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The polymorphism of vespid wasps (Hymenoptera: Vespidae) from Indonesia with morphology-based cladistic

Polimorfisme tawon vespid (Hymenoptera: Vespidae) asal Indonesia dengan morfologi berbasis cladistic

Yelsha Ramadhila[1], Hari Nugroho[2], Erfanus Jane[1], Intan Ahmad[1]*

[1]Sekolah Ilmu dan Teknologi Hayati, Institut Teknologi Bandung
Jalan Ganesha No. 10, Bandung 40132, Indonesia
[2]Museum Zoologicum Bogoriense, Pusat Riset Biosistematika dan Evolusi, Badan Riset dan Inovasi Nasional (BRIN)
Jalan Raya Jakarta-Bogor Km 46, Cibinong 16911, Indonesia

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ABSTRAK

Wasps in the family of Vespidae often have a yellowish black color with white or brown markings, but some species have variations in their markings and coloring. There is limited information available about the distribution of these marking patterns within the Vespidae Family. To clarify their taxonomic status, this study aims to examine the marking patterns of Vespid wasps that are widely distributed in the Indonesian Archipelago and to explore correlations with their biogeographical distribution patterns. In this study, specimens from three different locations (Bandung, Sumedang, and Purworejo) and specimens from the Museum Zoologicum Bogoriense (MZB) were examined. A total of 31 individuals from five different species were analyzed based on their morphological features. The data collected was coded and analyzed using cladistic methods, and the results were used to create cladogram trees for each of the five species i.e., *Phimenes flavopictus*, *Polistes stigma*, *Apodynerus troglodytes*, *Vespa affinis*, and *Vespa velutina*, showing their biogeographical distribution. The cladistic analysis in this study showed the relationships between the different species based on their morphological characteristics. The arrangements of the clades were determined using the Euclidean method in R studio. The results showed that *P. flavopictus* has two clades based on the marking patterns on their thorax and abdomen, while the other species i.e., *Po. stigma*, *V. affinis*, *V. velutina*, and *A. troglodytes* have three clades based on their coloring and marking patterns on all segments. The distribution of the Vespidae species appears to be scattered, with their patterns randomly distributed among locations.

Key words: aposematism, biogeographical distribution, marking pattern

ABSTRAK

Tawon dalam Famili Vespidae seringkali memiliki warna hitam kekuningan dengan corak putih atau cokelat, namun beberapa spesies memiliki variasi corak dan warna. Informasi mengenai distribusi pola penandaan ini dalam Famili Vespidae masih terbatas. Penelitian ini bertujuan untuk mengkaji pola penandaan tawon pada Famili Vespidae yang tersebar luas di Kepulauan Indonesia dan mengeksplorasi korelasinya dengan pola persebaran biogeografisnya untuk lebih memahami status taksonominya. Pada penelitian ini dilakukan pemeriksaan spesimen dari tiga lokasi (Bandung, Sumedang, dan Purworejo) dan spesimen dari Museum Zoologicum Bogoriense (MZB). Sebanyak 31 individu dari lima spesies berbeda dianalisis berdasarkan ciri morfologinya. Data yang dikumpulkan diberi kode dan dianalisis menggunakan metode kladistik, dan hasilnya digunakan untuk membuat

*Penulis korespondensi: Intan Ahmad. Sekolah Ilmu dan Teknologi Hayati, Institut Teknologi Bandung
Jalan Ganesha No. 10, Bandung 40132, Indonesia, Tel: 022-2511575, Email: intan@itb.ac.id

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pohon kladogram masing-masing lima spesies (*Phimenes flavopictus*, *Polistes stigma*, *Apodynerus troglodytes*, *Vespa affinis*, dan *Vespa velutina*), yang menunjukkan sebaran biogeografisnya. Analisis kladistik dalam penelitian ini menunjukkan hubungan antara spesies yang berbeda berdasarkan karakteristik morfologinya. Susunan *clades* ditentukan dengan menggunakan metode Euclidean di R Studio. Hasil penelitian menunjukkan bahwa *P. flavopictus* memiliki dua *clade* berdasarkan pola penandaan pada mesosoma dan metasoma, sedangkan spesies lainnya (*Po. stigma*, *V. affinis*, *V. velutina*, dan *A. troglodytes*) memiliki tiga *clade* berdasarkan pewarnaan dan pola penandaan pada seluruh ruas tubuhnya. Sebaran spesies Vespidae tampak tersebar, dengan pola yang tersebar secara acak antara lokasi.

Kata kunci: aposematisme, distribusi biogeografis, pola penandaan

INTRODUCTION

The Vespidae Family of Hymenoptera is found throughout the world and includes almost 4,600 known species. Vespid wasps are often black with yellow, white, or brown markings, but some species within this family have different patterns and variations in coloration, making them polymorphic. Some insects display color patterns that have evolved convergently and may serve important biological functions, such as aposematism and mimicry (Mora & Hanson 2019). This phenomenon has been studied primarily in Lepidoptera and Coleoptera but has not been extensively examined in Hymenoptera. In social Hymenoptera, Wilson (1953) noted that certain morphological forms or castes may occur within a single colony.

Blackith (1958) conducted a preliminary study on the analysis of polymorphism in Vespidae, examining the differences in form between adult queens, males, and workers in three species of social wasps. The study examined whether the differences between queens and workers were solely a matter of size or if there were also distinct changes in shape associated with caste formation. Additionally, Wilson (1971) noted that polymorphism among wasps is largely limited to queen-worker dimorphism, which is particularly prominent in the Vespinae. Jeanne & Fagen (1974) also reported the occurrence of complete queen-worker dimorphism in *Stelopolybia areata* (Say) (Vespidae; Polistinae) collected from Mexico.

There is limited information available about the taxonomic distribution of marking patterns in the Vespidae Family. Nugroho et al. (2020) is one of the few studies that has attempted to address this issue, by creating parallel distribution maps for several Eumeninae species. Some authors have questioned the usefulness of using morphological data for reconstructing phylogeny, as opposed to using molecular data (e.g., Rokas et al. 2003). However, Wiens (2004) and Scotland et al. (2003) have argued that morphological data can still be used for this purpose. One of the main reasons is to compare or clarify the phylogenetic relationships between fossils and living taxa (Jenner 2004). For example, according to data from 1999, out of 87 publications on polymorphism, 81.6% used morphological data and the remainder used either molecular or allozyme data (Kornet & Turner 1999). These studies used the characteristics occurring in the species being studied and scored the differences between each taxon for analysis.

Therefore, this study aims to examine the occurrence of forms with significantly different color patterns in widely distributed species, in order to establish their taxonomic status. Specifically, the study aims to determine whether these differences represent variations within a given area of Indonesia or if they indicate the presence of different species. This information is necessary for understanding the relationships between these wasps and for accurately classifying them.

MATERIAL AND METHOD

A total of 31 female Vespidae wasps from five species with distinct characteristics were examined from the Museum Zoologicum Bogoriense (MZB) in Indonesia. These specimens were collected from various locations across the country, including Bali, Banten, Bengkulu, Central Java, East Java, East Kalimantan, East Nusa Tenggara, Jambi, Lampung, North Maluku,

North Sulawesi, North Sumatra, South Sulawesi, Southeast Sulawesi, West Java, West Kalimantan, West Papua, West Sumatra, and Yogyakarta. The sample included three subfamilies (Vespinae, Polistinae, and Eumeninae) and four genera (*Phimenes*, *Apodynerus*, *Vespa*, and *Polistes*). The data on these species was coded and converted into numerical form (Table 1 & 2) for analysis using cladistic hierarchy methods in R studio. Seven colors (black, pale yellow, average yellow, bright yellow, orange, reddish, and brownish) (see Table 2) and five categories of marking pattern spots (0, ≤25, >25, ≤50, and >50%) (see Table 1) were used to evaluate 18 distinct segments (mandible, clypeus, frons, vertex, yellow line along ocular sinus, pronotum, mesoscutum, scutellum, metanotum, propodeum, propodeal spine, tegula, and metasomal tergum 1–6) on all specimens (Figure 1).

RESULTS

In this study, a total of 18 marking pattern characteristics were examined in 31 specimens from five different species. All specimens were adult female wasps (worker caste for the social wasps). This choice was made because some wasp species exhibit dimorphism between males and females, although the differences may be minor. Additionally, sterile female wasps, particularly in social species, are more commonly encountered because male wasps are only produced at certain times.

Apodynerus troglodytes (de Saussure, 1855)

Based on the color and marking patterns (Figure 2), the populations from Kolaka, South Sulawesi and Magelang, Central Java show the closest relationship. The Euclidean height among the species in these populations is almost 2. These populations have similar marking patterns on the head, mesosoma, and metasoma, with only slight differences on the tegula.

According to the cladogram analysis, the two forms of marking patterns found in the Bandung area show the most distant relationships with their contrasting markings. The individuals with the most distant relationship are from Bandung, West Java (left), and differ from others in almost all segments. The head has a brown mandible and only the upper part of the clypeus is yellow, while the mesosoma segments are mostly black with some yellow spots. Similarly, the metasoma is mostly black, except for a posterior band on the second tergum.

All of the specimens have yellow mandibles and resemble the mesosoma, except for *Apodynerus troglodytes* from Bandung, West Java (left).

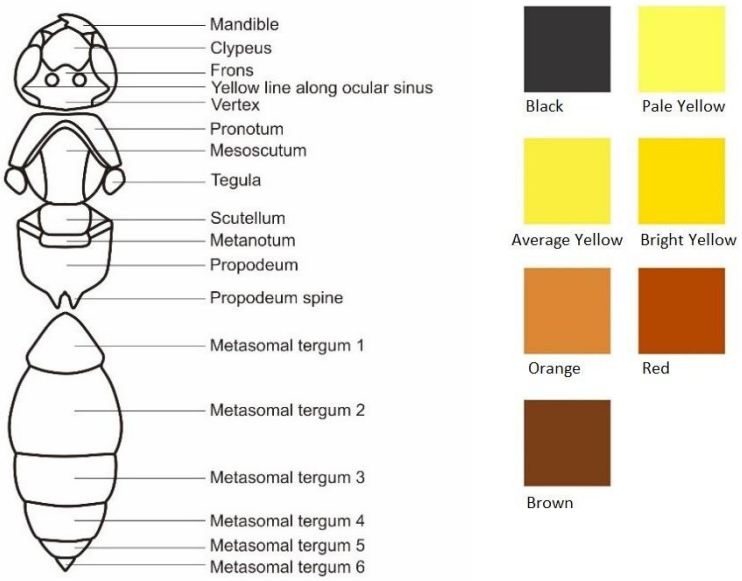


Figure 1. Analyzed segments of the wasps; mandible, clypeus, frons, vertex, yellow line along ocular sinus, pronotum, mesoscutum, scutellum, metanotum, propodeum, propodeal spine, tegula, and metasomal tergum 1–6 and seven colour grading; black, pale yellow, average yellow, bright yellow, orange, reddish, and brownish.

Table 1. Species segment's marking code. I: mandible; II: clypeus; III: frons; IV: vertex; V: yellow line along ocular sinus; VI: pronotum; VII: mesoscutum; VIII: scutellum; IX: metanotum; X: propodeum; XI: propodeum spine; XII: tegula; XIII: metasomal tergum 1; XIV: metasomal tergum 2; XV: metasomal tergum 3; XVI: metasomal tergum 4; XVII: metasomal tergum 5; XVIII: metasomal tergum 6

Species	Location	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Phimenes flavopictus blanchardi	Sumedang, West Java	1	1	1	1	4	1	1	1	1	2	5	1	3	4	4	4	4	1
Phimenes flavopictus continentalis	Jambi	1	5	4	1	5	5	3	5	5	5	5	5	3	4	4	4	4	1
Phimenes flavopictus maidly	Mentawai, West Sumatra	1	1	1	1	4	1	1	1	1	1	1	1	2	5	5	5	4	1
Phimenes flavopictus kalimantenus	Pujungan, East Kalimantan	1	1	1	1	4	4	3	4	5	5	5	4	2	3	3	3	1	1
Phimenes flavopictus baweanus	Bawean Island, East Java	1	2	2	1	4	1	1	1	1	1	1	1	1	1	1	1	1	1
Phimenes flavopictus engganensis	Enggano, Bengkulu	1	1	3	1	5	1	2	2	4	5	5	3	3	4	4	4	4	1
Apodynerus troglodytes	Kep. Seribu, Jakarta	5	5	2	1	4	5	1	5	1	3	1	2	1	1	1	1	1	1
Apodynerus troglodytes	Tanah Lot, Bali	5	5	2	1	5	5	1	5	1	5	1	5	1	3	1	1	1	1
Apodynerus troglodytes	Bandung, West Java	1	4	1	2	3	4	1	3	1	1	1	4	1	1	1	1	1	1
Apodynerus troglodytes	Bandung, West Java	5	5	2	1	4	5	1	5	1	3	1	4	1	3	1	1	1	1
Apodynerus troglodytes	Minahasa Peninsula, North Sulawesi	5	4	1	2	3	5	1	4	1	5	1	4	1	3	1	1	1	1
Apodynerus troglodytes	Kolaka, Southeast Sulawesi	5	3	2	1	4	5	1	5	1	5	1	4	1	3	1	1	1	1
Apodynerus troglodytes	Magelang, Central Java	5	3	2	1	4	5	1	5	1	5	1	5	1	3	1	1	1	1
Polistes stigma	Raja Ampat, West Papua	5	5	1	1	1	2	1	3	5	3	5	1	5	5	5	5	1	1
Polistes stigma	Pandeglang, Banten	5	5	4	1	4	2	5	3	5	5	5	1	5	5	5	5	1	1
Polistes stigma	Gunungkidul, Yogjakarta	5	5	4	1	4	2	5	3	5	5	5	1	5	5	5	5	1	1
Polistes stigma	Nusabarung, East Java	5	5	4	1	4	5	5	3	5	5	5	1	5	5	5	5	1	1
Polistes stigma	Kuku Timor, NTT	5	5	4	1	4	2	5	1	5	3	5	1	5	5	5	5	1	1
Polistes stigma	Ternate, North Maluku	5	1	1	4	1	1	4	1	5	1	1	1	1	4	1	1	1	1
Polistes stigma	Talaud, North Sulawesi	5	1	5	5	1	2	4	1	5	3	5	1	5	5	5	5	1	1
Vespa affinis	Aceh	1	1	1	1	1	1	1	1	1	1	1	1	1	5	1	1	1	1
Vespa affinis	Karimata Island, West Kalimantan	1	1	1	1	1	1	1	1	1	1	1	1	4	5	1	1	1	1

Table 1. Species segment's marking code. I: mandible; II: clypeus; III: frons; IV: vertex; V: yellow line along ocular sinus; VI: pronotum; VII: mesoscutum, VIII: scutellum; IX: metanotum; X: propodeum; XI: propodeum spine; XII: tegula; XIII: metasomal tergum 1; XIV: metasomal tergum 2; XV: metasomal tergum 3; XVI: metasomal tergum 4; XVII: metasomal tergum 5; XVIII: metasomal tergum 6 (Continue...)

Species	Location	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Vespa affinis	Raja Ampat, West Papua	1	4	1	5	1	5	1	4	1	1	5	4	5	5	1	1	1	1
Vespa affinis	Bogor, West Java	1	5	1	5	1	5	1	5	1	1	5	1	5	5	1	1	1	1
Vespa affinis	Bogor, West Java	1	5	1	1	1	1	1	1	1	1	5	1	5	5	1	1	1	1
Vespa affinis	Kolaka, Southeast Sulawesi	1	4	1	5	1	5	1	1	1	1	5	5	5	5	1	1	1	1
Vespa velutina	Bandung, West Java	5	5	5	4	5	4	1	4	1	1	1	5	1	1	2	4	4	1
Vespa velutina	Bali	5	5	5	5	5	5	4	5	1	1	1	5	1	1	2	4	5	1
Vespa velutina	Sulawesi	5	3	1	1	4	1	1	1	5	1	1	1	1	1	1	1	1	1
Vespa velutina	Bulusaraung, South Sulawesi	5	5	1	1	1	1	1	1	1	1	1	1	1	3	5	5	5	5
Vespa velutina	Magelang, Central Java	5	5	5	4	5	3	1	1	1	1	1	1	1	1	2	4	4	1

Number 1: no yellow spot in the segment; 2: yellow spot covered less than 25% segment; 3: yellow spot covered around 25% segment; 4: yellow spot covered around or almost 50% of the segment; and 5: yellow spot covered above 50% or almost all of the segment.

Table 2. Species segment's marking code. I: mandible; II: clypeus; III: frons; IV: vertex; V: yellow line along ocular sinus; VI: pronotum; VII: mesoscutum; VIII: scutellum; IX: metanotum; X: propodeum; XI: propodeum spine; XII: tegula; XIII: metasomal tergum 1; XIV: metasomal tergum 2; XV: metasomal tergum 3; XVI: metasomal tergum 4; XVII: metasomal tergum 5; XVIII: metasomal tergum 6

Species	Location	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Phimenes flavopictus blanchardi	Sumedang, West Java	A	A	A	A	C	A	A	A	A	A	C	A	C	C	C	C	C	A
Phimenes flavopictus continentalis	Jambi	A	C	C	A	C	C	C	C	C	C	C	C	C	C	C	C	C	A
Phimenes flavopictus maidli	Mentawai, West Sumatra	A	A	A	A	D	A	A	A	A	A	A	A	D	D	D	D	D	A
Phimenes flavopictus kalimantenus	Pujungan, East Kalimantan	A	A	A	A	D	C	C	C	C	C	C	C	C	C	C	C	C	A
Phimenes flavopictus baweanus	Bawean Island, East Java	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A
Phimenes flavopictus engganensis	Enggano, Bengkulu	A	A	C	A	C	A	C	C	C	C	C	C	C	C	C	C	C	A
Apodynerus troglodytes	Kep. Seribu, West Java	B	B	B	A	B	B	A	B	A	B	A	A	A	A	A	A	A	A
Apodynerus troglodytes	Tanah Lot, Bali	B	B	B	A	B	B	A	B	A	B	A	B	A	B	A	A	A	A

Table 2. Species segment's marking code. I: mandible; II: clypeus; III: frons; IV: vertex; V: yellow line along ocular sinus; VI: pronotum; VII: mesoscutum; VIII: scutellum; IX: metanotum; X: propodeum; XI: propodeum spine; XII: tegula; XIII: metasomal tergum 1; XIV: metasomal tergum 2; XV: metasomal tergum 3; XVI: metasomal tergum 4; XVII: metasomal tergum 5; XVIII: metasomal tergum 6 (Continue...)

Species	Location	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Apodynerus troglodytes	Bandung, West Java	G	A	B	A	B	B	A	B	A	A	A	B	A	A	A	A	A	A
Apodynerus troglodytes	Bandung, West Java	B	B	B	A	B	B	A	B	A	B	A	B	A	B	A	A	A	A
Apodynerus troglodytes	Minahasa Peninsula, North Sulawesi	B	B	B	A	B	B	A	B	A	B	A	B	A	B	A	A	A	A
Apodynerus troglodytes	Kolaka, Southeast Sulawesi	B	B	B	A	B	B	A	B	A	B	A	B	A	B	A	A	A	A
Apodynerus troglodytes	Magelang, Central Java	B	B	B	A	B	B	A	B	A	B	A	B	A	B	A	A	A	A
Polistes stigma	Raja Ampat, West Papua	E	D	A	A	A	E	A	D	E	A	D	C	D	E	E	E	E	E
Polistes stigma	Pandeglang, Banten	D	D	G	G	D	G	G	D	G	D	D	G	D	E	E	E	E	E
Polistes stigma	Gunungkidul, Yogjakarta	D	D	G	G	D	G	G	D	G	D	D	G	D	E	G	E	E	E
Polistes stigma	Nusabarung, East Java	D	D	G	G	D	D	G	D	G	D	D	G	D	E	G	G	G	E
Polistes stigma	Kuku Timor, East Nusa Tenggara	D	D	F	F	D	F	F	F	F	F	D	F	D	F	F	F	F	F
Polistes stigma	Ternate, North Maluku	F	F	F	A	F	F	A	F	F	A	A	A	A	F	A	A	A	A
Polistes stigma	Talaud, North Sulawesi	E	E	E	A	E	E	E	E	E	E	D	E	E	E	E	E	E	E
Vespa affinis	Aceh	A	A	A	A	A	A	A	A	A	A	A	A	A	E	A	A	A	A
Vespa affinis	Karimata Island, West Kalimantan	A	A	A	A	A	A	A	A	A	A	A	A	E	E	A	A	A	A
Vespa affinis	Raja Ampat, West Papua	A	G	G	G	G	G	A	G	A	A	E	G	E	E	A	A	A	A
Vespa affinis	Bogor, West Java	A	E	E	E	E	E	A	G	A	A	E	A	E	E	A	A	A	A
Vespa affinis	Bogor, West Java	A	E	E	E	E	A	A	A	A	A	E	A	E	E	A	A	A	A
Vespa affinis	Kolaka Southeast Sulawesi	A	G	G	G	G	G	A	A	A	A	E	G	E	E	A	A	A	A
Vespa velutina	Bandung, West Java	D	D	D	A	D	D	A	E	A	A	A	E	A	A	A	D	D	A
Vespa velutina	Bali	D	D	D	D	D	D	D	D	A	A	A	D	A	A	A	D	D	A
Vespa velutina	Sulawesi	D	D	A	A	D	A	A	A	D	A	A	A	A	A	A	A	A	A
Vespa velutina	Bulusaraung, South Sulawesi	G	D	A	A	A	A	A	A	A	A	A	A	A	D	D	D	D	D
Vespa velutina	Magelang, Central Java	D	D	D	A	D	D	A	A	A	A	A	A	A	A	A	D	D	A

Letter A: yellow is not available (black); B: pale yellow; C: average yellow; D: bright yellow; E: orange; F: reddish; and G: brownish.

Figure 2. Cladogram produced by hierarchy cluster analysis; represents the consensus of 7 individuals of *Apodynerus troglodytes* in several locations.

The clypeus is mostly black, except in Kepulauan Seribu, Tanah Lot, and Bandung (right). In Bandung (left) and Kepulauan Seribu, the metasomal tergum 2 does not have a yellow spot.

The cladogram for *A. troglodytes* shows two main clades in terms of color pattern. The first clade is from Bandung, West Java (left) and has a more extensive brownish color on the mandible, while the other individuals are yellow. The propodeum is entirely black without any markings, while the other populations have yellow spots. The pronotum and metasomal segments tend to have less extensive marking patterns compared to the other individuals.

***Phimenes flavopictus* (Blanchard, 1845)**

The populations with the closest resemblance are those originating from Sumedang, West Java and Bawean Island, East Java. These populations have similar characteristics on their head, but the thorax does not have any yellow markings, except for a few parts on the propodeal spine in the subspecies *blanchardi* from Sumedang.

For the metasoma, the subspecies *baweanus* has no markings at all, while the subspecies *blanchardi*, *continentalis*, and *engganensis* all have yellow markings. The mandibles and clypei of all subspecies are almost entirely black, except for the clypeus of the subspecies *continentalis* from Jambi. The forms from Mentawai, Sumedang, and Bawean Island do not have any yellow patterns on their mesosoma. The most distant relationship is observed between the subspecies *kalimantenus* and *baweanus*, as the Kalimantan form has some yellow spots on the segments (mesosoma, tegula, propodeum, and metasoma), while the Bawean Island form has no markings.

The cladogram (Figure 3) showed two clades in the color pattern of *Phimenes flavopictus*. The first clade is from Pujungan, Jambi, and Enggano, which generally has extensive yellow color patterns on the head, thorax, and abdomen. The second clade, from Mentawai, Sumedang, and Bawean Island, tends to have less-extensive color patterns on the head and mesosoma compared to the first clade.

***Polistes stigma* (Fabricius, 1793)**

According to the cladogram analysis (Figure 4), the *Polistes stigma* has two clades, but it

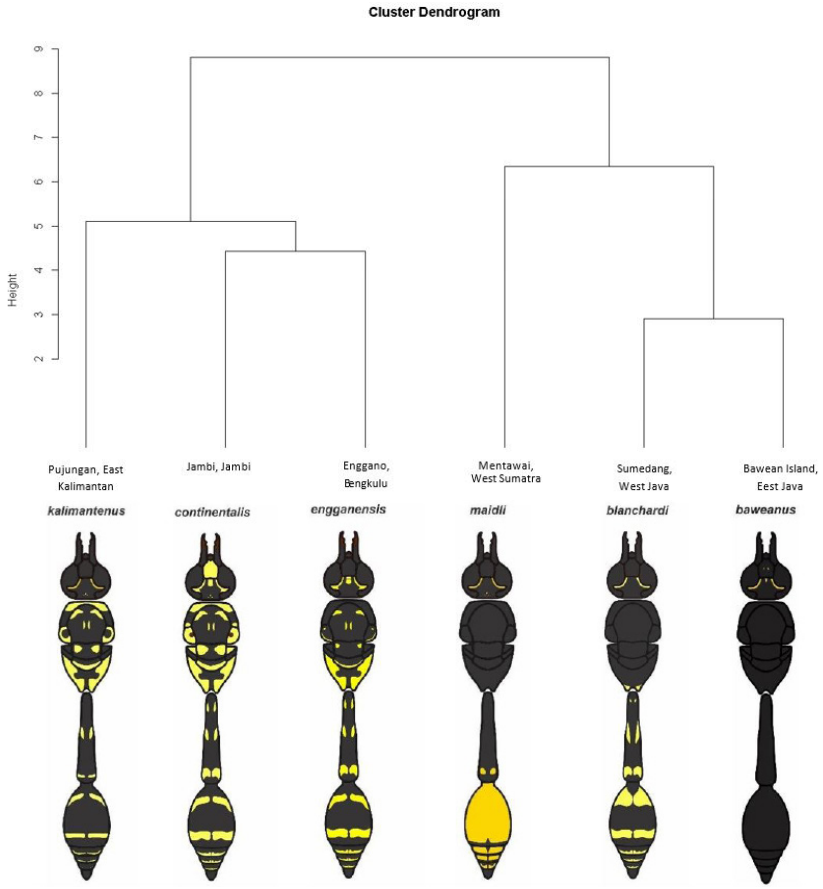


Figure 3. Cladogram produced by hierarchy cluster analysis; represents consensus of 6 individual of *Phimenes flavopictus* in several locations.

tends to have three clades based on their marking pattern. The first clade is the largest, and it is from North Maluku, and it generally has darker color in every segment from the head to the metasoma. The other clades are divided into two sub-clades of reddish-yellow marking members, with color grading randomly from west to east Indonesia.

The first clade tends to have a darker color and fewer marking patterns on almost all segments compared to the other sub-clade because the color base is black. The specimens from Banten and Yogyakarta are the closest and have similar markings, with only slight differences on the third metasomal tergum. Both specimens have the closest characteristics to those of East Java, while the latter has a black anterior band on metasomal terga 3-4. Meanwhile, the specimen from North Maluku has a distant resemblance because it differs completely in color and marking pattern from the others. The color is generally darker and often nearly red, with a narrow apical band on metasomal terga. In general, this species has a black color base but seems to have a color loss due to the marking pattern covered on the segment with various percentages of area. All specimens almost have patterns on their propodeum covered by orange or reddish color, except for the specimen from North Maluku with 0% of the marking pattern covering the segment. This might be due to aposematism to warn predators.

Vespa affinis (Linnaeus, 1764)

According to the cladogram analysis (Figure 5), the distribution of *Vespa affinis* wasps is divided into three main clades based on their marking patterns and color gradations. The first clade includes populations from Aceh and West Kalimantan, which have similar characteristics in most segments except for the yellow markings on the first metasomal tergum of the West Kalimantan population. The second clade consists of populations from West Papua and Southeast Sulawesi, which have similar marking patterns on the head, mesosoma, and metasoma, but differ in the reddish-brown scutellum of the West Papuan form.

The third clade includes species from Bogor, West Java, which have unique markings and are considered as one clade because they share

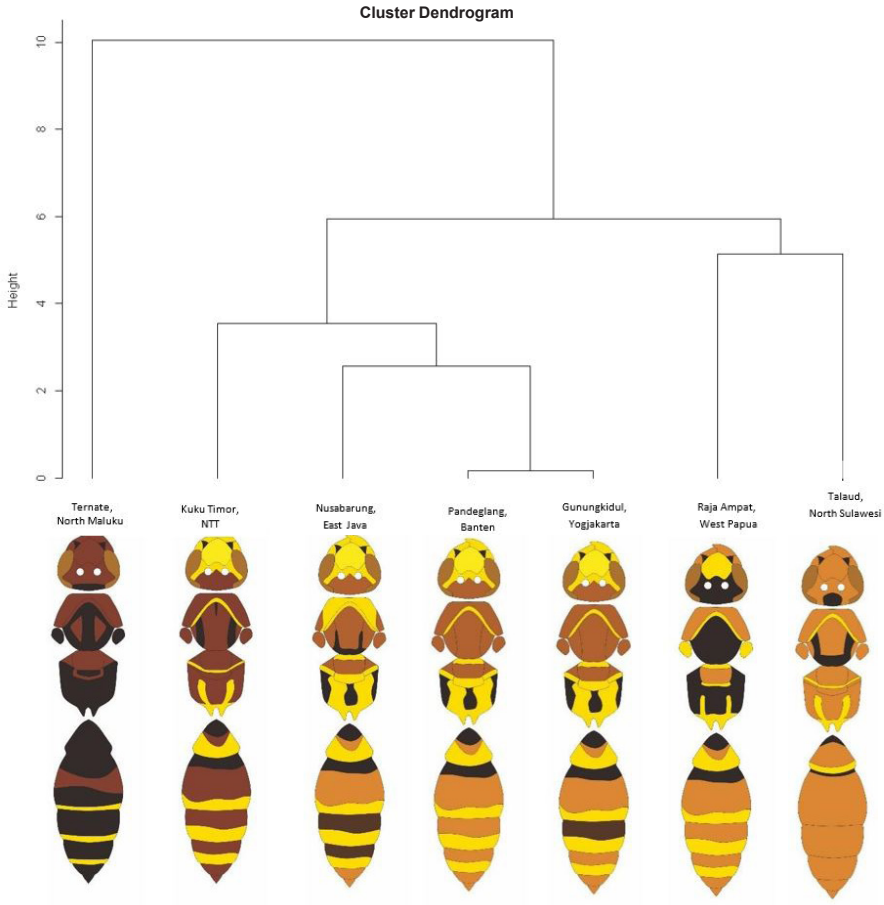


Figure 4. Cladogram produced by hierarchy cluster analysis; represents the consensus of 6 individuals of *Polistes stigma* in several locations.

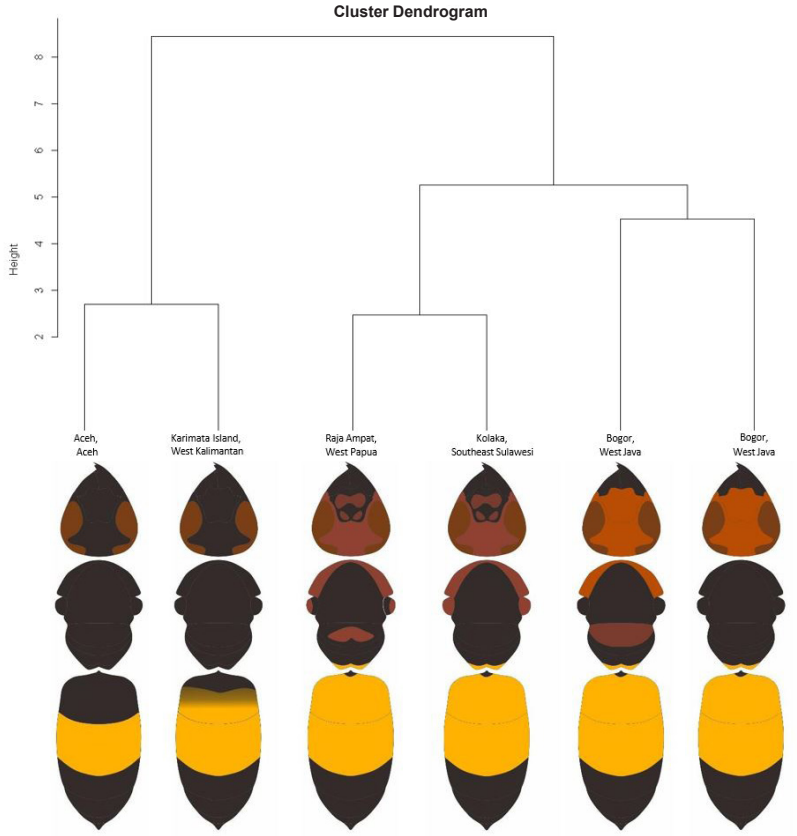


Figure 5. Cladogram produced by hierarchy cluster analysis; represents consensus of 6 individual of *Vespa affinis* in several locations.

almost all identical marking patterns. The closest resemblance is between specimens from Papua and South Sulawesi, while the least resemblance is between specimens from Bogor, West Java. The distribution of marking patterns among this species appears to be scattered.

***Vespa velutina* Lepeletier, 1836**

The analysis of the color and marking patterns of Vespidae wasps in this study showed that there are two clades among the species examined (Figure 6). The first clade consists of forms from Sulawesi and South Sulawesi, and the second clade consists of forms from Bali, West Java, and Central Java. The difference between the head characteristics of these two clades is subtle, as all specimens have a fully yellow clypeus except for those from Sulawesi, which only have 25% yellow on the clypeus. The mesosoma of the first clade tends to have a black color without any marking patterns, while the second clade has marking patterns on the pronotum and mesoscutum.

The last three metasomal terga of the second clade are similar, with the same marking patterns covered. The populations from South Sulawesi show the least resemblance to the other specimens, as they have a brownish mandible and no marking on the frons and vertex, while the mesosoma is entirely black. The populations from West Java and Central Java show the closest resemblance, with similar colors and patterns in the head and metasoma. The population from West Java has reddish-brown spots on the scutellum and tegula, while the Central Java population does not.

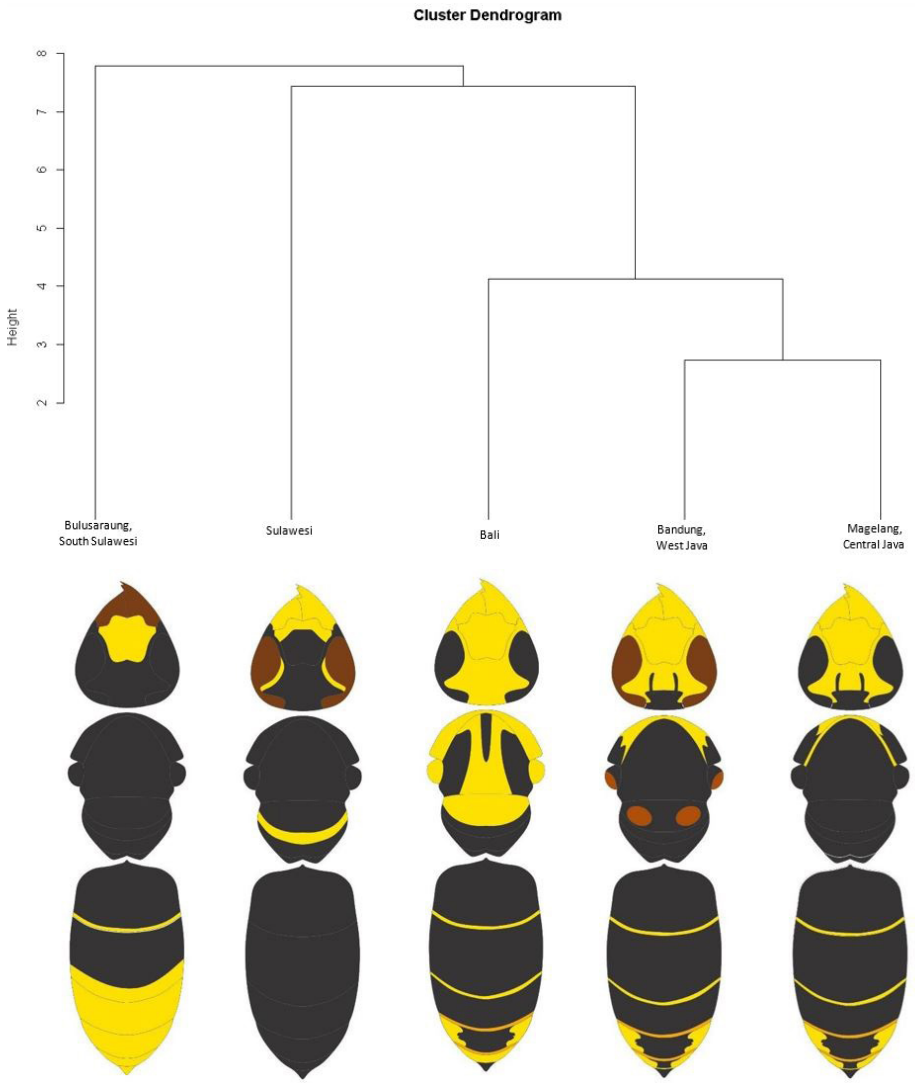


Figure 6. Cladogram produced by hierarchy cluster analysis; represents consensus of 6 individual of *Vespa velutina* in several locations.

Inter-species clades

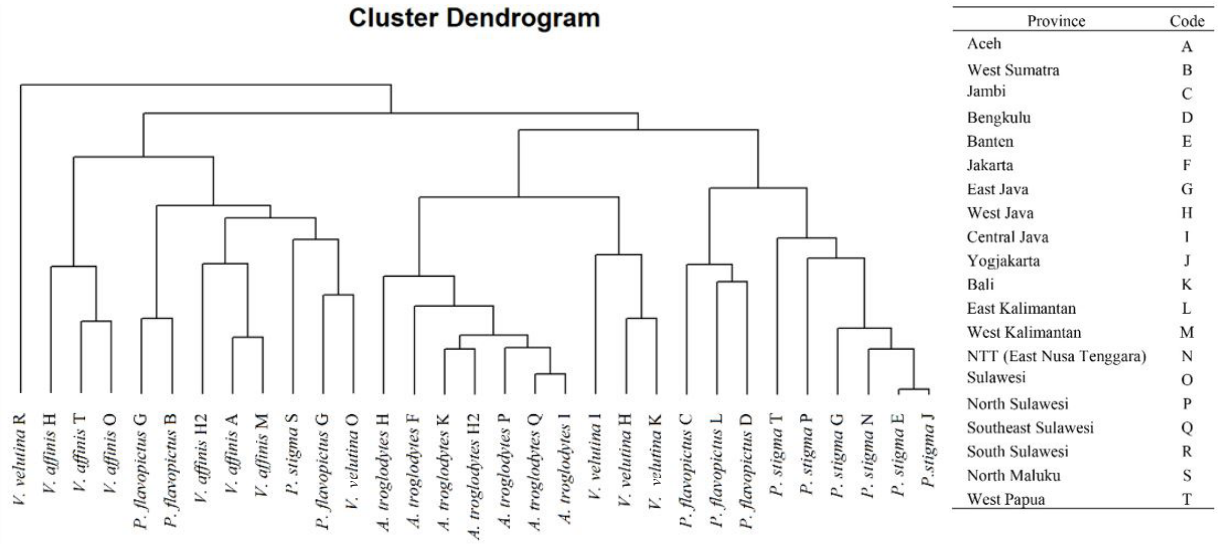
The specimens were tested for their relationship to one another in Figure 7. In this subfamily, multiple individuals from each genus had similar markings and color gradations, leading to the segregation of three clades. The specimens with the closest resemblance were *Po. stigma* from Banten and Yogyakarta, followed by *A. troglodytes* from Southeast Sulawesi and Central Java. Also a close intra-species similarity between East Java's *P. flavopictus* and Sulawesi's *Vespa velutina*.

The mesosoma, or the middle section of the body, is the most noticeable feature in determining the three clades. The first clade, shown in Figure 8, typically has a darker mesosoma and lacks marking patterns. The second clade, shown in Figure 9, usually has a marking pattern extending from the pronotum to the mesoscutum, scutellum, propodeum, and tegula, with a general yellow color on the mesoscutum. All species in the second clade have marking patterns on the pronotum. Similarly, all species in the third clade, shown in Figure 10, have marking patterns on the pronotum, propodeum, and metasoma. The marking patterns and gradations in the third clade are significantly different from those in the other clades, with nearly all segments exhibiting a varied pattern size.

Maps distribution

Solitary wasps. The distribution of the marking patterns of a solitary wasp species, as shown in Figure 11, is difficult to determine definitively because there are only two species available for comparison with those from West Java. However, when looking at individual species, it appears that the distribution of marking patterns and color gradations is scattered. This may be because species in the same area do not have similar marking patterns or color gradations compared to those in other areas. It is possible that the gradual changes in color and marking patterns seen in these species are due to a process of learning behaviors from other species or previous species in order to survive predators. These adjustments may be made in response to the environment, with darker colors helping the species blend in with their surroundings and avoid being preyed upon, while brighter colors may be used to deter predators who may avoid bright colors due to the belief that they indicate poison.

Social wasps. The comparison of the marking patterns and color gradations of three wasp species, as shown in Figure 12, in various locations suggests that wasps tend to have similarities within a specific area. For instance, the color gradation of the three wasp species from West Java tends to be brighter compared to those from Sulawesi and Papua. The farther east the location, the darker the color gradation of the wasp species tends to be. This may be due to the contrasting climates, where dark-colored insects are able to absorb more sunlight and increase their body temperature, which is more common in cooler climates. But not all the specific segments have the gradual color, some of the metasoma species look similar to each other. For the example, the metasoma of West Papuan



Province	Code
Aceh	A
West Sumatra	B
Jambi	C
Bengkulu	D
Banten	E
Jakarta	F
East Java	G
West Java	H
Central Java	I
Yogjakarta	J
Bali	K
East Kalimantan	L
West Kalimantan	M
NTT (East Nusa Tenggara)	N
Sulawesi	O
North Sulawesi	P
Southeast Sulawesi	Q
South Sulawesi	R
North Maluku	S
West Papua	T

Figure 7. Cladogram produced by hierarchy cluster analysis; represents consensus of all specimens in several locations.

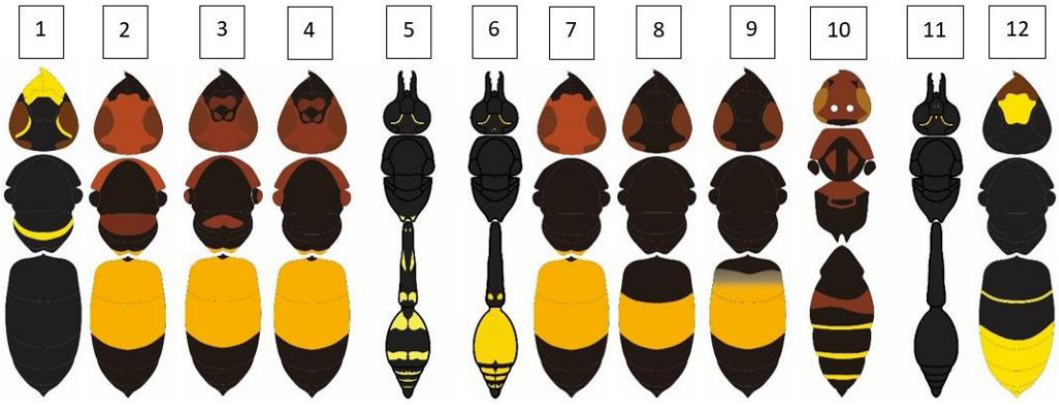


Figure 8. First clade of interspecies comparison based on marking pattern and color gradation. 1: *Vespa velutina* from Bulusaraung, South Sulawesi.; 2: *Vespa affinis* from Bogor, West Java; 3: *Vespa affinis* from Raja Ampat, West Papua: 4: *Vespa affinis* from Kolaka, Southeast Sulawesi; 5: *Phimenes flavopictus* from Sumedang, West Java; 6: *Phimenes flavopictus* from Mentawai, West Sumatra; 7: *Vespa affinis* from Bogor, West Java; 8: *Vespa affinis* from Aceh; 9: *Vespa affinis* from Pujungan, East Kalimantan; 10: *Polistes stigma* from Ternate, North Maluku; 11: *Phimenes flavopictu*s from Bawean Island, East Java; 12: *Vespa velutina* from Bulusaraung, South Sulawesi.

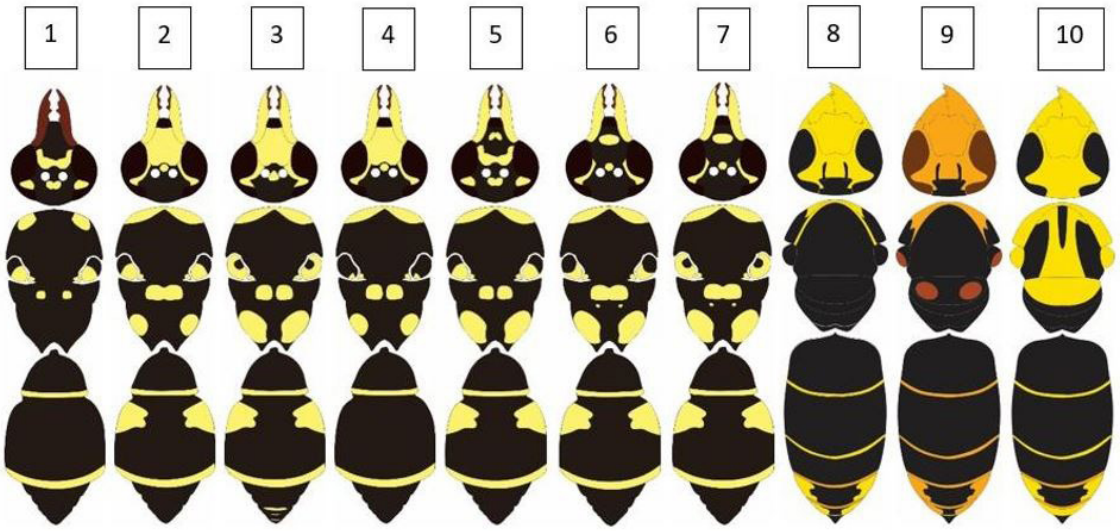


Figure 9. Second clade of interspecies comparison based on marking pattern and color gradation. 1: *Apodynerus troglodytes* (H2) from bandung, West Java; 2: *Apodynerus troglodytes* from bandung, West Java; 3: *Apodynerus troglodytes* from Tanah Lot, Bali; 4: *Apodynerus troglodytes* from Kep. Seribu, Jakarta; 5: *Apodynerus troglodytes* from Minahasa Peninsula, North Sulawesi; 6: *Apodynerus troglodytes* from Kolaka, South Sulawesi; 7: *Apodynerus troglodytes* from Magelang, Central Java; 8: *Vespa velutina* from Magelang, Central Java; 9. *Vespa velutina* from Bandung, West Java; 10. *Vespa velutina* from Bali.

Po. stigma have the same color with the specimen from Banten. Also, metasoma in *V. affinis* in West Papua also look similar with the species from West Java. This is indicated that the marking pattern in social wasp tends to be scattered than to be gradual. The difference in behavior can also affect the marking patterns and color gradations of each species as they adapt to different ways of living and avoiding predators. However, the results of the distribution marking pattern are not definitive, and more samples need to be analyzed for a more accurate result.

DISCUSSION

Marking pattern and color gradation

The variation in color gradation and marking patterns of female social and solitary wasps has been described and quantified. While it is

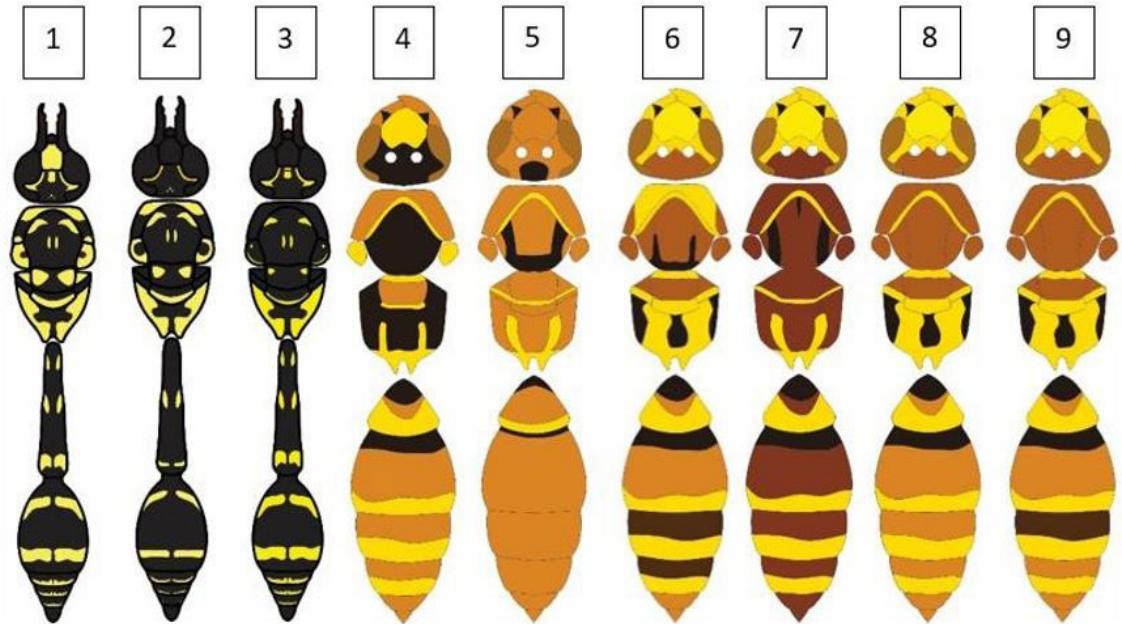


Figure 10. Third clade of interspecies comparison based on marking pattern and color gradation. 1: *Phimenes flavopictus* from Jambi; 2: *Phimenes flavopictus* from Pujungan, East Kalimantan; 3: *Phimenes flavopictus* from Enggano, Bengkulu; 4: *Polistes stigma* from Raja Ampat, West Papua; 5: *Polistes stigma* from Talaud, North Sulawesi; 6: *Polistes stigma* from Nusabarung, East Java; 7: *Polistes stigma* from Kuku Timor, East Nusa Tenggara (NTT); 8: *Polistes stigma* from Pandeglang, Banten; 9: *Polistes stigma* from Gunugkidul, Yogjakarta.

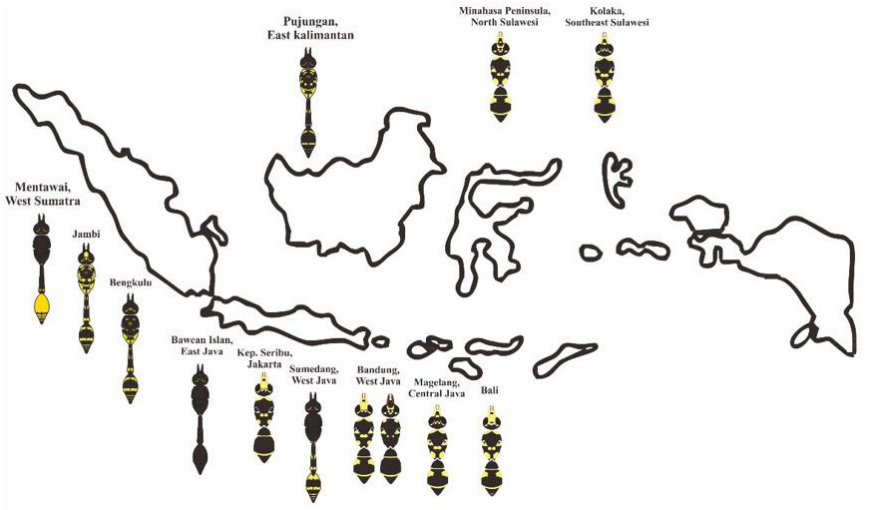


Figure 11. Marking pattern maps distribution of solitary wasps (*Apodynerus troglodytes* and *Phimenes flavopictus*).

generally easy to distinguish between different species of wasps based on dimorphism, it can be more challenging to identify differences within a species. According to a study by Clapperton et al. (1989), only 0.012% of over 50,000 wasps could not be assigned to a specific species based on the color markings on their head and thorax. From hundreds of species and subspecies in the sample specimens, only five were identified as polymorphic based on their marking patterns. The analysis shows the variety of patterns within each species and the extent to which they are covered. *A. troglodytes*, for example, has yellow markings on the mandible, clypeus, ocular sinus, pronotum, tegula, scutellum, propodeum, and metasomal tergum II. According to Kumar (2013), this species is a black wasp with yellow markings on various parts of its body, including the mandibles (except at the lateral and apical portions), clypeus (except for a waved transverse band that encircles the

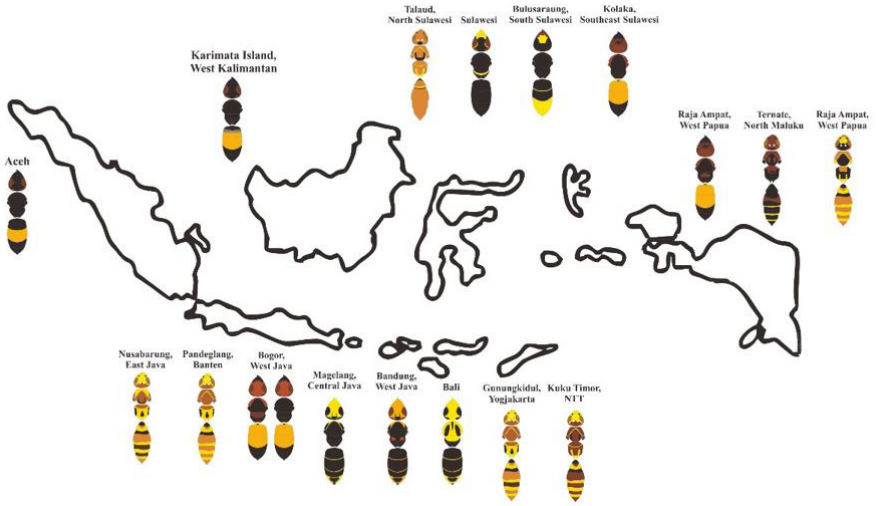


Figure 12. Marking pattern maps distribution of social wasps (*Polistes stigma*, *Vespa affinis*, and *Vespa velutina*).

posterolateral and apical margins), ocular sinus, an elongated spot on the upper part of the temple near the eye margin, scape in front, a median interrupted band on the dorsal side of the pronotum, tegula at both apex, two large spots on the scutellum, two small spots on the metanotum, larger and oval spots on the sides of the propodeum posteriorly, and metasomal tergum II with a large round spot on each side at its base. However, the species from Bandung (C, Figure 2) has a slightly different appearance, with a darker (brown) mandible.

The marking patterns of *P. flavopictus* from Kalimantan and Jambi are more extensively marked with yellow than other wasp species. This is in line with the study by Nugroho et al. (2020), which found that the subspecies *continentalis*, found in continental Asia and Sumatra, are more or less extensively marked with yellow. In contrast, the Bornean subspecies *kalimantenus* has a marking pattern similar to those of subspecies *continentalis*, but smaller, thinner, or reduced.

Species *Po. stigma* exhibits the most variable marking patterns among all segments. According to a study by Nguyen et al. (2017), this species generally has a dark brown body with yellow to orange marking patterns on the clypeus, a spot at the base of the mandible, a band along the inner eye margin extending from the bottom of the frons to the middle of the eye emargination, an apical band on tergum I, and a medial band on tergum IV. It also has black color markings on the propodeum posteriorly and the metasoma segments, except for the yellow parts. This description matches the characters from East Java, Banten, Yogyakarta and East Nusa Tenggara (NTT) as described above.

The marking patterns of *V. affinis* from South Sulawesi and West Papua are similar to those of the species from Aceh and West Kalimantan, according to Handru et al. (2020). The Sulawesian population is similar to those found in Borneo and North Moluccas, with the head mostly ferruginous and the first two metasomal terga entirely orange-yellow. *V. velutina*, on the other hand, has the most diverse marking pattern among the species. According to Carpenter and Kojima (1997), this species has a wide range of local color forms distributed throughout the Oriental Region. The analysis of the social group showed that there are three main clusters of populations, those from Java Island, Sulawesi, and the eastern species (from Maluku and Papua). The similarity in character traits among populations on each island within the social group supports report by Perrard et al. (2014) that some wasp populations in Indonesia and on the continent have very dark color patterns, while a population in southern Indonesia has the lightest color morph. This may suggest that certain biotic or environmental factors influence the development of color markings in these species.

The body color markings of solitary wasps tend to be limited to yellow and black, with little similarity between populations on different islands. This aligns with the findings of Nugroho et al. (2020) that the darkness of these markings varies significantly among local populations of a given species, resulting in a mosaic pattern of

distribution. This suggests that the variation in coloration may be driven more by aposematic factors, such as warning predators, rather than environmental variables.

Potential factors

There are several factors that may lead to the occurrence of different marking patterns and color gradations in wasp species, including aposematism. Aposematic coloration is a defensive strategy used by some animals to warn potential predators of their danger. This is often achieved through the use of bright and eye-catching colors. This strategy is used to protect against predation (Mallet & Joron 1999). Birds are the primary predators of Vespid wasps. An example of a predatory behavior that demonstrates aposematism can be seen in the Mexican butterfly-eating bird *(Danaus plexippus)*. These predatory birds repeatedly regurgitate the butterfly, more or less unharmed, until they find an individual that is palatable to eat (Calvert et al. 1979).

Wasps typically have black and yellow coloring. According to True (2003), the dark coloring may help with crypsis, while the yellow coloring appears to serve as a warning color that bird predators instinctively avoid (Hauglund et al. 2006). Warning colors are important for the defense of social wasps, particularly their queens during their solitary phase. As the queens are responsible for producing the next generation, they must survive for several weeks.

The marking patterns and color gradations of certain wasp species vary in size, which may be influenced by the presence and behavior of predators in the area. This can lead to the evolution of aposematic coloration as a means of predator avoidance, as predators learn to avoid prey with eye-catching hues. As a result, the prey benefits from having aposematic coloration by not needing to be toxic; this was proposed by Pfennig et al. (2001).

To enhance the accuracy of analysis and gain deeper insights, future studies should incorporate molecular analysis as a necessary component to aid in understanding the historical biogeography of wasp populations, tracing their migration patterns, and exploring how past geological events might have shaped their distribution. Such insights could offer valuable clues about the evolutionary forces that have influenced their diversity and adaptation to various environments. This would further contribute to our understanding of the intricate patterns and evolutionary dynamics within this fascinating group of wasps.

CONCLUSION

Our research delved into the marking patterns of wasps (Hymenoptera: Vespidae) in the Indonesian Archipelago and revealed a consistent trend of two to three distinct clades based on their morphological patterns and color gradations. Based on their social behavior, we identified that the marking pattern variation among solitary wasps (Hymenoptera: Vespidae) in the Indonesian Archipelago tends to exhibit dispersion across different locations, while the social wasp tends to be scattered among locations than to be gradual. We suggest that future research incorporating molecular to provide a more comprehensive understanding of the intricate patterns and evolutionary dynamics within this group of wasps. Furthermore, it is essential to expand the sample size and ensure a robust, representative dataset for analysis. Adequate sample size and representativeness are crucial for statistical significance and to avoid potential biases in the study findings.

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