

Review of the potter wasps (Hymenoptera: Vespidae, Eumeninae) with a petiolate metasoma from Indonesian Archipelago

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Abstract. The taxonomy and biogeography of potter wasps with a petiolate metasoma occurring in the Indonesian Archipelago are reviewed. Literature review and specimens examination were carried out for the present study. Within the Eumeninae, the wasps with a petiolate metasoma distributed in the region have been more or less well studied compared with those with a non-petiolate metasoma, but their generic affinities and the concepts of some species yet remain unestablished. A total of 80 species belonging to 16 genera of the “petiolate metasoma” are known to occur from the region. Sumatra, Java, Bali and Borneo have mainly Oriental eumenine fauna, including several area-specific species of the Oriental genera. New Guinean fauna is comprised of Papua-Australian species of the widely distributed genera, together with widely distributed species and species endemic to New Guinea. The Wallacean fauna is constituted mainly with the area-specific species in the rather widely distributed genera; in the western part of Wallacea, they are represented mainly by widely distributed genera, together with Oriental genera; in the eastern part of Wallacea, they are constituted mainly by area endemic species of widely distributed Oriental genera. Widely distributed species generally show a wide range of variation in the marking patterns, and occurs sympatrically in some areas, even the peripheral populations usually characterized by the island(s)-specific marking patterns. Sympatric occurrences of forms with quite different color patterns in widely distributed species need further study to establish their taxonomic status, namely whether they are variations within a given area or different species.

1 Introduction

The subfamily Eumeninae is cosmopolitan and the largest subfamily in the Vespidae, consisting of more than 3,500 described species in 210 genera [1, 2, table 1]. Most of eumenine wasps are solitary even though they gather around a suitable nesting site and a few genera are known to be communal nesters [2, 3]; some genera, such as *Orancistrocerus* and *Calligaster*, are subsocial. Many eumenine wasps construct nests with soil/mud mixed with relatively small amount of wasps’ oral secretion or saliva, but *Calligaster* species use plant materials, and *Epsilon* is known to make their nests with plant-origin resin. Others use pre-existing cavities as their nesting places, and some are burrowers in the soil or wood, in which cell partitions or closing plugs are usually made of soil/mud or only sometimes plant material such as in *Zethus* [2, 4, 5].

Eumenine wasps are predaceous on terrestrial insects, hunting mainly lepidopterous caterpillars or sometimes coleopterous larvae as food for their larvae ([6, 7]; Iwata, 1971 *in* [3]), and thus they are more or less at higher positions in a food web of terrestrial arthropods. They also visit flowers for nectar as their own energy source and thus are considered as potential pollinators of many plants [5, 6, 7].

The Indonesian Archipelago, consisting of about 17,500 islands spreading from Sumatera in the west to New Guinea in the east, is known for the mega biodiversity. In the archipelago, four (Eumeninae, Stenogastrinae, Polistinae and Vespinae) of the six vespid subfamilies occur, of which the Eumeninae are the most diverse, with a total of 226 species in 51 genera so far recorded in the archipelago. The species recorded from Sarawak, Sabah, Brunei, Timor Leste and Papua New Guinea were included in the total biodiversity of

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Eumeninae from Indonesian Archipelago, since the countries' border may have no biological meaning in the distribution of species.

Compared with the other three vespidae subfamilies, to which the species belonging are all social, the taxonomy of the Eumeninae, in general, is yet much more poorly studied. Of the eumenine wasps known from the archipelago, 16 genera are among those treated as "potter wasps with a petiolate metasoma", which are characterized by having the first metasomal tergum at least twice as long as its apical width. These eumenine wasps with a petiolate metasoma were originally described in the genus *Eumenes* Latreille, 1802, genera in the so-called "Zethinae" and in the genus *Labus*.

Within the Eumeninae, the wasps with a petiolate metasoma distributed in the Indo-Australian Region have been more or less well studied compared with those with a non-petiolate metasoma, but their generic affinities and the concepts of some species yet remain unestablished. In the present study, the taxonomy and distribution (or biogeography) of potter wasps with a petiolate metasoma occurring in the Indonesian Archipelago are reviewed.

2 Material and Methods

2.1. Specimens examined

Examination of the specimens was carried out to study the morphological characters and clarify the distributional record, including determining the color/markings pattern within local populations. The specimens examined in the present study were those having deposited in the collections of the Museum Zoologicum Bogoriense, Cibinong, Bogor, Indonesia (MZB), the Natural History Collection at Ibaraki University, Mito, Japan (IUNH), the Systematic Entomology Institute, Hokkaido University Museum, Sapporo, Japan (SEIHU), the Natural Resources Inventory Center, National Institute for Agro-Environmental Sciences, Tsukuba, Japan (NRIC), the National Museum of Nature and Science, Tsukuba, Japan (NSMT), and Institute of Ecology and Biological Resources, Hanoi, Vietnam (IEBR). In addition to those specimens in the collections, we have collected many specimens in various places in the Indonesian Archipelago, which were pinned and dried and deposited in the MZB and IUNH.

2.2 Literature review

A literature review was conducted to study the taxonomic history of Eumeninae at the genus, species and subspecies levels. Placements of the genera into the tribes are based on Hermes et al. [2], and the use of the "Labus group" is based on the authors' opinion, since the taxonomic treatment has not been carried out to clarify their phylogenetic position.

3 Results and Discussion

3.1. Taxonomic history

Hermes et al. [2] performed a comprehensive cladistic analysis of the Eumeninae and corroborated a natural classification of Eumeninae at the tribal level to recover the Eumenini, Odynerini and Zethini, which had been previously available. They also clearly showed that the potter wasps with a petiolate metasoma do not form a monophyletic group, but they are placed in all the three monophyletic tribes, namely Zethini, Odynerini and Eumenini, suggesting that the shape of the first metasomal segment is a weak character due to its high heterogeneity (see also [8]). However, their study did not include several Oriental and/or Afrotropical genera with a petiolate metasoma, such as *Calligaster* de Saussure, 1852, *Labus* de Saussure, 1867 and *Cyrtolabulus* van der Vecht, 1969, and their phylogenetic positions have not yet been discussed.

Many species originally described in the genus *Eumenes* have been transferred to several genera as the results of taxonomic works, including the establishment of new genera, by subsequent authors. The most important taxonomic studies on the Oriental Eumeninae with a petiolate metasoma are van der Vecht [9,10,11,12,13] and Giordani Soika [14,15], which resulted in a proliferation of generic names in the Eumeninae: *Omicroides* Giordani Soika, 1935, *Pseumenes* Giordani Soika, 1935, *Nortozumia* van der Vecht, 1937, *Coeleumenes* van der Vecht, 1963 and *Cyrtolabulus* van der Vecht, 1969. These taxonomic treatments to split the preexisting genera were then continued by Giordani Soika [16] and Gusenleitner and Gusenleitner [17], in which *Phimenes* Giordani Soika, 1992 and *Flavoleptus* Giordani Soika, 1992, and *Norteumenes* Gusenleitner and Gusenleitner, 2013 were proposed.

The first record of potter wasps under *Zethus* from the Indonesian Archipelago was Cameron [18], who described *Z. quadridentatus* and *Z. varipunctatus* from Borneo. The other Oriental genus in the so-called "Zethini", *Calligaster* de Saussure, 1852, was described based on *C. cyanoptera* de Saussure, 1852 from Java, but since de Saussure (1855) treated *Calligaster* as a division of *Zethus* its taxonomic position had been ambiguously interpreted until Bequaert [19] definitely reinstated its generic status.

The *Labus* group is an Oriental and Ethiopian eumenine fauna. Two genera are recognized, *Labus* from the Oriental region and *Cyrtolabulus* from Indo-Ethiopian region. The genus *Labus* was described by de Saussure (1867) based on *L. spiniger* de Saussure, 1867 from Java, and since then received many interpretations, as it differs in many characters from its related genera [8, 20]. However, Bequaert [20] discussed the generic characters and established good diagnosis based on Ethiopian species. Van der Vecht [9] newly described another three species from Java, having contributed to a better understanding of the *Labus* fauna in the Indonesian

Archipelago. The genus *Cyrtolabus* was described by van der Vecht [13] to accommodate two species from the Indian subcontinent; subsequently *Cyrtolabus* van der Vecht, 1969 was established as a replacement name for *Cyrtolabus* van der Vecht, 1963.

3.2. Diversity and biogeography

Potter wasps with a petiolate metasoma in the Indonesian Archipelago consisting of 131 species-group taxa (80 species and 51 subspecies; table 1). The diversity of a petiolate metasomal genera in the archipelago consisted of widely distributed species (33) and endemic species (47). Sumatra, Java, Bali and Borneo are more likely representing Oriental element with less endemic species occurs; Sulawesi, Lesser Sunda Islands and Moluccas species more or less consisting mainly with the occurrence of endemic species; New Guinea species probably underrate, as they may less explore areas (Fig. 1).

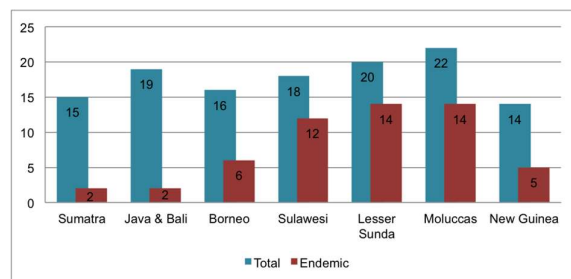


Fig. 1. Total species and number of endemic species of potter wasps with a petiolate metasoma in Indonesian Archipelago.

The tribe Eumenini includes four genera known to occur in the Indonesian Archipelago: *Eumenes* Latreille, 1802, *Delta* de Saussure, 1855, *Phimenes* Giordani Soika, 1992 and *Omicroides* Giordani Soika, 1935. *Delta*, *Eumenes* and *Phimenes* have widely distributed genera, while *Omicroides* is representing Oriental element. In this tribe, a total of 38 species in four genera with a petiolate metasoma are recognized from the Indonesian Archipelago. They are nine species in the genus *Delta*; 20 species in the genus *Eumenes*; the species in the monotypic genus *Omicroides*; and eight species in the genus *Phimenes*.

The tribe Odynerini is consist of eight genera known to occur in the Indonesian Archipelago: *Coeleumenes* van der Vecht, 1963, *Ectopioglossa* Perkins, 1912, *Flavoleptus* Giordani Soika, 1992, *Norteumenes* Gusenleitner & Gusenleitner, 2013, *Nortozumia* van der Vecht, 1937, *Pareumenes* de Saussure, 1855, *Pseudozumia* de Saussure, 1875 and *Pseumenes* Giordani Soika, 1935. *Flavoleptus*, *Norteumenes*, *Nortozumia* and *Pseudozumia* are representing the Oriental genera in the Odynerini; *Coeleumenes*, *Ectopioglossa*, *Pareumenes* and *Pseumenes* are widely distributed genera and occur along the archipelago. In the Odynerini, the following 26 species in eight genera are recognized in the Indonesian archipelago: three species in the genus *Pareumenes*, three species in the genus *Pseumenes*, six species in the genus

Coeleumenes, seven species in the genus *Ectopioglossa*, two species in the genus *Nortozumia*, three species in the genus *Pseudozumia*, and each of the monotypic genera *Flavoleptus* and *Norteumenes*.

The tribe Zethini consists of three genera known to occur in the Indonesian Archipelago: *Calligaster* de Saussure, 1852, *Elimus* de Saussure, 1852 and *Zethus* Fabricius, 1804. In the Zethini, eight species in three genera are recognized in the Indonesian Archipelago; namely, three species in the genus *Calligaster*, four species in the genus *Zethus* and one species in the genus *Elimus*.

The *Labus* group is consisting only single genus known to occur in the Indonesian Archipelago, representing by eight species and distributed from Sumatra in the west to the Lesser Sunda Islands in the east. In the genus *Labus*, which may form, together with the Indo-Ethiopian genus *Cyrtolabus*, an independent tribe, eight species are recognized in the Indonesian Archipelago.

With extremely high biodiversity characterized by a high level of endemism and complex geological history, the Indonesian Archipelago, the islands between continental Southeast Asia and Australia, has long attracted the attention of biologists from biogeographical and evolutionary (in terms of speciation) points of view. From the geological perspective, the Indonesian Archipelago is comprised of two major components, namely the Sunda Shelf component (Borneo, Sumatra, Java and Bali), where the fauna consists of mainly Oriental elements; and the Sahul Shelf component (New Guinea and its adjacent islands, including Aru Islands), where the fauna is comprised of Papua-Australian elements.

In the fauna of potter wasps with a petiolate metasoma of the Indonesian Archipelago, genera such as *Calligaster*, *Zethus*, *Flavoleptus*, *Norteumenes*, *Nortozumia*, *Pseudozumia*, *Omicroides* and *Labus* are the Oriental elements (Figs 2, 3), while *Elimus* is the Papua-Australian element (Fig. 2). Sumatra, Java, Bali and Borneo, as a part of Sunda Shelf/Oriental component, have mainly Oriental eumenine fauna, including several area-specific species of the Oriental genera (Fig. 4). New Guinean fauna is comprised of Papua-Australian species of the widely distributed genera, together with widely distributed species and species endemic to New Guinea (Fig. 4).

The islands lying between the two shelves form a particular area, known as Wallacea, which is considered as the harbour of endemic species, as well as those on potter wasps with a petiolate metasoma (Fig. 4). The fauna of potter wasps with a petiolate metasoma in the Wallacea is constituted mainly with the area-specific species in the rather widely distributed genera, such as *Eumenes*, *Delta*, *Phimenes*, *Coeleumenes*, *Ectopioglossa*, *Pareumenes*, and *Pseumenes*; in the western part of Wallacea, namely Sulawesi and Lesser Sunda Islands, they are represented mainly by widely distributed genera,

together with Oriental genera *Calligaster*, *Zethus* and *Labus* (Fig. 2); in the eastern part of Wallacea, namely the Moluccas (excluding Aru Islands), they are constituted mainly by area endemic species of widely distributed

Oriental genera. Occurrences of four Papua-Australian species in the Moluccas show that the area is the transition zone between Oriental and Australasian faunae (Fig. 4).

Table 1. An updated list of the Potter Wasps (Hymenoptera: Vespidae, Eumeninae) with a Petiolate Metasoma from Indonesia Archipelago (based and modified from Nugroho et al. [21]).

No.	Species	Distribution
EUMENINI		
<i>Delta</i> de Saussure, 1855		
1.	a. <i>Delta campaniforme campaniforme</i> (Fabricius, 1775)	India; Nepal; Myanmar; Vietnam; Thailand; Malaysia: Peninsular Malaysia; Singapore; Philippines; Papua New Guinea; Australia; adventive in U. S. A.: Hawaii; Indonesia: Sumatra, Java, Bawean I., Kangean Is., Borneo, Sulawesi, Lombok, Bali, Sumba, Sumbawa, Timor, Moluccas (including Kei Is.), Papua.
	b. <i>Delta campaniforme keyense</i> Giordani Soika, 1972	Indonesia: Moluccas (Kei Islands)
	c. <i>Delta campaniforme megalospilus</i> (Cameron, 1911)	Indonesia: Papua
	d. <i>Delta campaniforme tricoloratum</i> (Cameron, 1906)	Indonesia: Papua
	e. <i>Delta campaniforme urvillei</i> (de Saussure, 1852)	Indonesia: Papua, Moluccas
2.	<i>Delta eremnum</i> (van der Vecht, 1959)	Indonesia: Sumba, Flores
3.	a. <i>Delta latreillei latreillei</i> (de Saussure, 1852)	Indonesia: Papua, Java; Australia
	b. <i>Delta latreillei petiolare</i> (Schulz, 1905)	Papua New Guinea; Admiralty Is.; Trobriand Is.; Solomon Islands; adventive in U. S. A.: Hawaii; Indonesia: Papua
4.	<i>Delta nigriculum</i> Giordani Soika, 1986	Indonesia: Lombok, Sumbawa, Flores, Rinca I., Sumba
5.	a. <i>Delta pyriforme butonense</i> (Schulz, 1905)	Thailand; Indonesia: Sulawesi (including Buton Island), Moluccas
	b. <i>Delta pyriforme circinale</i> (Fabricius, 1804)	Pakistan; India; Sri Lanka; Bhutan; Nepal; China; Myanmar; Thailand; Peninsular Malaysia; Philippines; Indonesia: Sumatra, Java, Krakatau, Bawean Island, Kangean Islands, Bali, Borneo, Sulawesi (including Buton Island), Lombok, Sumbawa, Komodo, Flores, Timor, Tanimbar Islands, Sumba, Moluccas, New Guinea; adventive in U. S. A.: Hawaii.
	c. <i>Delta pyriforme malayanum</i> (Giordani Soika, 1958)	Indonesia: Sumatra
	d. <i>Delta pyriforme miraculum</i> Gusenleitner, 2008	Indonesia: Tanimbar Islands
	e. <i>Delta pyriforme nigrocinctum</i> Giordani Soika, 1993	Indonesia: Sumba
	f. <i>Delta pyriforme novaeguineae</i> (Giordani Soika, 1935)	Papua New Guinea
	g. <i>Delta pyriforme rufonigerrimum</i> Giordani Soika, 1973	Indonesia: Moluccas
6.	<i>Delta rumphii</i> (van der Vecht, 1959)	Indonesia: Moluccas

7.	<i>Delta sciarum</i> (van der Vecht, 1959)	Indonesia: Lombok, Sumba, Sumbawa, Komodo Island, Flores
8.	<i>Delta viridipenne</i> (van der Vecht, 1959)	Indonesia: Sumatra (Riau Islands)
9.	<i>Delta wieneckeii</i> (van der Vecht, 1959)	Indonesia: Timor
<i>Eumenes</i> Latreille, 1802		
1.	<i>Eumenes achterbergi</i> Giordani Soika, 1992	Indonesia: Sulawesi
2.	<i>Eumenes affinissimus</i> de Saussure, 1852	Kyrgyzstan; India; Myanmar; Malaysia: Peninsular Malaysia; Indonesia: Java
3.	<i>Eumenes agillimus</i> Dalla Torre, 1894	Indonesia: Papua, Moluccas
4.	<i>Eumenes architectus</i> Smith, 1859	India; China; Myanmar; Malaysia: Peninsular Malaysia; Singapore; Philippines; Indonesia: Sumatra, Java (including Krakatau, Kangean Is.), Sulawesi, Moluccas
5.	<i>Eumenes batantanensis</i> Nugroho, 2010	Indonesia: Papua (Batanta Island)
6.	a. <i>Eumenes blandus blandus</i> Smith, 1861	Indonesia: Moluccas
	b. <i>Eumenes blandus sumbanus</i> Giordani Soika, 1992	Indonesia: Sumba
7.	<i>Eumenes dichrous</i> Maindron, 1882	Indonesia: Moluccas
8.	<i>Eumenes diligens</i> Smith, 1864	Indonesia: Moluccas (Buru Island)
9.	<i>Eumenes dorycus</i> Maindron, 1882	Papua New Guinea; Indonesia: Papua
10.	<i>Eumenes floralis</i> Smith, 1859	Indonesia: Sulawesi
11.	<i>Eumenes inconspicuus</i> Smith, 1858	Vietnam, Thailand; Malaysia: Peninsular Malaysia, Sarawak; Indonesia [Sumatra, Kalimantan, Krakatau Islands, Java, Bali, Lesser Sunda Islands (Sumbawa), Sulawesi, Ceram, Papua]
12.	<i>Eumenes insolens</i> Smith, 1865	Indonesia: Moluccas
13.	<i>Eumenes koriensis</i> Giordani Soika, 1992	Indonesia: Sumba
14.	<i>Eumenes macrops</i> de Saussure, 1852	India; Malaysia: Peninsular Malaysia; Indonesia: Bali
15.	<i>Eumenes multipictus</i> de Saussure, 1855	Vietnam; Malaysia: Peninsular Malaysia, Sarawak; Singapore; China; Indonesia: Sumatra (including Bangka Island), Java, Kalimantan
16.	<i>Eumenes piriformis</i> de Saussure, 1862	Nepal; Philippines; Thailand; Indonesia: Sumatra, Java, Sulawesi, Lesser Sunda Islands (Lombok, Sumbawa)
17.	a. <i>Eumenes pius nigrorufus</i> Giordani Soika, 1992	Indonesia: Sumba
	b. <i>Eumenes pius pius</i> Giordani Soika, 1986	Indonesia: Komodo, Timor
18.	<i>Eumenes simplicilamellatus</i> Giordani Soika, 1935	Papua New Guinea; Australia; Indonesia: Papua
19.	<i>Eumenes tricolor</i> Smith, 1861	Indonesia: Sulawesi, Moluccas
20.	<i>Eumenes truncatus</i> Nugroho, 2010	Indonesia: Papua
<i>Omicroides</i> Giordani Soika, 1935		
1.	<i>Omicroides singularis</i> (Smith, 1858)	Vietnam; Malaysia: Sarawak; Myanmar; Thailand; Singapore; Indonesia: Sumatra, Kalimantan
<i>Phimenes</i> Giordani Soika, 1992		
1.	a. <i>Phimenes arcuatus amboinensis</i> (van der Vecht, 1959)	Indonesia: Moluccas
	b. <i>Phimenes arcuatus arcuatus</i> (Fabricius, 1775)	Papua New Guinea; Australia; Indonesia: Moluccas (Damma, Aru and Kei Islands), Papua (including Raja Ampat Islands, Biak Island)

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| c. | <i>Phimenes arcuatus buruanus</i> (van der Vecht, 1959) | Indonesia: Moluccas (Buru Island) |
| d. | <i>Phimenes arcuatus lyratus</i> (van der Vecht, 1959) | Indonesia: Moluccas |
| e. | <i>Phimenes arcuatus muruensis</i> (van der Vecht, 1960) | Papua New Guinea |
| f. | <i>Phimenes arcuatus obiensis</i> (van der Vecht, 1959) | Indonesia: Moluccas (Obi Island) |
| g. | <i>Phimenes arucatus praslinius</i> (Guérin-Méneville, 1831) | Papua New Guinea: Bismarck Islands. |
| h. | <i>Phimenes arcuatus transilis</i> (van der Vecht, 1959) | Indonesia: Papua (Misool Island) |
| 2. | a. <i>Phimenes curvatus sangirensis</i> (van der Vecht, 1959) | Indonesia: Sulawesi (Sangir Islands) |
| | b. <i>Phimenes curvatus talaudense</i> (van der Vecht, 1959) | Indonesia: Sulawesi (Talaud Islands) |
| 3. | a. <i>Phimenes flavopictus baweanus</i> (van der Vecht, 1959) | Indonesia: Bawean Island (north coast of Java) |
| | b. <i>Phimenes flavopictus blanchardi</i> (de Saussure, 1852) | Indonesia: Java (including Panaitan I., Karimunjawa and Kangean Is.), Bali, Lombok, Sumbawa, Sumba, Komodo, Flores. |
| | c. <i>Phimenes flavopictus continentalis</i> (Zimmermann, 1931) | India: Arunachal Pradesh, Karnataka, Kerala, Meghalaya, Sikkim, Uttarakhand, West Bengal; Nepal; China; Myanmar; Thailand; Vietnam; Malaysia; Indonesia: Sumatra, Krakatau. |
| | d. <i>Phimenes flavopictus dammae</i> (Dalla Torre, 1904) | Indonesia: Moluccas [Damma I. (= Pulau Damar), Kei] |
| | e. <i>Phimenes flavopictus engganensis</i> (van der Vecht, 1959) | Indonesia: Sumatra (Enggano Island) |
| | f. <i>Phimenes flavopictus kalimantenus</i> (van der Vecht, 1959) | Malaysia: Sarawak; Indonesia: Kalimantan |
| | g. <i>Phimenes flavopictus maidli</i> (Giordani Soika, 1934) | Malaysia: Peninsular Malaysia; Indonesia: Mentawai Islands (west coast of Sumatra) |
| | h. <i>Phimenes flavopictus simalurensis</i> (Giordani Soika, 1934) | Indonesia: Simalur Island [=Simeleue Island, Aceh, northwest of Sumatra] |
| | i. <i>Phimenes flavopictus telonus</i> (van der Vecht, 1959) | Indonesia: Batu Islands (west coast of Sumatra) |
| | j. <i>Phimenes flavopictus timorensis</i> (van der Vecht, 1959) | Indonesia: Timor, Wetar Island, Tanimbar Islands (Yamdena Island) |
| | k. <i>Phimenes flavopictus umbripennis</i> (van der Vecht, 1959) | Indonesia: Nias Island (west coast of Sumatra) |
| 4. | a. <i>Phimenes fulvipennis fulvipennis</i> (Smith, 1857) | Indonesia: Sulawesi (including Buton Island), Moluccas (Sula Islands) |
| | b. <i>Phimenes fulvipennis niasanus</i> (Zimmermann, 1931) | Indonesia: Nias Island (west coast of Sumatra) |
| | c. <i>Phimenes fulvipennis saleyerensis</i> (Zimmermann, 1931) | Indonesia: Selayar Islands (South of Sulawesi) |
| 5. | a. <i>Phimenes incola aruense</i> (Giordani Soika, 1935) | Indonesia: Moluccas (Aru and Kei Islands, near Papua); Australia (Queensland) |
| | b. <i>Phimenes incola incola</i> (Giordani Soika, 1935) | Papua New Guinea |
| | c. <i>Phimenes incola mauritsi</i> (van der Vecht, 1959) | Indonesia: Papua |

d.	<i>Phimenes incola octomaculatus</i> (van der Vecht, 1959)	Indonesia: Misool Island (Northwest of Papua)
e.	<i>Phimenes incola zonites</i> (van der Vecht, 1959)	Papua New Guinea; Indonesia: Papua
6.	<i>Phimenes perplexus</i> (Smith, 1864)	Indonesia: Moluccas (Buru Island)
7.	<i>Phimenes violaceipennis</i> (van der Vecht, 1959)	Indonesia: Java, Bali
8.	<i>Phimenes zamenes</i> (van der Vecht, 1959)	Indonesia: Sulawesi, Moluccas (Sula Islands)
ODYNERINI		
<i>Coeleumenes</i> van der Vecht, 1963		
1.	a. <i>Coeleumenes impavidus conformis</i> van der Vecht, 1963	Indonesia: Java
	b. <i>Coeleumenes impavidus impavidus</i> (Bingham, 1897)	India; Sri Lanka; Myanmar; Thailand; Malaysia; Singapore; Indonesia: Kalimantan.
2.	<i>Coeleumenes multicolor</i> (Giordani Soika, 1935)	Indonesia: Sumba, Sumbawa
3.	<i>Coeleumenes ruficrus</i> van der Vecht, 1963	Indonesia: Moluccas
4.	<i>Coeleumenes secundus</i> (Dalla Torre, 1889)	Indonesia: Moluccas
5.	<i>Coeleumenes timorensis</i> van der Vecht, 1963	Indonesia: Timor
6.	<i>Coeleumenes vindex</i> (Smith, 1859)	Indonesia: Sulawesi
<i>Ectopioglossa</i> Perkins, 1912		
1.	<i>Ectopioglossa henseni</i> Gusenleitner, 1990	Thailand; Borneo: Baret-Sekadu, West Kalimantan
2.	<i>Ectopioglossa mediana</i> (Smith, 1864)	Indonesia: Moluccas (Ceram Island)
3.	<i>Ectopioglossa mutata</i> Gusenleitner, 1991	Indonesia: Sulawesi
4.	<i>Ectopioglossa palustris</i> van der Vecht, 1963	Indonesia: Java
5.	a. <i>Ectopioglossa polita polita</i> (Smith, 1861)	Indonesia: Moluccas (Bacan Island)
	b. <i>Ectopioglossa polita volatilis</i> (Smith, 1864)	Papua New Guinea; Indonesia: Papua (including Misool Island), Moluccas (Aru Islands)
6.	<i>Ectopioglossa sublaevis</i> (Smith, 1857)	Vietnam; Malaysia: Sarawak; Philippines; Indonesia: Sumatra, Java, Kalimantan
7.	<i>Ectopioglossa sumbana</i> van der Vecht, 1963	Indonesia: Sumba
<i>Flavoleptus</i> Giordani Soika, 1992		
1.	<i>Flavoleptus flavobalteatus</i> (Cameron, 1903)	Malaysia: Sarawak, Sabah
<i>Norteumenes</i> Gusenleitner & Gusenleiter, 2013		
1.	<i>Norteumenes hiesli</i> Gusenleitner & Gusenleitner, 2013	Sabah
<i>Nortozumia</i> van der Vecht, 1937		
1.	<i>Nortozumia pulchella</i> (Smith, 1858)	Malaysia: Sarawak
2.	<i>Nortozumia rufofemorata rufofemorata</i> (Cameron, 1903)	Malaysia: Sarawak
<i>Pareumenes</i> de Saussure, 1855		
1.	<i>Pareumenes nigerrimus</i> van der Vecht, 1963	Indonesia: Sumbawa, Sumba, Flores, Timor
2.	<i>Pareumenes pullatus</i> (Smith, 1864)	Indonesia: Moluccas (Ceram Island)
3.	a. <i>Pareumenes quadrispinosus interjectus</i> van der Vecht, 1937	Malaysia: Peninsular Malaysia, Sarawak; Indonesia: Sumatra
	b. <i>Pareumenes quadrispinosus javanus</i> van der Vecht, 1937	Indonesia: Java
<i>Pseudozumia</i> de Saussure, 1875		

- | | | | |
|----|----|---|---|
| 1. | a. | <i>Pseudozumia indica borneana</i> Giordani Soika, 1960 | Malaysia (including Sarawak); Indonesia: Kalimantan |
| | b. | <i>Pseudozumia indica indica</i> (de Saussure, 1855) | India; Sri Lanka; China; Taiwan; Vietnam; Malaysia: Peninsular Malaysia; Borneo: Sarawak; Indonesia: Sumatra, Java, Bali, Lombok. |
| | c. | <i>Pseudozumia indica wallacei</i> (Meade-Waldo, 1910) | Indonesia: Sumatra |
| 2. | | <i>Pseudozumia orientalis</i> (Gribodo, 1892) | Indonesia: Kalimantan |
| 3. | | <i>Pseudozumia viridipennis</i> Giordani Soika, 1960 | Indonesia: Sulawesi |

***Pseumenes* Giordani Soika, 1935**

- | | | | |
|----|----|---|-------------------------------------|
| 1. | a. | <i>Pseumenes depressus hamanni</i> van der Vecht, 1963 | Indonesia: Sulawesi |
| | b. | <i>Pseumenes depressus insignis</i> van der Vecht, 1963 | Indonesia: Sumba |
| | c. | <i>Pseumenes depressus pictifrons</i> (Smith, 1861) | Indonesia: Sulawesi |
| | d. | <i>Pseumenes depressus thoracicus</i> (van der Vecht, 1937) | Indonesia: Java, Bali |
| 2. | a. | <i>Pseumenes eximius arcuatoides</i> van der Vecht, 1963 | Indonesia: Moluccas (Ambon), Papua. |
| | b. | <i>Pseumenes eximius eximius</i> (Smith, 1861) | Indonesia: Moluccas |
| 3. | | <i>Pseumenes laboriosus</i> (Smith, 1861) | Indonesia: Sulawesi |

ZETHINI

***Calligaster* de Saussure, 1852**

- | | | |
|----|--|--------------------------|
| 1. | <i>Calligaster cyanoptera</i> de Saussure, 1852 | Indonesia: Java, Sumatra |
| 2. | <i>Calligaster etchellsii</i> (Cameron, 1909) | Malaysia: Sarawak |
| 3. | <i>Calligaster viridipennis</i> Giordani Soika, 1960 | Indonesia: Sulawesi |

***Elimus* de Saussure, 1852**

- | | | |
|----|---|------------------|
| 1. | <i>Elimus papuanus</i> Borsato and Giordani Soika, 1995 | Papua New Guinea |
|----|---|------------------|

***Zethus* Fabricius, 1804**

- | | | |
|----|---|--|
| 1. | <i>Zethus celebensis</i> Giordani Soika, 1960 | Indonesia: Sulawesi |
| 2. | <i>Zethus mandibularis</i> Giordani Soika, 1995 | Indonesia: Flores, Sumba |
| 3. | <i>Zethus quadridentatus</i> Cameron, 1902 | Borneo |
| 4. | <i>Zethus varipunctatus</i> Cameron, 1902 | Malaysia: Peninsular Malaysia, Serawak |

***Labus* Group**

***Labus* de Saussure, 1867**

- | | | |
|----|--|---|
| 1. | <i>Labus amoenus</i> van der Vecht, 1935 | India: Assam; China; Laos; Vietnam; Malaysia; Singapore; Indonesia: Java, Sumatra (including Bangka Island) |
| 2. | <i>Labus angularis</i> van der Vecht, 1935 | India; China; Myanmar; Thailand; Indonesia: Java |
| 3. | <i>Labus clypeatus</i> van der Vecht, 1935 | Indonesia: Java; Vietnam |
| 4. | <i>Labus robustus</i> Li & Carpenter, 2018 | Indonesia: Java |
| 5. | <i>Labus rufomaculatus</i> van der Vecht, 1963 | Indonesia: Sumba |
| 6. | <i>Labus spiniger</i> de Saussure, 1867 | Indonesia: Sumatra, Java; China |
| 7. | <i>Labus sumatrensis</i> Giordani Soika, 1991 | Indonesia: Sumatra |
| 8. | <i>Labus vandervechti</i> Giordani Soika, 1960 | Indonesia: Lombok, Sumbawa, Flores |
-

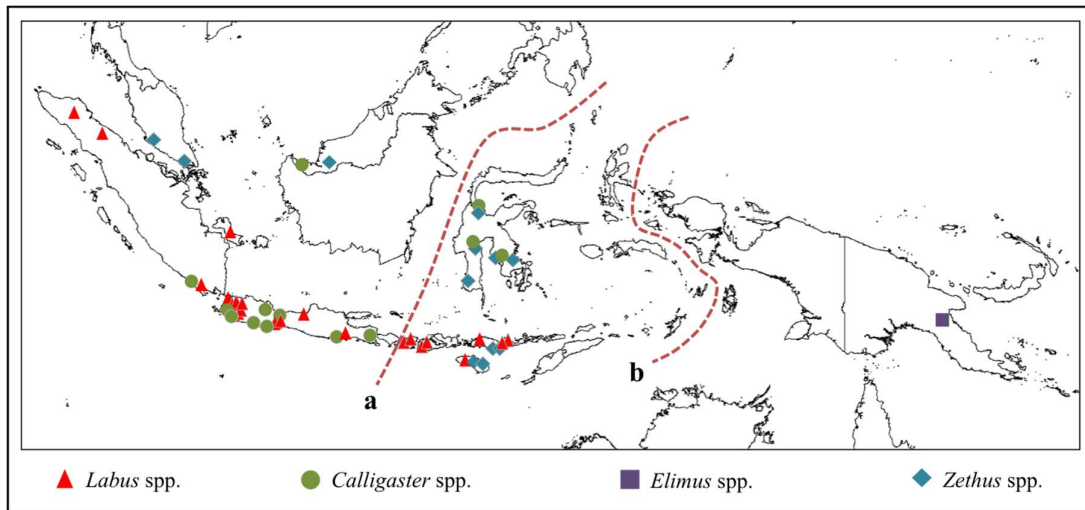


Fig. 2. Map showing the collection records of the *Labus* group and Zethini at the generic level in the Indonesian Archipelago. (a) Wallace's line. (b) Lydekker's line

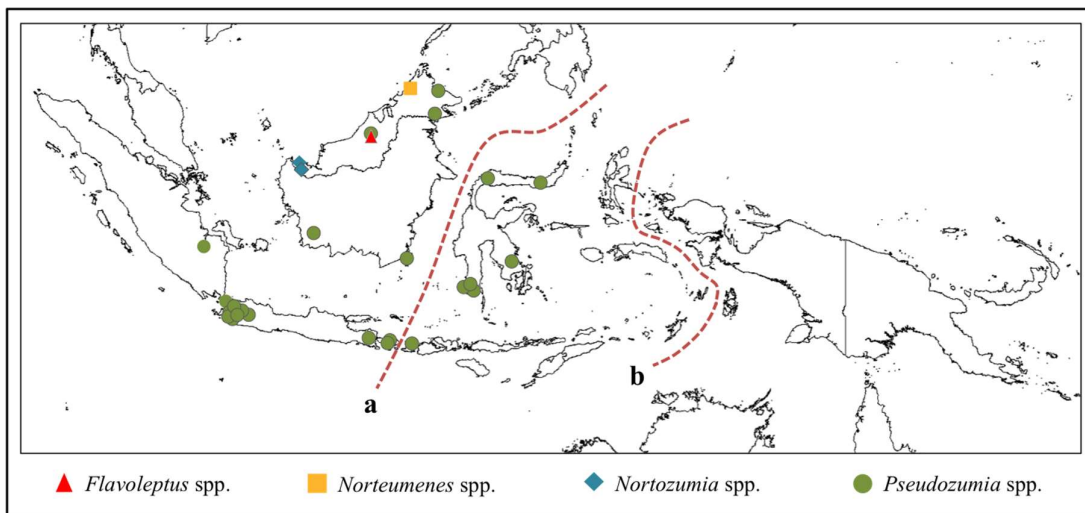


Fig. 3. Map showing the collection records of Oriental genera of Odynerini in the Indonesian Archipelago. (a) Wallace's line. (b) Lydekker's line

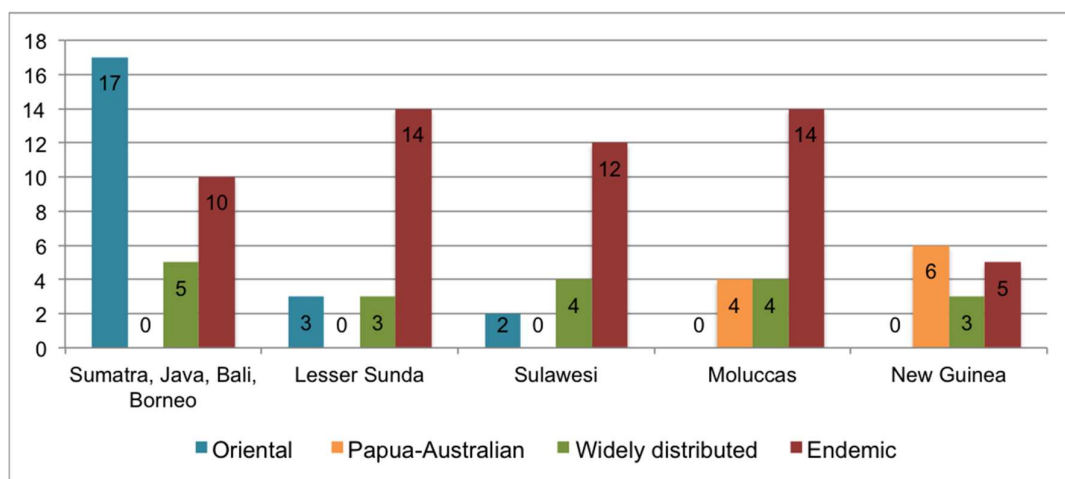


Fig. 4. Number of species of the potter wasps with a petiolate metasoma in the Indonesian Archipelago. Sumatra, Java, Bali and Borneo are part of Sunda Shelf; Wallacea consists of Lesser Sunda, Sulawesi and Moluccas; New Guinea is Sahul Shelf component, and including Aru Islands

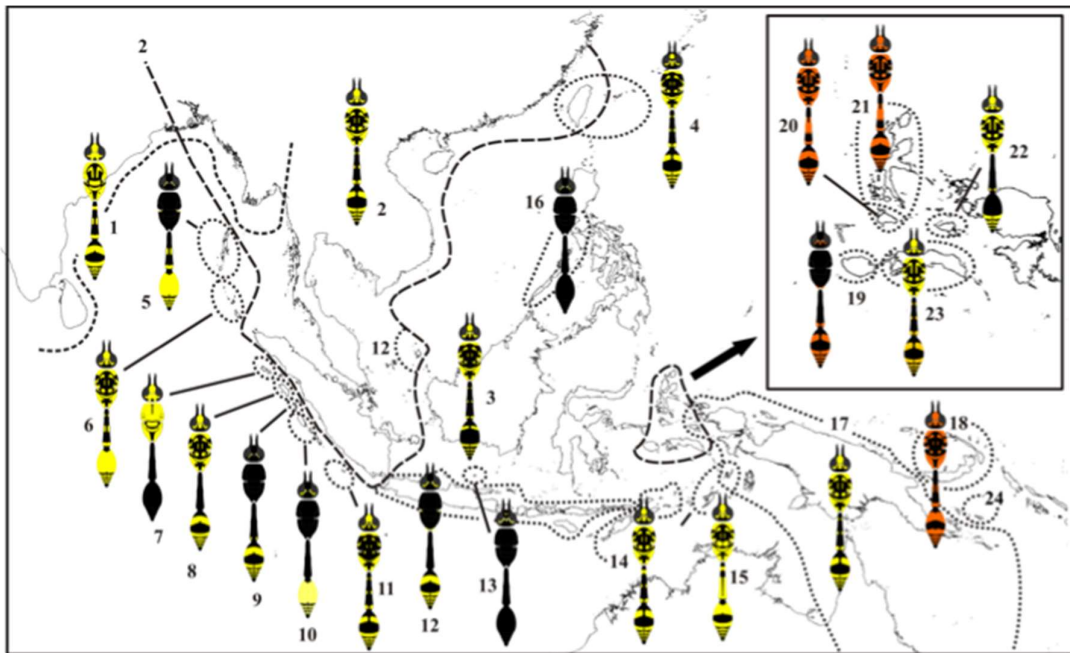


Fig. 5. Marking pattern and distribution of the subspecies *Phimenes flavopictus* and *Phimenes arcuatus* [modified from van der Vecht (1959)]: **1–16:** *Phimenes flavopictus*. (1) *P. f. flavopictus*. (2) *P. f. continentalis*. (3) *P. f. kalimantenus*. (4) *P. f. formosanus*. (5) *P. f. andamanicus*. (6) *P. f. nicobaricus*. (7) *P. f. simalurensis*. (8) *P. f. umbripennis*. (9) *P. f. telonus*. (10) *P. f. maidli*. (11) *P. f. engganensis*. (12) *P. f. blanchardi*. (13) *P. f. baweanus*. (14) *P. f. timorensis*. (15) *P. f. dammae*. (16) *P. f. aidrytus*. **17–24:** *Phimenes arcuatus*. (17) *P. a. arcuatus*. (18) *P. a. praslinius*. (19) *P. a. buruanus*. (20) *P. a. obiensis*. (21) *P. a. lyratus*. (22) *P. a. transilis*. (23) *P. a. amboinensis*. (24) *P. a. muruensis*

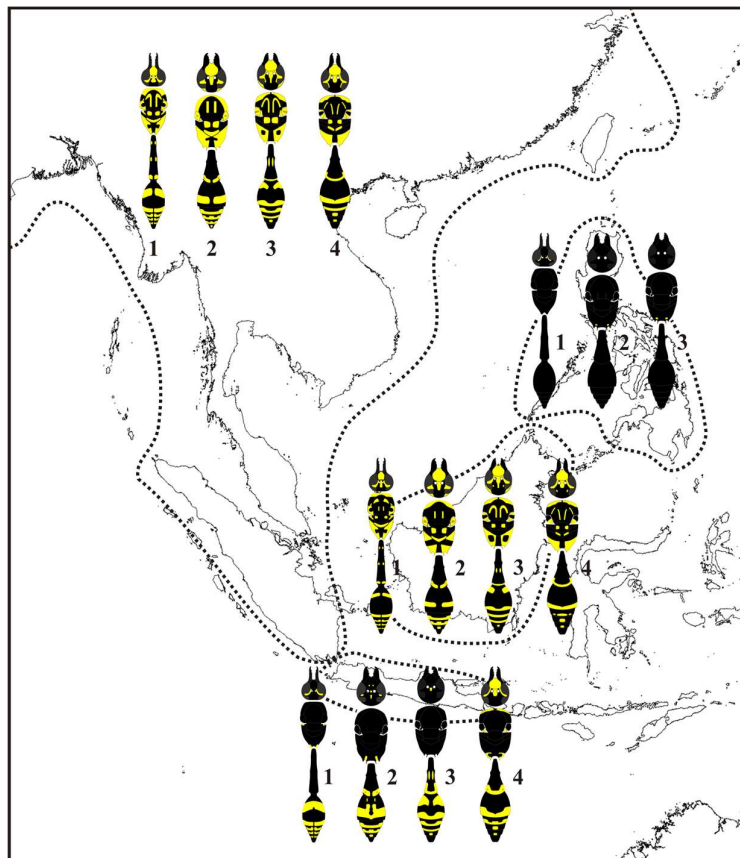


Fig. 6. Map showing the parallel distribution of marking pattern in four species: (1) *Phimenes flavopictus*, (2) *Pareumenes quadrispinosus*, (3) *Pseumenes depressus*, (4) *Coeleumenes impavidus*

3.3. Color variation and marking pattern

Species that are widely distributed generally show wide range of variation in the marking patterns, such as *Phimenes flavopictus*, *P. arcuatus*, *Pareumenes quadrispinosus*, *Pseumenes depressus* and *Coeleumenes impavidus*. The marking patterns of two closely related polymorphic species, Oriental *Phimenes flavopictus* and Papuan *P. arcuatus*, are remarkable (Fig. 5). Their marking patterns consist of those of the “mainland populations (or subspecies)” that inhabit a wide range of geographical areas and those of “peripheral populations (or subspecies)” inhabiting adjacent islands (van der Vecht, 1961). The mainland subspecies of *P. flavopictus*, *flavopictus* in continental Asia (Fig. 5 [1]), *continentalis* occurring in continental Asia and Sumatra (Fig. 5 [2]) and *formosanus* in Taiwan (Fig. 5 [4]), are more or less extensively marked with yellow, and occur sympatrically in some areas. The Bornean subspecies, *kalimantenus* (Fig. 5 [3]), has the marking pattern similar to those of these mainland subspecies but its yellow markings are constantly narrower or reduced. The peripheral subspecies of *P. flavopictus* inhabiting small islands from the Andaman Islands, through the group of islands off the west coast of Sumatra and Java, to Lesser Sunda Islands and Tanimbar, and also the Philippines, are characterized by the island(s)-specific marking patterns. In some subspecies, mosaic marking patterns are recognized, that is, in some body parts yellow markings are more extensive than those in mainland subspecies and in other body parts the yellow markings are reduced or even absent (Fig. 5 [5–7, 9, 10]). In other subspecies, yellow markings are much reduced, or even the body is nearly entirely black (Fig. 5 [12, 13, 16]), while others have the marking pattern with yellow marking only slightly reduced and/or only slightly extensive than those of the mainland subspecies (Fig. 5 [8, 11, 14, 15]).

The mainland subspecies of *P. arcuatus*, *arcuatus* (Fig. 5 [17]), has the marking pattern similar to those of the mainland subspecies of *P. flavopictus*, and occurs in New Guinea (including Aru Islands) and North Queensland of Australia, and also in Kei Islands, where *P. flavopictus dammae* [Fig. 5 (15)] with the marking pattern similar to *P. a. arcuatus* occurs. The peripheral subspecies of *P. arcuatus* are found in the Moluccas and adjacent islands of New Guinea [Fig. 5 (18–24)]. They show, as the peripheral subspecies of *P. flavopictus*, the island(s)-specific marking patterns, which are generally characterized by orange markings instead of yellow markings [Fig. 5 (18–21)] or reduction of yellow markings [Fig. 5 (22)]. Subspecies *ambonensis* is similar to mainland subspecies, but the markings on the metasoma are slightly darker [Fig. 5 (23)].

As mentioned above, their marking patterns often consist of those of the “mainland populations (or subspecies)” that inhabit a wide range of geographical areas and those of “peripheral populations (or subspecies)” inhabiting adjacent islands; the mainland subspecies more or less show similar markings with only

slightly reduced and/or only a slightly extensive variation and occurs sympatrically in some areas, while the peripheral subspecies usually characterized by the island(s)-specific marking patterns (Fig. 5). Sympatric occurrences of forms with quite different color patterns in widely distributed species may invite us to make a further intensive study to establish their taxonomic status, namely whether they are variations within a given area or different species.

Body color markings in aculeate wasps are commonly found to be contrasted patterns of bright and dark (usually black) color as a warning signal to their predators, despite the fact that the degree of darkness drastically varies among local populations of a given species. The color variations in the polymorphic and widely distributed eumenine species with a petiolate metasoma in the Indonesian Archipelago show mosaic pattern of distribution but they do not change along geographical clines, and thus such the color variations have been more likely driven by aposematic pressure rather than by abiotic factors. Sympatric occurrences of nearly the same marking pattern in four species (*Phimenes flavopictus*, *Pareumenes quadrispinosus*, *Pseumenes depressus*, and *Coeleumenes impavidus*), probably have resulted from the Müllerian mimicry, and are recognized in the continental Asia, the Philippines, Borneo and Java (Fig. 6).

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