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

Compared with the other three vespid 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 “Zethinace” 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/marking 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 (SEIIU), 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, *Norteumenes* 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. quadridens* and *Z. varipunctatus* from Borneo. The other Oriental genus in the so-called “Zethinace”, *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** Delta de Saussure, 1855 |
| 1. a. | *Delta campaniforme campaniforme* (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. | *Delta campaniforme keyense* Giordani Soika, 1972 | Indonesia: Moluccas (Kei Islands) |
| c. | *Delta campaniforme megalospilus* (Cameron, 1911) | Indonesia: Papua |
| d. | *Delta campaniforme tricoloratum* (Cameron, 1906) | Indonesia: Papua |
| e. | *Delta campaniforme urvillei* (de Saussure, 1852) | Indonesia: Papua, Moluccas |
| 2. | *Delta eremnum* (van der Vecht, 1959) | Indonesia: Sumba, Flores |
| 3. a. | *Delta latreillei latreillei* (de Saussure, 1852) | Indonesia: Papua, Java; Australia |
| b. | *Delta latreillei petiolare* (Schulz, 1905) | Papua New Guinea; Admiralty Is.; Trobriand Is.; Solomon Islands; adventive in U. S. A.: Hawaii; Indonesia: Papua |
| 4. | *Delta nigriculum* Giordani Soika, 1986 | Indonesia: Lombok, Sumbawa, Flores, Rinca I., Sumba |
| 5. a. | *Delta pyriforme butonense* (Schulz, 1905) | Thailand; Indonesia: Sulawesi (including Buton Island), Moluccas |
| b. | *Delta pyriforme circinale* (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. | *Delta pyriforme malayanum* (Giordani Soika, 1958) | Indonesia: Sumatra |
| d. | *Delta pyriforme miraculum* Gusenleitner, 2008 | Indonesia: Tanimbar Islands |
| e. | *Delta pyriforme nigrocinctum* Giordani Soika, 1993 | Indonesia: Sumba |
| f. | *Delta pyriforme novaeguineae* (Giordani Soika, 1935) | Papua New Guinea |
| g. | *Delta pyriforme rufonigerrimum* Giordani Soika, 1973 | Indonesia: Moluccas |
| 6. | *Delta rumphii* (van der Vecht, 1959) | Indonesia: Moluccas |
mainly by area endemic species of widely distributed Moluccas (excluding Aru Islands), they are constituted together with Oriental genera

Table 1.

| No. | Species                                      | Distribution                                                                 |
|-----|----------------------------------------------|------------------------------------------------------------------------------|
| 7   | *Delta sciarum* (van der Vecht, 1959)        | Indonesia: Lombok, Sumba, Sumbawa, Komodo Island, Flores                      |
| 8   | *Delta viridipenne* (van der Vecht, 1959)    | Indonesia: Sumatra (Riau Islands)                                            |
| 9   | *Delta vienecet* (van der Vecht, 1959)       | Indonesia: Timor                                                             |

**Eumenes Latreille, 1802**

1. *Eumenes achterbergi* Giordani Soika, 1992
   - Indonesia: Sulawesi
2. *Eumenes affinisimus* de Saussure, 1852
   - Kyrgyzstan; India; Myanmar; Malaysia: Peninsular Malaysia; Indonesia: Java
3. *Eumenes agilinus* Dalla Torre, 1894
   - Indonesia: Papua, Moluccas
4. *Eumenes architectus* Smith, 1859
   - India; China; Myanmar; Malaysia: Peninsular Malaysia; Singapore; Philippines; Indonesia: Sumatra, Java (including Krakatau, Kangean Is.), Sulawesi, Moluccas
5. *Eumenes batatanensis* Nugroho, 2010
   - Indonesia: Papua (Batanta Island)
6. a. *Eumenes blandus blandus* Smith, 1861
    - Indonesia: Moluccas
   b. *Eumenes blandus sumbanus* Giordani Soika, 1992
    - Indonesia: Sumba
7. *Eumenes dichrous* Maindron, 1882
   - Indonesia: Moluccas
8. *Eumenes diligens* Smith, 1864
   - Indonesia: Moluccas (Buru Island)
9. *Eumenes dorycus* Maindron, 1882
   - Papua New Guinea; Indonesia: Papua
10. *Eumenes floralis* Smith, 1859
    - Indonesia: Sulawesi
11. *Eumenes inconspicuus* Smith, 1858
    - Vietnam, Thailand; Malaysia: Peninsular Malaysia, Sarawak; Indonesia [Sumatra, Kalimantan, Krakatau Islands, Java, Bali, Lesser Sunda Islands (Sumbawa), Sulawesi, Ceram, Papua]
12. *Eumenes insolens* Smith, 1865
    - Indonesia: Moluccas
13. *Eumenes koriensis* Giordani Soika, 1992
    - Indonesia: Sumba
14. *Eumenes macrops* de Saussure, 1852
    - India; Malaysia: Peninsular Malaysia; Indonesia: Bali
15. *Eumenes multipictus* de Saussure, 1855
    - Vietnam; Malaysia: Peninsular Malaysia, Sarawak; Singapore; China; Indonesia: Sumatra (including Bangka Island), Java, Kalimantan
16. *Eumenes piriformis* de Saussure, 1862
    - Nepal; Philippines; Thailand; Indonesia: Sumatra, Java, Sulawesi, Lesser Sunda Islands (Lombok, Sumbawa)
17. a. *Eumenes plus nigrorufus* Giordani Soika, 1992
    - Indonesia: Sumba
   b. *Eumenes plus plus* Giordani Soika, 1986
    - Indonesia: Komodo, Timor
18. *Eumenes simplicilamellatus* Giordani Soika, 1935
    - Papua New Guinea; Australia; Indonesia: Papua
19. *Eumenes tricolor* Smith, 1861
    - Indonesia: Sulawesi, Moluccas
20. *Eumenes truncatus* Nugroho, 2010
    - Indonesia: Papua

**Omicroides Giordani Soika, 1935**

1. *Omicroides singularis* (Smith, 1858)
   - Vietnam; Malaysia: Sarawak; Myanmar; Thailand; Singapore; Indonesia: Sumatra, Kalimantan

**Phimenes Giordani Soika, 1992**

1. a. *Phimenes arcuatus amboinensis* (van der Vecht, 1959)
    - Indonesia: Moluccas
   b. *Phimenes arcuatus arcuatus* (Fabricius, 1775)
    - Papua New Guinea; Australia; Indonesia: Moluccas (Damma, Aru and Kei Islands), Papua (including Raja Ampat Islands, Biak Island)
c. *Phimenes arcuatus buruanus* (van der Vecht, 1959) 
   Indonesia: Moluccas (Buru Island)

d. *Phimenes arcuatus lyratus* (van der Vecht, 1959) 
   Indonesia: Moluccas

e. *Phimenes arcuatus muruensis* (van der Vecht, 1960) 
   Papua New Guinea

f. *Phimenes arcuatus obiensis* (van der Vecht, 1959) 
   Indonesia: Moluccas (Obi Island)

g. *Phimenes arcuatus praslinius* (Guérin-Méneville, 1831) 
   Papua New Guinea: Bismarck Islands.

h. *Phimenes arcuatus transilis* (van der Vecht, 1959) 
   Indonesia: Papua (Misool Island)

2. a. *Phimenes curvatus sangirensis* (van der Vecht, 1959) 
   Indonesia: Sulawesi (Sangir Islands)

b. *Phimenes curvatus talaudense* (van der Vecht, 1959) 
   Indonesia: Sulawesi (Talaud Islands)

3. a. *Phimenes flavopictus baweanus* (van der Vecht, 1959) 
   Indonesia: Bawean Island (north coast of Java)

b. *Phimenes flavopictus blanchardi* (de Saussure, 1852) 
   Indonesia: Java (including Panaitan I., Karimunjawa and Kangean Is.), Bali, Lombok, Sumbawa, Sumba, Komodo, Flores.

c. *Phimenes flavopictus continentalis* (Zimmermann, 1931) 
   India: Arunachal Pradesh, Karnataka, Kerala, Meghalaya, Sikkim, Uttarakhnad, West Bengal; Nepal; China; Myanmar; Thailand; Vietnam; Malaysia; Indonesia: Sumatra, Krakatua.

d. *Phimenes flavopictus dammae* (Dalla Torre, 1904) 
   Indonesia: Moluccas [Damma I. (= Pulau Damar), Kei]

e. *Phimenes flavopictus engganensis* (van der Vecht, 1959) 
   Indonesia: Sumatra (Enggano Island)

f. *Phimenes flavopictus kalimantenus* (van der Vecht, 1959) 
   Malaysia: Sarawak; Indonesia: Kalimantan

g. *Phimenes flavopictus maidli* (Giordani Soika, 1934) 
   Malaysia: Peninsular Malaysia; Indonesia: Mentawai Islands (west coast of Sumatra)

h. *Phimenes flavopictus simalurensis* (Giordani Soika, 1934) 
   Indonesia: Simalur Island [=Simeleue Island, Aceh, northwest of Sumatra]

i. *Phimenes flavopictus telonus* (van der Vecht, 1959) 
   Indonesia: Batu Islands (west coast of Sumatra)

j. *Phimenes flavopictus timorensis* (van der Vecht, 1959) 
   Indonesia: Timor, Wetar Island, Tanimbar Islands (Yamdena Island)

k. *Phimenes flavopictus umbripennis* (van der Vecht, 1959) 
   Indonesia: Nias Island (west coast of Sumatra)

4. a. *Phimenes fulvipennis fulvipennis* (Smith, 1857) 
   Indonesia: Sulawesi (including Buton Island), Moluccas (Sula Islands)

b. *Phimenes fulvipennis niasanus* (Zimmermann, 1931) 
   Indonesia: Nias Island (west coast of Sumatra)

c. *Phimenes fulvipennis saleyerensis* (Zimmermann, 1931) 
   Indonesia: Selayar Islands (South of Sulawesi)

5. a. *Phimenes incola aruense* (Giordani Soika, 1935) 
   Indonesia: Moluccas (Aru and Kei Islands, near Papua); Australia (Queensland)

b. *Phimenes incola incola* (Giordani Soika, 1935) 
   Papua New Guinea

c. *Phimenes incola mauritii* (van der Vecht, 1959) 
   Indonesia: Papua
|   | Scientific Name                                      | Distribution                                                                 |
|---|-----------------------------------------------------|-------------------------------------------------------------------------------|
| d. | *Phimeipes incola octomaculatus* (van der Vecht, 1959) | Indonesia: Misool Island (Northwest of Papua)                                 |
| e. | *Phimeipes incola zonites* (van der Vecht, 1959)     | Papua New Guinea; Indonesia: Papua                                             |
| 6. | *Phimeipes perplexus* (Smith, 1864)                  | Indonesia: Moluccas (Buru Island)                                             |
| 7. | *Phimeipes violaceipennis* (van der Vecht, 1959)     | Indonesia: Java, Bali                                                        |
| 8. | *Phimeipes zamenes* (van der Vecht, 1959)            | Indonesia: Sulawesi, Moluccas (Sula Islands)                                  |

**ODYNERINI**

|   | Scientific Name                                      | Distribution                                                                 |
|---|-----------------------------------------------------|-------------------------------------------------------------------------------|
| 1. | *Coeleumenes impavidus conformis* van der Vecht, 1963 | Indonesia: Java                                                              |
| 2. | *Coeleumenes multicolor* (Giordani Soika, 1935)      | Indonesia: Sumba, Sumbawa                                                   |
| 3. | *Coeleumenes ruficrus* van der Vecht, 1963           | Indonesia: Moluccas                                                          |
| 4. | *Coeleumenes secundus* (Dalla Torre, 1889)          | Indonesia: Moluccas                                                          |
| 5. | *Coeleumenes timorensis* van der Vecht, 1963         | Indonesia: Timor                                                             |
| 6. | *Coeleumenes vindex* (Smith, 1859)                   | Indonesia: Sulawesi                                                          |

**Ectopioglossa Perkins, 1912**

|   | Scientific Name                                      | Distribution                                                                 |
|---|-----------------------------------------------------|-------------------------------------------------------------------------------|
| 1. | *Ectopioglossa henseni* Gusenleitner, 1990          | Thailand; Borneo: Bate-Sekadu, West Kalimantan                               |
| 2. | *Ectopioglossa mediana* (Smith, 1864)                | Indonesia: Moluccas (Ceram Island)                                           |
| 3. | *Ectopioglossa mutata* Gusenleitner, 1991           | Indonesia: Sulawesi                                                          |
| 4. | *Ectopioglossa palustris* van der Vecht, 1963       | Indonesia: Java                                                              |
| 5. | a. *Ectopioglossa polita polita* (Smith, 1861)       | Indonesia: Moluccas (Bacan Island)                                           |
|    | b. *Ectopioglossa polita volatilis* (Smith, 1864)    | Papua New Guinea; Indonesia: Papua (including Misool Island), Moluccas (Aru Islands) |
| 6. | *Ectopioglossa sublaevis* (Smith, 1857)              | Vietnam; Malaysia: Sarawak; Philippines; Indonesia: Sumatra, Java, Kalimantan |
| 7. | *Ectopioglossa sumbana* van der Vecht, 1963         | Indonesia: Sumba                                                             |

**Flavoleptus Giordani Soika, 1922**

|   | Scientific Name                                      | Distribution                                                                 |
|---|-----------------------------------------------------|-------------------------------------------------------------------------------|
| 1. | *Flavoleptus flavobalteatus* (Cameron, 1903)         | Malaysia: Sarawak, Sabah                                                    |

**Nortozumia Gusenleitner & Gusenleiter, 2013**

|   | Scientific Name                                      | Distribution                                                                 |
|---|-----------------------------------------------------|-------------------------------------------------------------------------------|
| 1. | *Nortozumia hiesli* Gusenleitner & Gusenleiter, 2013 | Sabah                                                                       |

**Nortozumia van der Vecht, 1937**

|   | Scientific Name                                      | Distribution                                                                 |
|---|-----------------------------------------------------|-------------------------------------------------------------------------------|
| 1. | *Nortozumia pulchella* (Smith, 1858)                 | Malaysia: Sarawak                                                            |
| 2. | *Nortozumia rufofemorata rufofemorata* (Cameron, 1903) | Malaysia: Sarawak                                                            |

**Pareumenes de Saussure, 1855**

|   | Scientific Name                                      | Distribution                                                                 |
|---|-----------------------------------------------------|-------------------------------------------------------------------------------|
| 1. | *Pareumenes nigerrimus* van der Vecht, 1963         | Indonesia: Sumbawa, Sumba, Flores, Timor                                      |
| 2. | *Pareumenes pullatus* (Smith, 1864)                  | Indonesia: Moluccas (Ceram Island)                                           |
| 3. | a. *Pareumenes quadrir-spinosus interfectus* van der Vecht, 1937 | Malaysia: Peninsular Malaysia, Sarawak; Indonesia: Sumatra |
|    | b. *Pareumenes quadrir-spinosus javanus* van der Vecht, 1937 | Indonesia: Java                                                             |

**Pseudozumia de Saussure, 1875**
1. **Pseudozumia indica borneana** Giordani Soika, 1960  
   Malaysia (including Sarawak); Indonesia: Kalimantan
2. **Pseudozumia indica indica** (de Saussure, 1855)  
   India; Sri Lanka; China; Taiwan; Vietnam; Malaysia: Peninsular Malaysia; Borneo: Sarawak; Indonesia: Sumatra, Java, Bali, Lombok.
3. **Pseudozumia indica wallacei** (Meade-Waldo, 1910)  
   Indonesia: Sumatra

2. **Pseudozumia orientalis** (Gribodo, 1892)  
   Indonesia: Kalimantan

3. **Pseudozumia viridipennis** Giordani Soika, 1960  
   Indonesia: Sulawesi

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1. a. **Pseumenes depressus hamanni** van der Vecht, 1963  
   Indonesia: Sulawesi
2. b. **Pseumenes depressus insignis** van der Vecht, 1963  
   Indonesia: Sumba
3. c. **Pseumenes depressus pictifrons** (Smith, 1861)  
   Indonesia: Sulawesi
4. d. **Pseumenes depressus thoracicus** (van der Vecht, 1937)  
   Indonesia: Java, Bali

2. a. **Pseumenes eximius arcuatoides** van der Vecht, 1963  
   Indonesia: Moluccas (Ambon), Papua.
2. b. **Pseumenes eximius eximius** (Smith, 1861)  
   Indonesia: Moluccas
3. c. **Pseumenes laboriosus** (Smith, 1861)  
   Indonesia: Sulawesi

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**ZETHINI**

**Calligaster de Saussure, 1852**

1. **Calligaster cyanoptera** de Saussure, 1852  
   Indonesia: Java, Sumatra
2. **Calligaster etchellsii** (Cameron, 1909)  
   Malaysia: Sarawak
3. **Calligaster viridipennis** Giordani Soika, 1960  
   Indonesia: Sulawesi

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**Elimus de Saussure, 1852**

1. **Elimus papuanus** Borsato and Giordani Soika, 1995  
   Papua New Guinea

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**Zethus Fabricius, 1804**

1. **Zethus celebensis** Giordani Soika, 1960  
   Indonesia: Sulawesi
2. **Zethus mandibularis** Giordani Soika, 1995  
   Indonesia: Flores, Sumba
3. **Zethus quadridenticus** Cameron, 1902  
   Borneo
4. **Zethus variipunctatus** Cameron, 1902  
   Malaysia: Peninsular Malaysia, Sarawak

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**Labus Group**

**Labus de Saussure, 1867**

1. **Labus amoenus** van der Vecht, 1935  
   India: Assam; China; Laos; Vietnam; Malaysia; Singapore; Indonesia: Java, Sumatra (including Bangka Island)
2. **Labus angularis** van der Vecht, 1935  
   India; China; Myanmar; Thailand; Indonesia: Java
3. **Labus clypeatus** van der Vecht, 1935  
   Indonesia: Java; Vietnam
4. **Labus robustus** Li & Carpenter, 2018  
   Indonesia: Java
5. **Labus rufofuscatus** van der Vecht, 1963  
   Indonesia: Sumba
6. **Labus spiniger** de Saussure, 1867  
   Indonesia: Sumatra, Java; China
7. **Labus sumatrensis** Giordani Soika, 1991  
   Indonesia: Sumatra
8. **Labus vandervechti** Giordani Soika, 1960  
   Indonesia: Lombok, Sumbawa, Flores
1. a. *Pseudozumia indica borneana* Giordani Soika, 1960 Malaysia (including Sarawak); Indonesia: Kalimantan

b. *Pseudozumia indica indica* (de Saussure, 1855) India; Sri Lanka; China; Taiwan; Vietnam; Malaysia: Peninsular Malaysia; Borneo: Sarawak; Indonesia: Sumatra, Java, Bali, Lombok.

c. *Pseudozumia indica wallacei* (Meade-Waldo, 1910) Indonesia: Sumatra

2. *Pseudozumia orientalis* (Gribodo, 1892) Indonesia: Kalimantan

3. *Pseudozumia viridipennis* Giordani Soika, 1960 Indonesia: Sulawesi

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1. a. *Pseumenes depressus hamanni* van der Vecht, 1963 Indonesia: Sulawesi

b. *Pseumenes depressus insignis* van der Vecht, 1963 Indonesia: Sumba

c. *Pseumenes depressus pictifrons* (Smith, 1861) Indonesia: Sulawesi

d. *Pseumenes depressus thoracicus* (van der Vecht, 1937) Indonesia: Java, Bali

2. a. *Pseumenes eximius arcuatoides* van der Vecht, 1963 Indonesia: Moluccas (Ambon), Papua.

b. *Pseumenes eximius eximius* (Smith, 1861) Indonesia: Moluccas

3. *Pseumenes laboriosus* (Smith, 1861) Indonesia: Sulawesi

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*Zethini*  
1. *Calligaster cyanoptera* de Saussure, 1852 Indonesia: Java, Sumatra

2. *Calligaster etchellsii* (Cameron, 1909) Malaysia: Sarawak

3. *Calligaster viridipennis* Giordani Soika, 1960 Indonesia: Sulawesi

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*Elimus* de Saussure, 1852  
1. *Elimus papuanus* Borsato and Giordani Soika, 1995 Papua New Guinea

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*Zethus* Fabricius, 1804  
1. *Zethus celebensis* Giordani Soika, 1960 Indonesia: Sulawesi

2. *Zethus mandibularis* Giordani Soika, 1995 Indonesia: Flores, Sumba

3. *Zethus quadridentatus* Cameron, 1902 Borneo

4. *Zethus varipunctatus* Cameron, 1902 Malaysia: Peninsular Malaysia, Sarawak

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*Labus* Group  
1. *Labus amoenus* van der Vecht, 1935 India: Assam; China; Laos; Vietnam; Malaysia; Singapore; Indonesia: Java, Sumatra (including Bangka Island)

2. *Labus angularis* van der Vecht, 1935 India; China; Myanmar; Thailand; Indonesia: Java

3. *Labus clypeatus* van der Vecht, 1935 Indonesia: Java; Vietnam

4. *Labus robustus* Li & Carpenter, 2018 Indonesia: Java

5. *Labus rufomaculatus* van der Vecht, 1963 Indonesia: Sumba

6. *Labus spiniger* de Saussure, 1867 Indonesia: Sumatra, Java; China

7. *Labus sumatrensis* Giordani Soika, 1991 Indonesia: Sumatra

8. *Labus vandervechti* Giordani Soika, 1960 Indonesia: Lombok, Sumbawa, Flores

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**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. simalarensis. (8) P. f. umbripennis. (9) P. f. telonus. (10) P. f. maidii. (11) P. f. engganensis. (12) P. f. blanchardi. (13) P. f. baweanus. (14) P. f. timorensis. (15) P. f. dammae. (16) P. f. aidryus. 17–24: *Phimenes arcuatus*. (17) P. a. arcuatus. (18) P. a. praslinius. (19) P. a. buruanus. (20) P. a. obiensis. (21) P. a. lyraeus. (22) P. a. transilis. (23) P. a. amboinensis. (24) P. a. murrensis

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 Timor, 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 [11, 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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