

THE VESPINAE OF THE INDO-MALAYAN AND PAPUAN AREAS (HYMENOPTERA, VESPIDAE)

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INTRODUCTION

It is now more than fifty years ago since R. du Buysson published a monograph of the genus *Vespa*, a group of wasps which is at present regarded as representing a subfamily consisting of four or five different genera.

In the collections used for the preparation of that work, the fauna of the Indo-Australian archipelago was rather poorly represented. Furthermore, du Buysson did not yet have a clear idea of the relative value of structural and colour characters, and he was in several cases deceived by the remarkable resemblance in coloration of structurally different forms. For these reasons, his monograph is a far from reliable tool for the identification of the Oriental species, and a more modern treatment of the subject has been a desideratum for many years.

In the period 1934-9 some Oriental species of *Vespa* were studied by Bequaert (1934, 1936, 1939), while van der Vecht (1935, 1936) discussed

the species of the genus *Provespa*. However, only the Vespinae of the Philippine Islands were completely revised (Bequaert, 1941).

Some extensive collections from Indonesia, Malaya, and New Guinea, now available for study, have enabled me to prepare a revision of the Vespinae of the entire south-eastern part of their area of distribution¹⁾. Since these insects are fairly large and conspicuous, and as a rule rather numerous where they occur, they have been collected by many entomologists who did not pay special attention to Hymenoptera. I believe, therefore, that we have at present a fairly accurate idea of the species occurring in this part of the world. It seems very unlikely that new species will be discovered, although there remains much to learn about the distribution of some subspecies.

It should be stated here again²⁾ that the data on the distribution of the various species and "varieties", as given in the literature, are unreliable to a considerable extent. So many specimens in museum collections, obtained in the preceding century, have been found to bear incorrect locality labels, that it must be strongly advised not to use such specimens for records of distribution unless their data are confirmed by more recently collected material.

The area considered in this study comprises the Malay Peninsula or Malaya, Indonesia, the Philippine Islands, and New Guinea. Some notes are given on specimens from China, India, Siam, and Indo-China, but no attempt has been made to discuss all the species occurring in these countries.

The present revision is mainly based on the collections of the Museum Zoologicum at Bogor, Java, Indonesia, and the Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands. The former collection includes the material obtained by the Netherlands-American Archbold Expedition to New Guinea in 1938-9; the latter contains some hundreds of Vespinae collected by myself in Indonesia, besides many older specimens from this area.

The study of this subject was considerably facilitated by a visit to the "Muséum National d'Histoire Naturelle" in Paris, where an important part of the material studied by du Buysson and by Pérez is preserved. I am much indebted to the "Buitendijk-fonds" for financial aid, and to Professor E. Séguy for his kind permission to study these wasps. Du Buysson has often marked two or more specimens of his new species as "type" and unless the

1) No Vespinae are known from the Solomon Islands, New Caledonia, Australia and New Zealand.

2) Compare van der Vecht, 1950. No less than eight species of Vespinae have been recorded from Java, where only three species occur!

whole typical series came from one locality, I have indicated one specimen as the lectotype. The types of Pérez's new forms were not marked as such; they are in the collection Pérez, under the original labels, and have not yet been incorporated in the general collection.

Additional material was received from various other sources, and the valuable assistance of several museums is gratefully acknowledged. Mr. H. T. Pagden kindly sent me several specimens from his private collection and allowed me to reproduce some of his photographs. To indicate the present location of the specimens that I have examined, the following abbreviations are used:

- BM = British Museum (Natural History), London.
 IRSNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles.
 MA = Zoölogisch Museum, Amsterdam.
 LEW = Laboratorium voor Entomologie, Wageningen.
 MB = Museum Zoologicum, Bogor, Indonesia.
 MBA = Naturhistorisches Museum, Basel.
 ML = Rijksmuseum van Natuurlijke Historie, Leiden.
 MP = Muséum National d'Histoire Naturelle, Paris.
 USNM = United States National Museum, Washington, D. C.
 HTP = Mr. H. T. Pagden, Penang (formerly Kuala Lumpur).

References of literature under the species and subspecies are restricted to the original description and one or more recent papers. A complete bibliography will be presented at a later date in a catalogue of Oriental Vespidae.

TAXONOMIC STUDIES

Key to the Vespinae of Malaya and the Indo-Australian Archipelago

1. Head small, with short vertex and narrow temples. Ocelli very large, posterior ocelli much closer to the eyes than to each other, about as far from the occiput as from the eyes. First abdominal segment cup-shaped, the tergite convex anteriorly. Coloration uniformly brown, clypeus sometimes yellowish
 (Genus *Provespa* Ashmead) 2
- Head large, with long vertex and broad temples. Ocelli normal, posterior ocelli much closer to each other than to the eyes (except in *V. binghami* Buyss.), and at least twice as far from the occiput as from the eyes. First abdominal segment transverse, the tergite truncate and abruptly sloping anteriorly
 (Genus *Vespa* Linnaeus) 7
2. Females and workers (antennae 12-segmented, abdomen 6-segmented) 3
- Males (antennae 13-segmented, abdomen 7-segmented) 5
3. Anterior margin of clypeus distinctly emarginate, the edges of the emargination roundly prominent, slightly raised. Thorax elongate. Clypeus brownish. Length (h. + th. + t. 1 + 2): ♀ 17-20 mm, ♂ 14-16 mm. *Provespa nocturna* v. d. Vecht
- Anterior margin of clypeus nearly straight 4

4. Body slender; thorax, as seen from above, nearly $1\frac{1}{2}$ times as long as wide (including the tegulae), mesoscutum distinctly longer than wide. First abdominal segment slender, as seen from above the width at apex about $1\frac{2}{3}$ times its length. Clypeus brownish. Length (h. + th. + t. 1 + 2): ♀ 14 mm. ♂ 11-13 mm.
Provespa anomala Saussure
- Body much stouter, the thorax less elongate, only $1\frac{1}{4}$ times as long as wide, the mesoscutum scarcely longer than wide. First abdominal tergite relatively shorter and wider, its width at apex approximately twice its length. Clypeus pale yellow, darker along the margins. Length (h. + th. + t. 1 + 2): ♀ probably 17-20 mm, ♂ 14-15 mm
Provespa barthelemyi Buysson
5. Anterior margin of clypeus distinctly, but shallowly emarginate in the middle (van der Vecht, 1935, fig. 1 B). (Antennae without tyloides. Genitalia: lower margin of valva externa almost straight, not toothed; apical branches of penis approximately triangular, sharply pointed laterally, the space between them oval, slightly longer than wide (du Buysson, 1905, pl. 5 figs. 1 and 2)). Length (h. + th. + t. 1 + 2): 14-16 mm
Provespa nocturna v. d. Vecht
- Anterior margin of clypeus scarcely emarginate, almost straight 6
6. Antennae without tyloides. Genitalia about as in *P. nocturna*. Length (h. + th. + t. 1 + 2): 12-13 mm.
Provespa anomala Saussure
- Antennae with linear, raised ridges (tyloides) at under side of the flagellar segments. Genitalia: lower margin of valva externa with a distinct blunt tooth before the apex; apical branches of penis with subparallel sides, the space between them long and narrow (du Buysson, 1905, pl. 5 figs. 3 and 4). Length (h. + th. + t. 1 + 2): 13-14 mm.
Provespa barthelemyi Buysson
7. Females and workers (antennae 12-segmented, abdomen 6-segmented) 8
- Males (antennae 13-segmented, abdomen 7-segmented) 19
8. Anterior margin of clypeus with a broad and rather deep median excision, the edges forming broad, rounded, slightly raised lobes, the notch with a median, triangular blunt tooth which projects only half as far as the lateral lobes (occasionally the tooth is small or rudimentary). Clypeus coarsely, in anterior half rugosely punctate; mesopleura very finely punctate, metapleura impunctate. Sixth abdominal segment yellow.
Vespa analis Fabricius
- Anterior margin of clypeus more or less excised, but without median tooth 9
9. Head strongly widened and produced behind the eyes; as the head is seen in profile, the temples more than twice as broad as the eyes. Posterior ocelli more than three times as far from the occiput as from the eyes. Clypeus coarsely punctate, with deep median excision, the lateral lobes large and broadly rounded. (Temples and mesopleura finely and sparsely punctate; metapleura very finely punctate in lower half only).
Vespa mandarinia Smith
- Head normal, the temples at most $1\frac{1}{2}$ times the width of an eye. Posterior ocelli less than three times as far from the occiput as from the eyes. 10
10. Basal half of clypeus distinctly, often rather coarsely, punctate. If the punctures are only moderately coarse (*luctuosa*-group), the lower, vertical area of the pronotum bears some distinct transverse ridges, and the postscutellum is mainly or entirely yellow. 11
- Basal half of clypeus at most with some fine, superficial and scattered punctures. Lower, vertical area of pronotum without distinct transverse ridges. Postscutellum black, reddish or yellowish brown, yellow in *V. bicolor* only. 17
11. First abdominal tergite short, as seen from above only half as long as the second tergite. Body black, more or less extensively marked with yellow 12
- First abdominal tergite relatively longer. Head and thorax black or more or less extensively ferruginous or dull red, not marked with yellow 15

12. Abdomen entirely black (♀), or black with narrow yellow band at apex of first tergite, rather densely covered with long and stiff, black hairs. Puncturation coarser than in the following species. (Celebes) *Vespa fervida* Smith
 — Abdominal tergites with yellow apical bands; if without bands or with only one band in the ♀, the clypeus as a rule entirely yellow 13
13. Abdominal tergites rather coarsely punctate, the punctures moderately deep and well defined. Declivous part of first abdominal tergite black. Clypeus entirely yellow, partly black in females from Mindanao. (Philippine Is.). *Vespa luctuosa* Saussure
 — Abdominal tergites more finely punctate, the punctures superficial and less distinctly defined. Declivous part of first abdominal tergite as a rule with yellow spots. Clypeus black with broad yellow band at sides and anterior margin, rarely yellow with free, median, dark spot. (Malaya, Sumatra, Borneo). 14
14. Mid and hind femora yellow beneath. Abdominal bands wide laterally, but narrowed towards the middle where they are more or less distinctly incised, or the whole band narrow except laterally *Vespa multimaculata* Pérez
 — Mid and hind legs black with brownish tarsi. Abdominal bands wide, somewhat irregular anteriorly, but not distinctly narrowed towards the middle; the band on tergite 2 often wider than the black base; visible part of tergites 4 and 5 entirely yellow, tergite 6 variable, yellow, or partly or entirely black
Vespa bellicosa Saussure
15. Anterior margin of clypeus with a bluntly triangular tooth on each side of the median excision. Lower, vertical area of pronotum with strong, transverse ribs. Body covered with strong and stiff bristles *Vespa tropica* Linnaeus
 — Anterior margin of clypeus on each side of the median excision with a short, broadly rounded lobe. Pubescence finer. 16
16. Vertex, temples, scutellum, postscutellum, metapleura, and propodeum more or less densely covered with distinct and well defined punctures. Lower, vertical area of pronotum without transverse ribs *Vespa affinis* Linnaeus
 — Vertex etc. sparsely, finely and superficially punctate, scutellum and metapleura almost impunctate. Lower, vertical area of pronotum with some transverse ribs (indistinct in the worker) *Vespa mocsaryana* Buysson
17. Anterior half of clypeus almost impunctate. Mid tibiae densely covered with long hairs (longer than width of tibia) *Vespa basalis* Smith
 — Anterior half of clypeus distinctly punctate. Mid tibiae at most with a few long hairs 18
18. Abdomen rather densely covered with erect pubescence; the hairs on the second abdominal tergite about as long as the width of the hind metatarsus. (Body mainly yellow; mesoscutum black). *Vespa bicolor* Fabricius
 — Pubescence of abdomen shorter and less conspicuous, the hairs on the second abdominal tergite much shorter than the width of the hind metatarsus. (Body more extensively black, or the mesoscutum partly orange-yellow).
Vespa velutina Lepeletier
19. 1) Sides of clypeus nowhere touching the eyes, separated from them by exceedingly narrow extensions of the inner orbits 20
 — Sides of clypeus touching the eyes 22
20. Incision at apex of sixth abdominal sternite broad and semi-elliptical, its sides curving gradually toward the sides of the hind margin. Fourth antennal segment with only the basal tyloide. Clypeus rather coarsely punctate
Vespa tropica Linnaeus

1) The key does not include the male of *Vespa mandarinia* Smith, which presumably differs from all other species by the shape of the head (see characters of ♀ and ♂).

- Incision at apex of sixth abdominal sternite as wide as deep, with angular edges. Fourth antennal segment with two tyloides. Clypeus finely punctate. 21
21. Body yellow, vertex and mesoscutum black. *Vespa bicolor* Fabricius
- Body more extensively black, or mesoscutum partly orange-yellow
Vespa velutina Lepeletier
22. Antennae long and slender, their fourth segment twice as long as wide, without tyloides. Clypeus very sparsely and superficially punctate. Mid and hind tibiae densely covered with long hairs *Vespa basalis* Smith

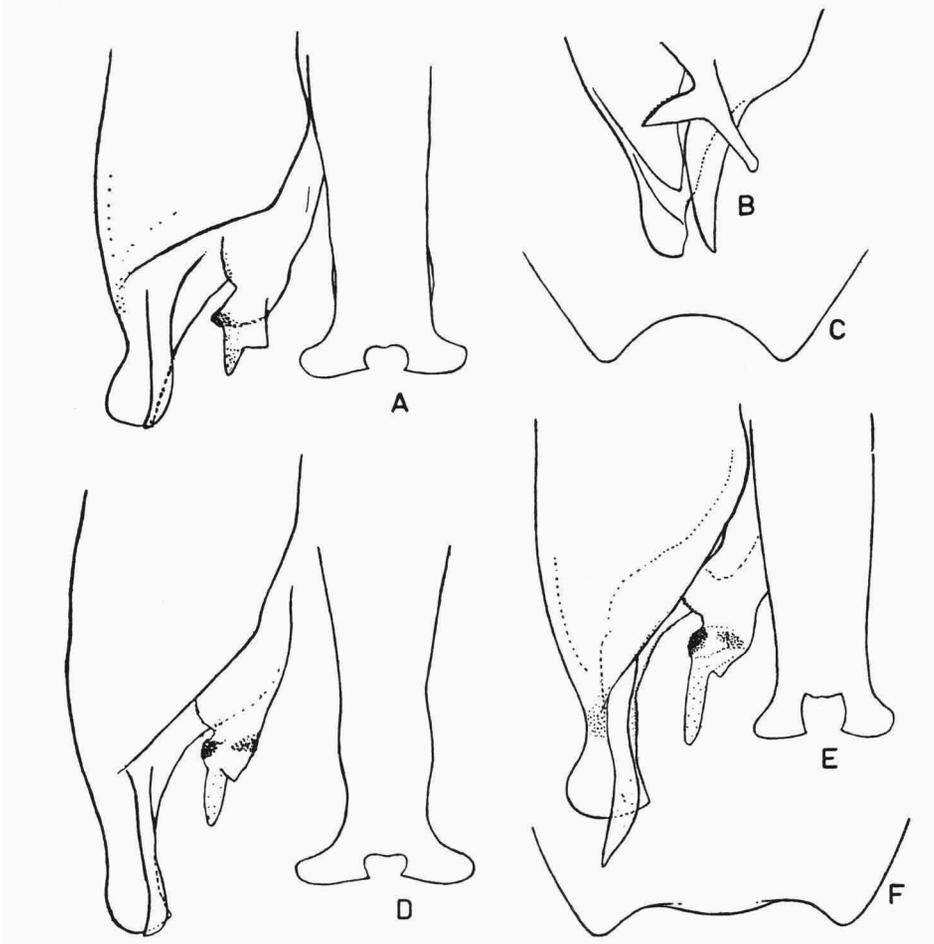


Fig. 1. Details of some males of the group of *Vespa luctuosa* Saussure. A-C, *Vespa multimaculata pendleburyi* v. d. Vecht, ♂ (Bukit Kutu, Malaya; ML); A, part of genitalia, seen from above; B, inner side of paramere and volsella; C, posterior margin of last abdominal sternite. D, *Vespa luctuosa luctuosa* Saussure, ♂ (Forest School, Luzon, Philippine Is.; ML), part of genitalia, seen from above. E-F, *Vespa fervida* Smith, ♂ (Marinsow, N. Celebes; ML); E, part of genitalia, seen from above; F, posterior margin of last abdominal sternite.

- Antennae relatively shorter, their fourth segment less than twice as long as wide, with two distinct tyloides. Clypeus more coarsely punctate. Pubescence of mid and hind legs short and sparse 23
- 23. Clypeus yellow, or black and yellow; postscutellum yellow (*luctuosa*-group). 24
- Clypeus ferruginous or black, if ferruginous-yellow, the postscutellum dark 26
- 24. Oculo-malar space shorter than in any other oriental *Vespa*, less than half the length of the fourth antennal segment. Apex of sternite 7 shallowly emarginate, the median part slightly produced, and the excision therefore not regularly arcuate (fig. 1 F). (Philippine Is., Celebes). 25
- Oculo-malar space longer than half the length of the fourth antennal segment. Apex of sternite 7 more deeply emarginate, the excision regularly arcuate (fig. 1 C). (Malaya, Sumatra, Borneo). (Abdominal tergites with broad yellow bands of equal width: see *V. bellicosa* Saussure) *Vespa multimaculata* Pérez
- 25. Clypeus black with yellow band at anterior margin, rarely black at base only. Parameral spine protruding beyond tip of paramere; inner posterior angle of lamina parameralis rounded; digitus volsellaris long (fig. 1 E). (Celebes). *Vespa fervida* Smith
- Clypeus yellow. Parameral spine not distinctly protruding beyond tip of paramere; inner posterior angle of lamina parameralis blunt; digitus volsellaris shorter (fig. 1 D). (Philippine Is.) *Vespa luctuosa* Saussure
- 26. Metapleura rather densely covered with well-defined punctures. Seventh abdominal tergite with a short, sharp, median, apical notch *Vespa affinis* Linnaeus
- Metapleura almost impunctate. Seventh tergite without median notch. 27
- 27. Anterior margin of clypeus depressed, the depression often produced in the middle into a groove which reaches the middle of the clypeus. Incision of sixth sternite semi-elliptical, wider than deep *Vespa analis* Fabricius
- Anterior margin of clypeus hardly depressed, with short and blunt median carina. Incision of sixth sternite almost as deep as wide. Head thinner and body more slender *Vespa mocsaryana* Buysson

Provespa Ashmead

1903. Ashmead, W. H., Entom. News, vol. 14, p. 182.
 1903. Ashmead, W. H., Proc. Ent. Soc. Wash., vol. 5, p. 284.
 1936. Vecht, J. van der, Jl. Fed. Mal. St. Mus., vol. 18, pp. 159-166.
 Type: *Vespa anomala* Saussure (= *V. dorylloides* Saussure).

The genus *Provespa* includes three species of nocturnal habits and is known exclusively from the Oriental region. The distribution of these insects in the Indo-Malayan area is shown in fig. 2.

Provespa anomala Saussure

- 1853-4. Saussure, H. de, Études fam. Vespides, vol. 2, p. 112, pl. 14 fig. 2 (*Vespa anomala*, "l'île de Java"), p. 256 (*Vespa dorylloides*, in "Errata").
 1903. Ashmead, W. H., Entom. News, vol. 14, p. 182 (*Vespa anomala*, type of new genus *Provespa*).
 1935. Vecht, J. van der, Entom. Meded. Ned. Indië, vol. 1, pp. 41-44, figs. 2 A, 2 B, 2 C (*Provespa anomala*).
 1936. Vecht, J. van der, Jl. Fed. Mal. St. Mus., vol. 18, p. 163 (*Provespa anomala*, literature, distribution).

The northern and western limits of the distribution area of this species are not exactly known. In 1936 I have recorded specimens from Peninsular

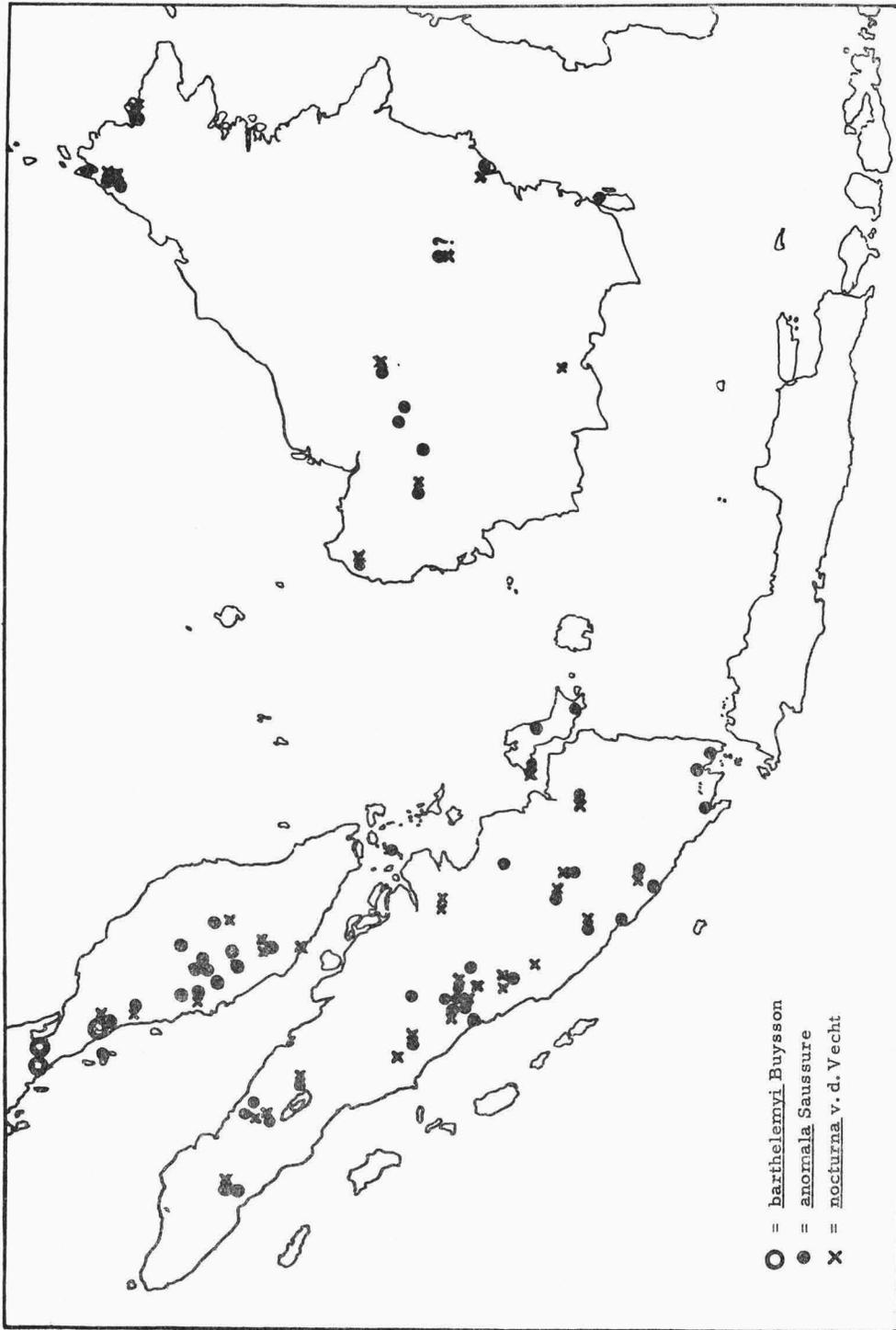


Fig. 2. The distribution of the *Protespa* species in Malaya and the Indo-Australian archipelago.

Siam, Malaya, Sumatra, and Borneo. Since then, the following material has been examined.

S u m a t r a: many specimens from various localities, ranging from Atjeh in the north (Blang Kedjeren and Mt. Kemiri, Leuser Expedition, 1937, C. G. G. J. van Steenis and A. Hoogerwerf) to the Lampong Districts in the south (MB); 4 ♀, 60 ♀, 8 ♂ from various localities (ML); 3 ♀ Durian Island, Riouw Is., 1923, K. W. Dammerman (MB, ML); some specimens from Bengkalis (MP).

B a n g k a: 1 ♀, 8 ♀, 4 ♂, Muntok, Pangkalpinang and Toboali, 1932-1939, van der Vecht (ML).

B o r n e o: 54 ♀, 6 ♂ from various localities (ML, MP); 1 ♀ Long Petak, Central East Borneo (MB); a series from Mentawir River, Balikpapan, Oct. 1950, A. M. R. Wegner (MB).

Provespa nocturna v. d. Vecht .

1935. Vecht, J. van der, Entom. Meded. Ned. Indië, vol. 1, p. 41, figs. 1 A, 1 B, 1 C (*Provespa nocturna*, Sumatra (type locality), Borneo; doubtfully recorded from Celebes; type in ML).

1936. Vecht, J. van der, Jl. Fed. Mal. St. Mus., vol. 18, pp. 161-163, figs. 1-3.

The doubtful record of this species from Celebes was based on a specimen in the Leiden Museum, bearing a label "Gorontalo, leg. Rosenberg". Since the publication of the two above-mentioned papers I have received two extensive collections of Hymenoptera from Celebes, the one made by the late Mr. F. Dupont in Menado and environs (1941), the other by Dr. C. J. H. Franssen in several localities throughout the island (1948-50). As *Provespa* was absent from both these collections, I am convinced that the specimen in the Leiden Museum is incorrectly labelled.

The following records are additions to those published in my previous papers.

I n d o - C h i n a: 1 ♀ Tonkin, rég. de Hoa-Binh, 1929, leg. A. de Cooman (MP).

S u m a t r a: Atjeh, 1 ♂ Blang Kedjeren, 1937, A. Hoogerwerf (MB); Deli, 1 ♀ Bandar Baru, J. C. van der Meer Mohr (MB), 1 ♂ Brastagi, 31 Dec. 1954, author (ML), 1 ♀ Sibolangit, 4 Jan. 1955, author (ML); Tapanuli, 2 ♀ Muarasipongi, Oct. 1925, Fuhnek and Karny (ML); Indragiri, 1 ♀ Kuala Tjinaku, 1 stylopized ♂, Rengat, Sept. 1940, Miss B. Polak (MB); Westcoast, 4 ♀ Rengkianglulus, May 1877, Sumatra-Exp. (ML); Benkulen, 1 ♀ 2 ♀ Tandjongsakti, 4 ♀ Muara Tenam, May-July 1935, Mrs. M. E. Walsh (ML).

B a n g k a I.: 1 ♂ Mt. Menumbing near Muntok, 440 m, Nov. 1939, van der Vecht (ML).

B o r n e o: West Borneo, 2 ♀ Sanggau, Kapuas River, 1894, Westenenk (ML); East Borneo, 7 ♀ 1 ♂ Mentawir River, Balikpapan, Oct. 1950, A. M. R. Wegner (MB, ML); South Borneo, 1 ♂ Pemanten-Sampit, July 1953, M. A. Lieftinck (MB).

Provespa barthelemyi (Buysson)

1905. Buysson, R. du, Ann. Soc. ent. Fr., vol. 73 (1904), p. 492, 497, 618, ♀, ♀, ♂, pl. 5 figs. 3, 4 (*Vespa Barthelemyi*; Indo-China; Bhutan; Birma).
1936. Vecht, J. van der, Jl. Fed. Mal. St. Mus., vol. 18, p. 165.

The typical series in the Paris Museum includes 1 ♀ Cambodge, Pnom Penh, 1888, leg. E. Fleutiaux; 2 ♀ Cochinchina, Cap St. Jacques, C^{te} de Barthélemy; 1 ♂ Bhoutan, leg. R. Oberthür. All these specimens are marked "type" in du Buysson's handwriting, but since only the first mentioned worker is marked "type!", I regard this as the lectotype.

Furthermore there are 2 ♀ from Baria in Cochinchina, A. Brebion, leg. Dr. J. V. Vautier, 1910, 1911, 2 ♀ 2 ♂ from Saigon, leg. Santschi, and 1 ♀ from Sikkim, leg. Fruhstorfer. The latter specimen is more densely pubescent than the others.

This species appears to reach the southern limit of its distribution area in Kedah in the Malay Peninsula.

Vespa Linnaeus

1758. Linnaeus, C., Systema Naturae, 10th Ed., vol. I, pp. 343 and 572.
1930. Bequaert, J., Bull. Brooklyn Ent. Soc., vol. 25, p. 64.
Type: *Vespa crabro* Linnaeus.

The species of this genus were divided into four groups by Bequaert (l.c., p. 65), but since it has been found that *V. analis*, *parallela*, and *nigrans* are conspecific, two groups consist each of a single species (*V. analis* and *V. binghami*), whereas the two others differ only in the length of the oculo-malar space. However, it is impossible to separate the groups sharply on the strength of this character and Bequaert himself remarked that the well-known *V. crabro* could be placed in group 3 equally well as in group 4.

Most of the species discussed below are markedly different from the others, and only *multimaculata*, *bellicosa*, *luctuosa*, and *fervida* form a group of very closely allied forms.

Vespa analis Fabricius (fig. 3)

1775. Fabricius, J. C., Systema entom., p. 363 (Cape of Good Hope, type in coll. Banks, BM). [actually probably from Java].
1939. Bequaert, J., Trans. Am. Ent. Soc., vol. 65, pp. 37-42.

This species is easily distinguished from all other Oriental Vespinae by the presence of a minute tooth in the emargination of the anterior margin of the clypeus. In the Indo-Malayan subspecies the sixth abdominal segment is always entirely yellow.

Bequaert (l.c.) enumerated the characters of *V. analis* and presented a key to the "colour forms" or "varieties". There is no doubt that most of

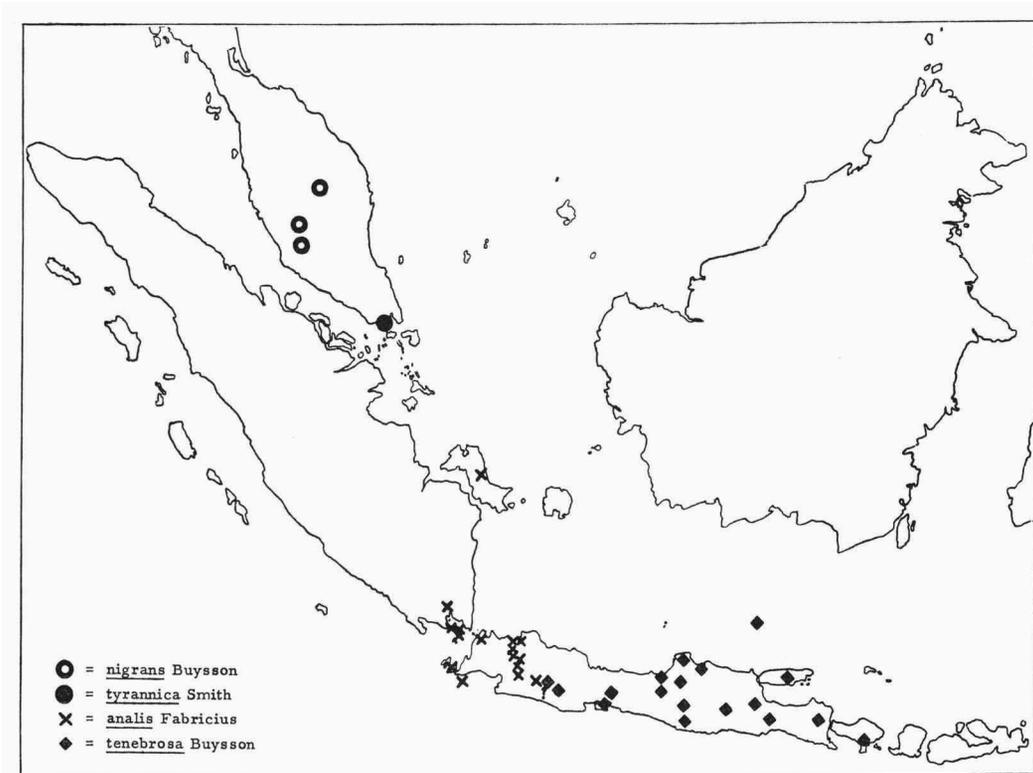


Fig. 3. The distribution of the subspecies of *Vespa analis* Fabricius inhabiting Malaya and the Indo-Australian archipelago.

these forms are geographically separated and represent true subspecies. Together with the subsp. *tenebrosa* Buysson, which was not distinguished by Bequaert as a separate form, I recognize the following subspecies: *parallela* André (China, Siberia); *nigrans* Buysson (Sikkim; Assam; South China; Yunnan; Formosa; Indo-China; Malaya); *insularis* Dalla Torre (Japan; Riukiu Is.; Hainan I.); *tyrannica* Smith (Singapore I.); *analis* F. (S. Sumatra; Bangka I.; W. Java); *tenebrosa* Buysson (E. Java; Bali).

The "varieties" *barbouri* and *kuangsiana*, described by Bequaert in 1939,

from Sikkim and Kuangsi, China, respectively, are both sympatric with one of the above mentioned subspecies, and probably represent individual variations. Both were described from a single specimen (worker).

Key to the Indo-Malayan subspecies of *V. analis* Fabricius

1. Head orange-yellow, either entirely or in the lower half only. Abdominal tergites 1-5 with yellow apical bands 2
- Head black or dark brown, often more or less extensively marked with dull ferruginous. Only tergites 1 and 2 with more or less distinct, ferruginous band at apex, in some specimens entirely dark 3
2. Upper half of head black, lower half yellow or orange-yellow. All abdominal segments with apical yellow fasciae, much reduced on first, extensive on the others. (Singapore Island) *tyrannica* Smith
- Head entirely yellow or orange-yellow, at most the vertex with a black spot about ocelli. Tergites 1-5 with narrow yellowish or orange apical bands, covering one-fourth or less of each segment. (Continental Asia, incl. Malaya) *nigrans* Buysson
3. Head, thorax, and abdominal segments 1-5 brownish black, only the scutellum more or less extensively ferruginous, and the posterior margins of tergites 1 and 2 often with narrow ferruginous or yellowish band. (Central and East Java; Bali).
tenebrosa Buysson
- Head and thorax extensively marked with dull ferruginous; first abdominal tergite ferruginous with dark transverse band on posterior half or two thirds of horizontal portion, the extreme apical margin often narrowly ferruginous; second tergite dark brown with irregular, ferruginous band on basal half and narrow band of the same colour at posterior margin. (West Java; South Sumatra; Bangka Island).
analis Fabricius

***Vespa analis nigrans* Buysson**

- ! 1903. Buysson, R. du, Bull. Soc. ent. France, 1903, p. 175, ♂ (*Vespa nigrans*, Tseku, Yunnan, leg. R. Oberthür, type in MP).
- ! 1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), pp. 487, 496, 527; pl. 5 fig. 6 (*Vespa nigrans*).
1905. Bingham, C. T., Fasc. Malay. Zool., vol. 3, p. 51 ("*Vespa magnifica* Smith", Malaya).
1931. Dover, C., Jl. Fed. Mal. St. Mus., vol. 16, p. 260 ("*Vespa magnifica* Smith", Malaya).

Up to the present *Vespa analis* had not been recorded from the mainland of the Malay Peninsula, but the collection of Malayan *Vespa*, kindly sent to me by Mr. H. T. Pagden, showed that the insect had been confused there with *Vespa magnifica*. The Malayan specimens recorded under this name by Dover (1931) all proved to belong to the present species, and only the Siamese specimens, mentioned at the same time, were correctly identified as *magnifica*. The "single small worker" of *Vespa magnifica*, recorded by Bingham (1905) from Bukit Besar, was undoubtedly also a specimen of *V. analis nigrans*. The remarkable resemblance in coloration of the subsp. *nigrans* with *V. magnifica*, responsible for the existing confusion, was

already noted by du Buysson, who wrote as follows (l.c.): "La *V. nigrans* porte la livrée de la *V. magnifica* Smith, mais c'est avec la *V. analis* F. qu'elle a le plus d'affinité".

In the Malayan specimens which I have seen (six workers, see below) the coloration is as follows: Head orange-red, brighter than in subsp. *analis* from W. Java; front above inter-antennal shield with a dark blotch, which laterally almost reaches the eyes and posteriorly encloses the ocellar area. Cutting edge and tip of mandibles black. Antennae dark brown, first segment ferruginous anteriorly. Thorax almost entirely black; pronotum brown below, scutellum reddish posteriorly. Abdominal segments 1-5 brownish black, with narrow orange-yellow bands at the posterior margins of the tergites; segment 6 entirely yellow.

In Malaya *V. analis nigrans* has been collected only in Selangor (Fraser's Hill, 4200', July 1931 and Sept. 1936; Bukit Kutu, 3500', Aug. 1915 and Jan. and Sept. 1929) and Pahang (Genting Sempak, 2000', July 1939). I have seen one or two workers from each of these localities. Furthermore I examined a ♂ from Mt. Tahan Padang, 5500', Pahang, Malaya, 27 Dec. 1922, leg. H. M. Pendlebury (BM).

***Vespa analis tyrannica* Smith**

1857. Smith, F., Cat. Hym. Ins. Br. Mus., vol. 5, p. 119, ♀ or ♂ (*Vespa tyrannica*, Singapore I., leg. A. Wallace, type in Mus. Oxford).
 ! 1905. Buysson, R. du., Ann. Soc. ent. France, vol. 73 (1904), p. 487, 513 (*Vespa parallela*, var. *Biroi*).
 1939. Bequaert, J., Trans. Am. Ent. Soc., vol. 65, p. 40 (*Vespa analis* var. *tyrannica*).

This remarkable form is known exclusively from Singapore Island. I have seen 6 ♀ and 1 ♂ from Singapore and Selitar (BM, ML), but none of these was collected after 1911. It would be very interesting to know more about the present distribution of this insect. If *tyrannica* is a forest inhabitant, like *nigrans* in the Malayan mainland, it may have become very scarce, occurring perhaps only in the restricted forest reserve in the island.

The type of *Vespa parallela* var. *Biroi* Buysson is a worker in the Paris Museum, bearing a label: "Singapore, Biro, 1898".

A male of this subspecies in the BM is labelled: "Singapore, S.S. Flower, 98-48" and "*Vespa bellicosa* Smith, var., det. du Buysson, 1903". It is at once distinguished from *bellicosa*, however, by the dark postcutellum and the narrow band on the first abdominal tergite. The genitalia of this specimen are in the Paris Museum, on a pin bearing a label: "appareil copulateur de *V. bellicosa* Sauss. var. *semperi* Buysson affinissima" in du Buysson's handwriting.

Vespa analis analis Fabricius

1775. Fabricius, J. C., *Systema entom.*, p. 363.

1905. Buysson, R. du, *Ann. Soc. ent. France*, vol. 73 (1904), pp. 487, 496, 514 (Java). [apparently erroneously recorded from some localities in continental Asia].

The typical form of *V. analis* is a common insect in the cultivated plains and on the mountain slopes (up to about 1200 m) of West Java. It has also been found in the Lampong districts in the extreme south of Sumatra, and in the island of Bangka (see fig. 3).

West Java: many specimens from various localities in MB, ML and MP; 2 ♀ Bogor, Nov. 1931, E. Handschin (MBA); 11 ♀ and ♀, Bogor and Tandjong Priok (LEW).

Islands in Sunda Straits: 2 ♀ 1 ♂ Sebesi I., K. W. Dammerman, April and Oct. 1921 (MB); 8 ♀ Sangijang I., 15 ♀ 1 ♂ Sebesi I., 10 ♀ Sebuku I., 8 ♀ 17 ♂ Legundi I., 1 ♀ Krakatau I., 1 ♀ Deli I., 1 ♂ Panaitan I., all collected by an expedition of the Bogor Museum under Mr. A. M. R. Wegner in June-July 1955 (MB, ML).

South Sumatra: 1 ♀ Mt. Tanggamus, 1000 m, 20 Dec. 1934, M. A. Lieftinck and L. J. Toxopeus (MB); 1 ♀ 1 ♂ Kedaton Estate near Tandjongkarang, April 1937, van der Vecht (ML).

Bangka I.: 1 ♀ "Banka" leg. Buddingh (ML); 1 ♀ Trak, March 1935, van der Vecht (ML).

The collection of the Paris Museum contains one worker from Bengal and one from Pondichéry, but I suspect that these specimens, both very old, are incorrectly labelled.

Vespa analis tenebrosa Buysson

! 1905. Buysson, R. du, *Ann. Soc. ent. France*, vol. 73 (1904), p. 516 (*Vespa analis* var. *tenebrosa*; Java; type in MP).

1940. Vecht, J. van der, *Entom. Meded. Ned. Indië*, vol. 6, p. 43 (a distinct subspecies).

As a rule this form can easily be distinguished from typical *analis*, but a few specimens from Ardjasari, on the northern slope of Mt. Malabar (ML), are transitional, having the base of tergites 1 and 2 somewhat tinged with ferruginous. Very probably there is a zone of hybridization, situated east of Bandung.

The lectotype is a worker labelled "Goban, Java, R. Oberthür, 1898" (MP). I have been unable to trace a locality of this name, but I suspect that the wasp comes from Gobang, a village in the district Grogol of the residency Semarang, Central Java.

Central and East Java: 26 ♀ and ♀, 3 ♂ from Garut, Tjilatjap,

Purwokerto, Semarang, Ambarawa, Telawa, Mt. Muria, Bangak near Surakarta, Wonosari, Rembang, Kediri, Ardjuno, Bajukidul on Idjen Mts. (ML); 6 ♀ or ♀ Mt. Smeru, R. Darungan, June 1941, M. A. Lieftinck (MB); 1 ♂ "Java", leg. Horsfield (BM, this specimen bears a label: "male of *V. binghami* Buyss. or *variabilis* Buyss."); 7 ♀ and ♀, 1 ♂ Salatiga, 1910, W. Roepke (LEW); 1 ♀ Pogal, Tengger, 1700', 14 Dec. 1936 (LEW); 2 ♀ Blawan, H. Lucht (LEW); 6 ♀ and ♀, Semarang, 1905, 1909, leg. Edw. Jacobson (MP); 2 ♀ Malang (coll. Pérez, MP).

B a w e a n I.: 2 ♀ or ♀, 3 ♂ (ML).

B a l i I.: 2 ♀ Den Pasar (ML).

***Vespa mandarinia* Smith**

1852. Smith, F., Trans. Ent. Soc. Lond., new series, vol. 2, pt. 2, p. 38, ♀ ♀ (*Vespa mandarinia*, "Tein-tung, near Ning-po-foo, amongst the mountains", leg. R. Fortune; type in BM).

This species is distinguished by the peculiar shape of the head with its unusually dilated temples and by the clypeus which has the anterior angles broadly rounded, without median tooth in the emargination. Vertex, temples, mesoscutum, and scutellum are finely and sparsely punctate.

Some of the subspecies of *V. mandarinia* have been confused with certain forms of *V. tropica* and *V. analis* with which they agree exactly in coloration. The geographic variation of this species therefore requires further study. The typical form appears to be common in many parts of China; the following notes refer only to two subspecies occurring in Indo-China and Peninsular Siam.

***Vespa mandarinia magnifica* Smith**

1852. Smith, F., Trans. Ent. Soc. Lond., new series, vol. 2, pt. 2, p. 45 (*Vespa magnifica*; Nepaul, India, leg. Hardwick; type in BM).

1936. Bequaert, J., Treubia, vol. 15, p. 345 (*V. mandarinia* var. *magnifica* homeochromic with *V. tropica* var. *esakii* Sonan).

The collection of the Paris Museum contains an extensive series of this form, including the specimens recorded by du Buysson from Darjiling, Yunnan and Yung-Chan.

P e n i n s u l a r S i a m: 1 ♀, Nakon Sri Tamarat, Khao Luang, 3000', 30 March 1922, leg. H. M. Pendlebury (BM). — Head and abdomen of this specimen are rather dark, perhaps somewhat discoloured.

I n d o - C h i n a: 1 ♀ Haut Laos, Xien-Khouang (Tranninh), leg. Delacour, 1927 (MP). I give this record with some doubt, because the label of this specimen is identical with those of a series of *V. mandarinia soror*

in the Paris Museum (see below). Evidently, the occurrence of two *mandarinia*-forms in the same locality needs confirmation. Moreover, head, thorax, and anterior part of first abdominal tergite of this specimen are ferruginous, and it agrees therefore with the description of *Vespa bellona* Smith from West Yunnan. The latter is usually regarded as identical with *magnifica*, but may eventually prove to be a separate subspecies.

Vespa magnifica was erroneously recorded by Dover (1931) from Malaya (see under *V. analis nigrans*).

***Vespa mandarinia soror* Buysson (n. comb.)**

! 1905. Buysson, R. du, Ann. Soc. ent. Fr., vol. 73 (1904), pp. 490, 519, ♀♂ (*Vespa ducalis* var. *soror*; China; India; Indo-China) [the record "India" is incorrect, v. d. V.].

This insect was described by du Buysson as a variety of *Vespa ducalis* Smith, a form which is at present regarded as a subspecies of *Vespa tropica* Linn. Bequaert (1936) treated *soror* as a variety of *V. tropica*, but although this interpretation was based on the examination of some "cotypes" from the Paris Museum collection, du Buysson's description leaves no doubt that *soror* is a form of *magnifica*, not of *tropica*. This is particularly demonstrated by the following characters: "Tête fortement dilatée dans sa partie postérieure, derrière les yeux... (p. 490); ... les angles antérieurs du clypeus arrondis ..." (p. 519).

It is of interest to note that Bequaert (1936, p. 344) wrote: "*V. tropica* var. *soror* is homeochromic with a peculiar (apparently unnamed) color form of *Vespa mandarinia* Smith, occurring together with it. No doubt the two have often been confused."

The typical series of *V. ducalis* var. *soror* Buysson in the Paris Museum proved to contain 1 ♀ from Kiangsi, A. David, 1875, and 1 ♀ from Tonkin, Bac Kan, 1902, M. Maindron (on a second label: "Song-Kan, Octobre, leg. Cne Bertrand"); I have labelled these specimens as lectotype and paratype, respectively, because they agree well with du Buysson's description. Several other specimens, including some from Bombay, belong to *V. tropica* Linnaeus.

Indo-China: 6 ♂ Tonkin, région de Hoa Binh, 1926-1934, leg. A. de Cooman (MP, ML); 1 ♀ Annam, col des Nuages près Tourane, 1923, leg. Mme Poilane (MP); 1 ♀ Haut-Laos, Xieng-Khouang (Tranninh), 1927, leg. Delacour (MP).

***Vespa tropica* (Linnaeus) (fig. 4)**

1758. Linnaeus, C., Systema Naturae, 10th Ed., vol. 1, p. 571 (*Sphex tropica*, "in Indiis").

1775. Fabricius, J. C., System. Entom., p. 362, Malabar (*Vespa cincta*, not *V. cincta* Degeer 1773, nor *V. cincta* Drury, 1773).
 1912. Schulz, W. A., Berlin. Ent. Zeitschr., vol. 57, p. 57 (*Vespa tropica*; type of *Sphex tropica* Linn. examined).
 1936. Bequaert, J., Treubia, vol. 15, pp. 329-345, fig. 1 (*Vespa tropica*: ethology, characters, colour forms, distribution, etc.).

The colour forms of this species, together with those of *V. affinis* (L.)¹), were the subject of a study by J. Bequaert (l.c.). In 1936 the material present in the Zoological Museum at Bogor was examined by the present author for inclusion in Dr. Bequaert's paper.

Since then much additional material has been obtained, and this makes it possible to define more exactly the distribution of some of the forms of these species, and to distinguish some new ones.

Bequaert pointed out that in several cases two or more of the colour forms of these species are found in the same area and often in the same locality, so that they could not be regarded as "geographical races". It appears, however, that in this respect much confusion has been created by incorrectly labelled specimens in several museum collections. Recent collections from several parts of the Indo-Malayan area have not only failed to demonstrate the occurrence of two different colour forms in the same locality, but they have even shown that the geographical segregation of certain forms is more strict than was hitherto supposed. For this reason it appears preferable to give to most of the forms, discussed by Bequaert as "varieties", subgeneric rank. It will be necessary to discard some of the locality records based on old specimens, such as the reported occurrence of *V. tropica trisignata* in Java, where actually only the typical form of this species can be found (compare Bequaert, 1936, p. 340).

According to Bequaert (1936), the typical form of *Vespa tropica* (L.) occurs in continental S.E. Asia, from Sikkim and Indo-China to Malaya, and in Sumatra, Borneo, and Java; furthermore he reports to have seen specimens from the Sulu Islands and from Lombok. However, a study of the extensive material now available has shown that the specimens from Java differ constantly from those from other localities and must be regarded as a separate subspecies. The question thus arose: what is the type locality of "*Sphex tropica*" of Linnaeus? Fortunately, the type of this insect, which is preserved in the collection of Queen Lovisa Ulrika, in "Zoologiska Institutionen", Uppsala, is still in excellent condition. A photograph of this specimen (pl. I fig. 1), kindly sent to me by Prof. Bertil Kullenberg, together with some notes and a drawing of the second sternite, leave no

1) During many years these two species have been confused under the name *Vespa cincta* Fabr.

doubt that this insect originates from Java. Accordingly the race occurring in continental S.E. Asia, Sumatra, and Borneo requires a new name. I have named this form in honour of the late Dr. S. Leefmans, who in 1922 pointed to the differences between *V. tropica* and *V. affinis* (his "var. b" and "var. c").

Four other forms are recorded by Bequaert from the Indo-Australian Archipelago, viz. *trisignata* Pérez, *deusta* Lep., *anthracina* Beq., and *philippinensis* Saussure.

V. tropica trisignata sensu Bequaert is considered by me to consist of two races, the second of which has received a new name.

V. tropica deusta was recorded by Bequaert from the Philippine Islands and from Buru. However, I prefer to regard the *tropica* population occurring in the latter island as a different subspecies. Evidently it is a melanistic form which has developed independently from the similar races living in the Philippine Islands.

Although *Vespa deusta* was described from material without locality label, and eventually might prove to originate from the Southern Philippines or from Buru, I have followed de Saussure and Bequaert who apply this name to the northern Philippines form, which has the basal half of the wings not strongly infuscated. It should be noted, however, that Lepeletier says: "alis fusco-rufis, basis fuscioribus", and "ailes roussâtres, plus brunes vers leur base". The name *unicolor* Smith is available for the Buru form.

Vespa tropica anthracina Bequaert is a dark form of the southern Philippine Islands, which is apparently well separated from the northern *deusta*.

V. tropica philippinensis, however, presents a problem which I have been unable to solve satisfactorily. This form agrees in wing colour with *deusta*, but the tergites 1-3 bear wide orange bands. It was recorded from "les Philippines" by de Saussure, from "Baliwag" by Ashmead, and from Mindanao by du Buysson.

Bequaert (1936) examined specimens from Luzon, Ubay (not located), Samar, Negros, and Mindanao. It seems to me that Samar and Negros do indeed form part of the area of distribution of this form, for the specimens from these islands undoubtedly are correctly labelled. The occurrence on Luzon and Mindanao, however, appears to need confirmation.

The distribution of the subspecies at present recognized by me is shown in fig. 4. Some doubtful points are: the eastern limit of the distribution area of subsp. *tropica* (Bequaert states to have seen typical *tropica* from Lombok), the nature of the *tropica*-populations of the Kei and the Tenimber islands, and the distribution of *Vespa tropica philippinensis*.

Key to the Indo-Malayan and Papuan subspecies of *V. tropica* (L.).

1. Thorax and abdomen wholly or almost wholly black; at most a narrow orange line at apex of second, or more rarely of first and second tergites; sternites wholly or almost wholly black. Head black 2
- Abdomen extensively marked with orange; one or more of the tergites almost entirely of that colour or with broad apical bands 4
2. Wings uniformly yellowish-russet, only slightly darker close to the costa. Tergites 2, or 1 and 2, or 1-3, often with orange line at posterior margin. (Northern Philippine Is.) *deusta* Lep.
- Wings very strongly infuscated in the basal half; apical portion yellowish-russet; especially the hind wings rather smoky. Tergites usually entirely black 3
3. Specimens from Buru I., South Moluccas *unicolor* Smith
- Specimens from Palawan and other southern Philippine Islands. Wings slightly darker than in *unicolor* (?) *anthracina* Beq.
4. First three tergites with wide apical orange-yellow bands (rarely also the fourth with such a fascia); sternites almost wholly black. Wings rather uniformly yellowish-russet, darker toward base and along costa; infuscated in specimens from Negros. (Philippine Is.) (pl. I fig. 2) *philippinensis* Saus.
- Second, or first and second, tergites mostly orange-yellow; if the third tergite bears an apical spot or band, the sternites are extensively marked with the same colour and the wings are darker at base 5
5. First abdominal tergite black, rarely with small yellowish spots or narrow border 6
- First abdominal tergite more extensively marked with orange-yellow 7
6. Orange band of second abdominal sternite deeply emarginate anteriorly, the dark basal area extending to or beyond the middle of the sternite, the band often divided in the middle by a dark line. The infuscated area at the base of the wing relatively small, the first discoidal cell almost entirely yellowish. (Java, Bali) *tropica* Linn.
- Second abdominal sternite more extensively orange, the dark area at base not reaching the middle of the segment; wings more extensively infuscated, the first discoidal cell almost entirely infuscated. (Indo-China to Sumatra and Borneo) *leefmansii* n. subsp.
7. First abdominal tergite with complete orange band (the declivous part black). (Celebes to New Guinea) *trimeres* n. subsp.
- Orange band on first abdominal tergite ragged on the sides and cut by three small black lines, one anterior and median, the other two lateral and transverse; in dark specimens these lines wider and connected, the orange area reduced to some separate spots. (Timor and some neighbouring islands; perhaps also South Moluccas?) *trisinata* Pérez

***Vespa tropica leefmansii*, new subspecies**

Female, worker, and male. — Head and thorax black; orange band on second abdominal sternite shallowly emarginate anteriorly, medially wider than half the length of the sternite, not divided by dark median line. First abdominal tergite black (sometimes with orange line or band at posterior margin), second tergite orange, third sternite sometimes with lateral orange spots. Basal two thirds of fore wings strongly infuscated, the first discoidal cell almost entirely dark; hind wings entirely fuscous.

Type: ♀ from Solok, Padang, Sumatra, leg. P. O. Stolz (ML; received July 1909, together with 24 ♀ and ♂ from the same locality).

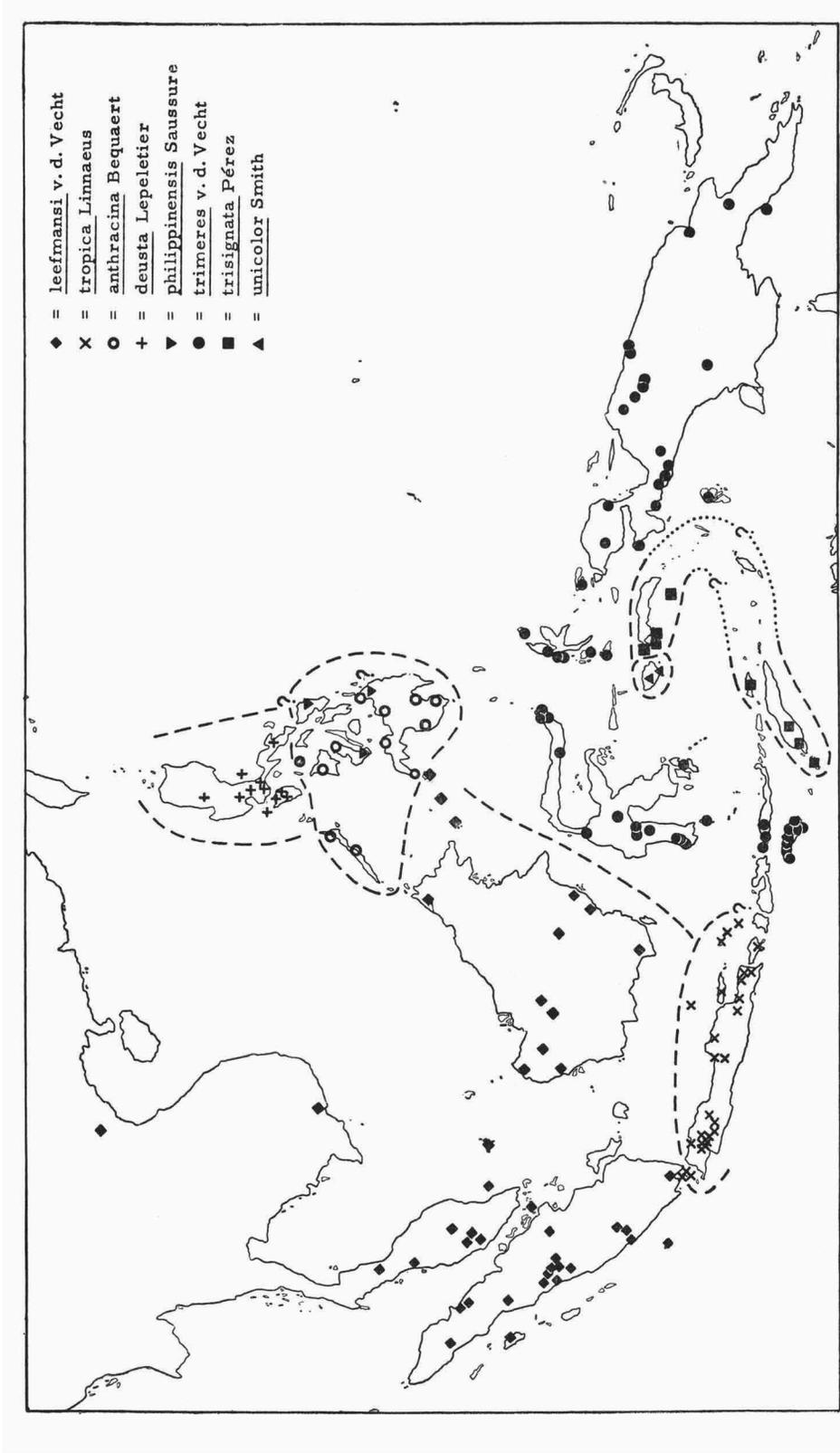


Fig. 4. The distribution of the Indo-Malayan subspecies of *Vespa tropica* (Linnaeus).

Indo-China: Tonkin, 1 ♀ Hoa Binh, 1927, A. de Cooman (MP); Cochinchine, 1 ♀ Baria, 1907, Capitaine Modest (MP).

Siam: Khao Ram: Nakon Sri Tamarat, leg. Pendlebury (BM).

Malaya: Pahang; Selangor; Kedah; Kedah Peak; Pulau Tioman; Langkawi Is.; collected by H. M. Pendlebury and by H. T. Pagden (BM, ML); (a specimen from Tioman Island with orange line at posterior border of first abdominal tergite).

Anambas Is.: 1 ♀ (BM).

Sumatra: many specimens: Atjeh; Deli; Indragiri; Lampong (all in MB); Deli; Padang; Palembang; Benkulen (ML).

Islands west of Sumatra: Nias, 7 ♀ ♀, leg. Kleiweg de Zwaan (ML); Enggano, 10 ♀ ♀, May-July 1936, leg. J. K. de Jong (MB).

Bangka I.: Aer Mesu; Aer Limau; leg. v. d. Vecht (ML).

Billiton I.: 1 ♀ leg. A. G. Vorderman (ML).

Borneo: British North Borneo; Mt. Kina Balu (3000'); Bettotan and Kudat (BM); Sambas; Pontianak; Sanggau; Smitau; Mahakkam River (ML); Balikpapan (MB).

Sulu Is.: Jolo I. (1 ♂, ML).

Basilan: 1 ♀ leg. Baker (USNM); the specimen has been wet and the orange-brown markings are not distinct.

A specimen in MB from Bandar Baru, collected by van der Meer Mohr, bears the following information on its label: "Batak name = sigrawak" (pron. seegra-wa').

Vespa tropica tropica (Linnaeus) (pl. I fig. 1)

Orange band on second tergite usually somewhat reduced anteriorly and laterally, in many specimens with a small blackish dot on each side; anterior margin as a rule with a small triangular incision in the middle.

In a series of 65 specimens only two workers (or females) have an orange line at the posterior margin of the first abdominal tergite; one of these (Batavia, 1908, E. Jacobson; ML) has also two vague orange marks in front of the band, thus approaching the *trisignata* pattern.

Third tergite and sternite black, but both with reduced apical orange band in one of the three males in the ML collection (old specimen, "Java, leg. Müller").

Easily distinguished from *V. tropica leefmansi* by the characters mentioned in the key. In the fore wing the submarginal and discoidal cells are almost entirely yellowish hyaline, the hind wing is infuscated, except for a yellowish area at anterior margin near the tip.

J a v a: common throughout the island, up to about 800 m above sea level, many specimens in MB, LEW, ML and MP.

I s l a n d s between Sumatra and Java: 1 ♀ Pulau Sangijang; 1 ♀ P. Sebesi, 1 ♀ P. Seuku, 1 ♀ P. Legundi, 1 ♂ P. Krakatau, 1 ♀ P. Panaitan leg. A. M. R. Wegner, June 1955 (ML).

B a w e a n I.: 2 ♀ (ML). Wings slightly more strongly infuscated than in specimens from Java, but coloration of second abdominal sternite not different.

M a d u r a: 1 ♀ (ML).

K a n g e a n I s.: 5 ♀ Bujutan, Djokang; Saobi; Batuputih, leg. A. Hoogerwerf (MB, ML). Specimens from these islands agree in wing colour with those from Bawean, but the orange band on the second abdominal sternite is slightly wider in the middle, and is not divided by a dark median line.

B a l i: 1 ♀ Den Pasar (ML).

***Vespa tropica trimeres*, new subspecies**

1936. Bequaert, J., *Treubia*, vol. 15, pp. 336, 339 (*Vespa tropica* var. *trisignata*; in part only).

This form has approximately the same coloration as certain subspecies of *Vespa affinis*, and was generally confused with that species until Bequaert (1936) pointed out the differences.

The subspecies *trimeres* is distinguished from *trisignata* by the coloration of the first abdominal tergite, which is almost entirely orange. Very rarely the specimens inhabiting the islands mentioned below show a tendency to develop the *trisignata*-pattern. Only two specimens of a series of 68 females and workers, collected in New Guinea by the Archbold Expedition (1938-39), have a brownish streak on each side of the first abdominal tergite. Second abdominal sternite with orange-yellow band over its entire width; this band as a rule rather deeply emarginate in the middle anteriorly, but rarely divided into two spots. Basal two thirds of fore wings strongly infuscated; hind wings entirely dark.

Type: 1 ♀ Palu, West Celebes, 1936, ex coll. v. d. Vecht (ML).

C e l e b e s: throughout the island; many specimens in MB and ML from: Menado, Tateli, Kinamang, Sonder, Panibi, Tomohon, Gorontalo (all in N. Celebes); Palu, Poso, Luwuk, Palopo, Rantepao (C. Celebes); Makassar, Bantimurung, Batu Koropa (S. Celebes); Buton and Salajar Is. (S. of Celebes).

L e s s e r S u n d a I s.: Komodo, Sumba (common), and Flores (MB, MBA, ML).

North Moluccas: Morotai, Halmahera, Tidore, Ternate, Batjan, Obi (MB, ML). (In a series of 12 specimens from Batjan Island (June 1953, A. M. R. Wegner) the wings are very dark and the band on the second abdominal sternite is deeply emarginate, sometimes broken up into two separate spots).

Waigeu: 2 ♀ leg. Bernstein (ML).

Aru: 2 ♀ leg. Rosenberg (ML).

New Guinea: apparently common throughout the island. The Leiden Museum possesses a series of 30 specimens from the following localities: Fakfak, Ajamaru, Etna Bay, Paniai, Pionier Bivak (Mamberamo River), Hollandia, Sentani Lake near Hollandia, Tanah Merah. — The Archbold Expedition (1938-9) collected 63 specimens, as follows: Hollandia, 14 ♀ and ♀ July 1938, 2 ♀ April 1939 (the latter specimens with brownish streak on each side of first tergite); Bernhard Camp, 50 m, 20 ♀ ♀, July-Nov. 1938, J. Olthof; do. 20 ♀ ♀, collected on 19 different days between 23 July and 14 Sept. 1938, 1 ♀ 23 Dec. 1938; Bernhard Camp B, 100 m, 1 ♀, 8 April 1939; mountain slope above Bernhard Camp, 800 m, 1 ♀ March 1939; Araucaria Camp, 800 m, 1 ♀ March 1939; Baliem Camp, 1600 m, 1 ♀ 6 Dec. 1938; Mist Camp, 1800 m, 1 ♀ 9 Jan. 1939; Top Camp, 2100 m, 1 ♂ 24 Jan. 1939. — Specimens collected in South New Guinea by E. Lindquist include: 2 ♀ Kaimana, 2 ♀ River Arja, west of Umar, 1 ♀ near mouth of River Aindua, June-July 1941 (MB).

***Vespa tropica trisignata* Pérez**

! 1910. Pérez, J., Act. Soc. Linn. Bord., vol. 64, p. 8 (*Vespa affinis* var. *trisignata*; Timor).

1936. Bequaert, J., Treubia, vol. 15, pp. 336, 339 (*Vespa tropica* var. *trisignata*; in part only).

Bequaert (l.c.) used the name *trisignata* Pér. for specimens from a great many localities¹⁾, but I have taken a more restricted view of this form.

Lesser Sunda Is.: 3 ♀ Timor, types, coll. Pérez (MP); 10 ♀ and ♀ Timor (ML); 3 ♀ 1 ♀ Timor (MBA); 1 ♀ 1 ♀ Roti (ML, MBA); 1 ♀ Wetar (ML); 2 ♀ "Wetar or Kisar" (ML). — In specimens from these islands the orange band of the first tergite is apparently always "ragged at the sides, and cut by three lines, one anterior and median, the other two lateral and transverse" (Bequaert's translation of part of original description). In dark specimens the lines flow together, and the orange band is then reduced to two lateral spots and a transverse band at apical margin, all very irregularly shaped.

1) Probably his material contained several incorrectly labelled specimens, such as those recorded from Sumatra, Nias, and Java!

Southern Moluccas: Amboina (2 ♀ ML); Haruku (2 ♂ ML); Ceram (6 ♀ and ♂, ML). — Specimens from these islands agree so well with those from Timor, that I have tentatively placed them under this subspecies. Further study of the *tropica* populations of Tenimbar, Kei, and neighbouring islands is necessary, however, before we can draw more definite conclusions.

Banda Is.: — Five specimens, probably 1 ♀ and 4 ♂, from these islands (coll. Rosenberg, ML) are more or less intermediate between *trisignata* and *trimeres*. The orange band on the first abdominal tergite is distinctly reduced anteriorly and at the sides, but not divided by dark lines. In a female from Great Banda in the Pérez collection (MP, see Pérez, l.c., p. 8) the first tergite has a broad black band at the base of the non-declivous part; the orange colour being reduced to a band occupying nearly the posterior half of this part, incised on each side by a transverse black line as in *trisignata* from Timor; orange band on second sternite reduced to two triangles which almost touch each other in the middle of the posterior margin.

***Vespa tropica unicolor* Smith**

1864. Smith, F., Jl. Proc. Linn. Soc. Zool., vol. 7, p. 44, ♀ (*Vespa unicolor*, Buru I., leg. Wallace; type in Oxford University Museum).
 ?! 1910. Pérez, J., Actes Soc. Linn. Bordeaux, vol. 64, p. 10 (*Vespa rubricans*, Lindi, Africa).
 1936. Bequaert, J., Treubia, vol. 15, p. 341 (syn. of *V. tropica* var. *deusta* Lep.).

The type of *V. rubricans* Pérez is in the Paris Museum; it is a somewhat discoloured specimen of subsp. *unicolor* or of *anthracina*, and is undoubtedly not African.

Buru I.: 1 ♀ leg. Hoedt (ML), 1 ♂ leg. Bernstein (ML), 1 ♂ leg. Denin (ML); 10 ♀ and ♂, Stations 1, 5, 7, 8, 9, and 22, April 1921-Jan. 1922, Buru-Exp. L. J. Toxopeus (MA, ML). — Twelve specimens are entirely black; in one worker the second tergite has a narrow ferruginous-yellow line, abbreviated laterally, at the posterior margin.

***Vespa tropica deusta* Lepeletier**

1836. Lepeletier, A. de, Hist. Nat. Ins. Hym., vol. 1, p. 506, ♀ (*Vespa deusta*, locality unknown, coll. Serville).
 1936. Bequaert, J., Treubia, vol. 15, p. 341 (*Vespa tropica* var. *deusta*; in part only).
 1941. Bequaert, J., Phil. Jl. Sci., vol. 75, p. 63.

In my opinion the identity of *V. deusta* Lep. is not entirely certain and it seems possible that the type originates from Buru and not from the Philippines (see p. 18). However, it is doubtful whether the type is still in existence.

Luzon: 5 ♀ and ♀ Los Baños (ML); in three specimens tergites 1 and 2 have a narrow, apical, orange band, one has such a band on tergite 2 only, and one is entirely black; 4 ♀ Los Baños, July 1952, Sept. 1952, and Dec. 1953, Townes family (coll. Townes; ML) (one ♀ with orange lines at apex of tergites 1 and 2, on 1 very short, the other ♀♀ black); 1 ♀ Guinoboton, Albay, 9 Dec. 1953, H. Townes (coll. Townes) (entirely black); 1 ♀ Clark Field, Pamp., 9 July 1952, Townes family (coll. Townes) (tergites 1 and 2 with orange lines at apex, on 1 very short); 4 ♀ "Manille" (MP); 16 ♀ and ♀, 2 ♂ from various localities (USNM).

Mindoro: 2 ♀ San Teodoro, 26 Aug. 1952, Townes family (coll. Townes; ML).

Bequaert has recorded this species from several localities in Luzon and from Mindoro and Lubang. The supposed occurrence in Sumatra, Celebes, Buru, and New Guinea is based on incorrectly labelled specimens or on misidentifications.

Vespa tropica anthracina Bequaert

1936. Bequaert, J., Treubia, vol. 15, p. 341, ♀♂♂ (*V. tropica* var. *anthracina*; Philippine Islands; type ♀ Sibuyan in USNM).

1941. Bequaert, J., Phil. Jl. Sci., vol. 75, p. 64 (*V. tropica* var. *anthracina*).

Palawan: 3 ♀ Puerto Princesa, leg. McGregor (USNM, ML); 1 ♀ Palawan, 1898, leg. Doherty, ex coll. Fruhstorfer (MP); 1 ♀ Puerto Princesa, leg. Baker (USNM).

Mindanao: 1 ♀ Lagao, Cotab., 10 Sept. 1952, H. Townes (coll. Townes); 1 ♀ Mindanao, leg. Montano, 1880 (MP; apex of tergite 2 with a narrow orange band); 2 ♀ Zamboanga, leg. Baker (USNM; tergite 2 with narrow apical band, abbreviated laterally, in one specimen interrupted medially; sternite 2 with more or less distinct L-shaped spot in each posterior corner); 1 ♀ Surigao (USNM); 1 ♀ Davao, leg. Baker (USNM).

Sibuyan: 1 ♀ 1 ♀ leg. Baker (USNM).

Negros: 1 ♀ Victorias, Dec. 1927 (USNM). — According to the collection of the USNM a dark-winged form of the subsp. *philippinensis* also occurs in this island (see below).

Bequaert has recorded *anthracina* also from Panay and Cebu.

Vespa tropica philippinensis Saussure (pl. I fig. 2)

1853-4. Saussure, H. de, Ét. fam. Vesp., vol. 2, p. 148, ♂ (*Vespa philippinensis*, Philippine Islands).

1936. Bequaert, J., Treubia 15, p. 342 (*V. tropica* var. *philippinensis*).

1941. Bequaert, J., Phil. Jl. Sci., vol. 75, p. 65.

This form has been recorded from several localities in the Philippines, but its distribution requires further study (see p. 18).

I have examined one female or worker from Samar, Mauo River, 9 April 1932, leg. Prince Léopold (IRSNB), one from Ubay, Oct. 1863, C. Semper (MP), a few incompletely labelled specimens (IRSNB), and 1 ♀ 1 ♂ from Negros, Cuernos Mts., leg. Baker (USNM). In both specimens from Negros the wings are rather dark, and the band on the third tergite is not sharply incised on each side as in the specimen from Samar (see pl. I fig. 2). I wonder if a ♂ in the USNM from Surigao, Mindanao, is correctly labelled, for *V. tropica anthracina*, which appears to occur throughout Mindanao, has also been found in this locality.

***Vespa affinis* (Linnaeus) (fig. 5)**

1764. Linnaeus, C., Mus. Ludov. Ulrica, p. 417 (*Apis affinis*, "in calidis regionibus").
 1936. Bequaert, J., Treubia, vol. 15, p. 345, ♀ ♂, fig. 2 (*Vespa affinis*: ethology, characters, colour forms, distribution, etc.).

This species was studied in detail by Bequaert (l.c.) and the following remarks and conclusions, based on the examination of additional material, are presented as a supplement to his paper.

Vespa affinis affinis L. is one of the forms of the Asiatic continent and should be distinguished from the subspecies occurring in the Indo-Australian archipelago.

The subspecies *indosinensis* Pérez was described from a series of specimens from various localities. The name should be restricted to a form occurring in Indo-China, Malaya and Sumatra. Specimens from Celebes, the Moluccas, and New Guinea, recorded by Bequaert under this name, belong to different subspecies.

The subspecies *alduini* Guérin, as understood by Bequaert, appears to consist of one form inhabiting the island of Buru (*alduini*) and another occurring in the Southern Moluccas, Kei Is., and part of New Guinea (*moluccana* n. subsp.).

The following key is restricted to the Indo-Malayan subspecies of *Vespa affinis*; it does not include the subspecies *affinis* L., *hainanensis* Beq. and *continentalis* Beq.

- | | |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------|
| 1. First abdominal tergite black | 2. |
| — First abdominal tergite marked with orange | 3 |
| 2. Abdomen entirely black. (South New Guinea) | <i>picea</i> Buysson |
| — Second abdominal tergite with two irregular orange spots or with a transverse band which is incompletely interrupted in the middle. (Buru I.) | <i>alduini</i> Guérin |
| 3. Head black, sometimes with some dark red markings on front, vertex and temples. (Indo-China to Sumatra; Philippine Islands) | 4 |
| — Head dark red, clypeus often black | 5 |
| 4. Second abdominal sternite on each side with large orange or brownish mark which covers about one third of the width of the sternite. Apical third of wings with | |

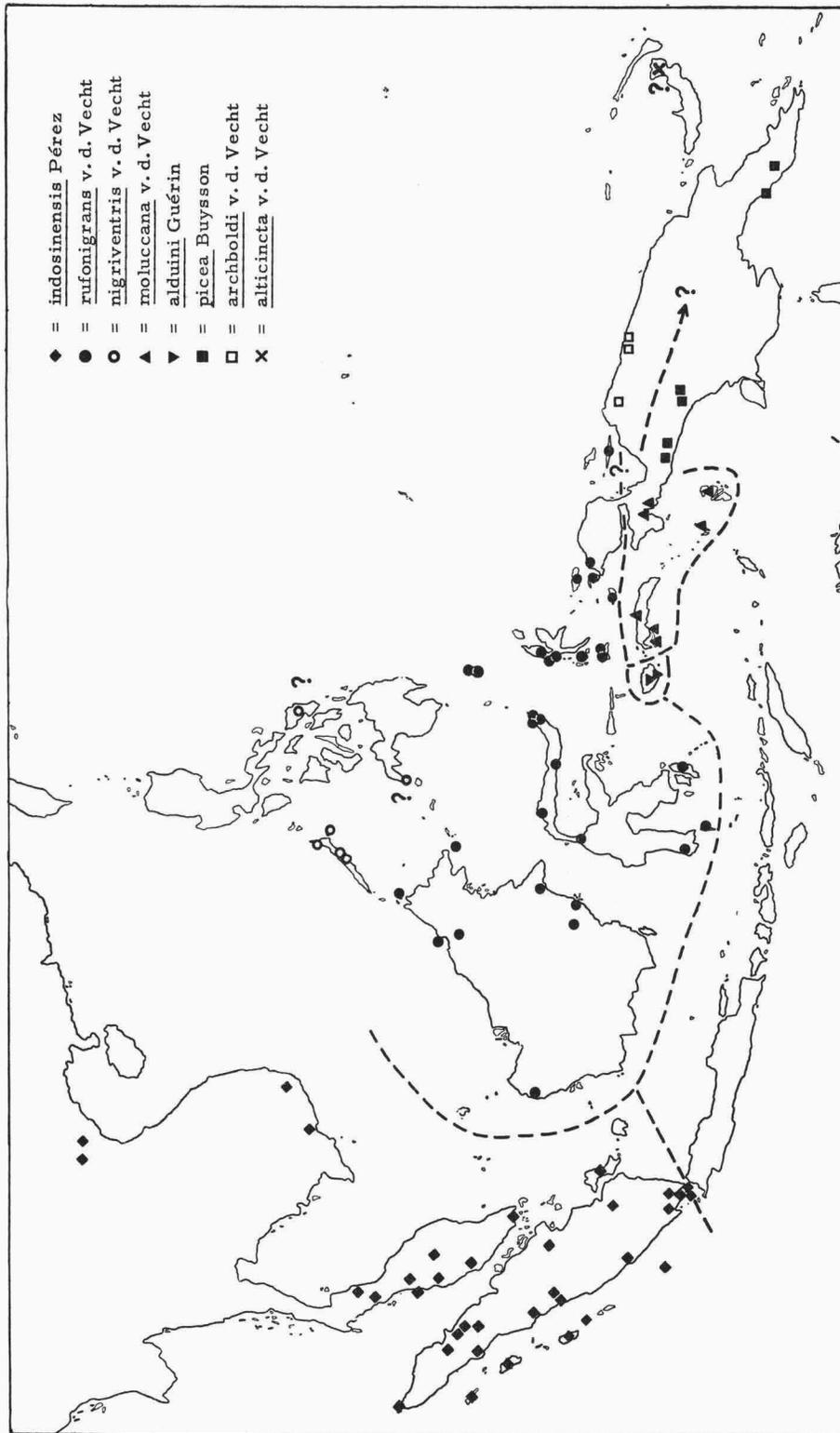


Fig. 5. The distribution of the Indo-Malayan and Papuan subspecies of *Vespa affinis* (Linnaeus).

- yellowish tinge. Front, vertex, and temples often partly reddish (Indo-China to Sumatra) *indosinensis* Pérez
- Second abdominal sternite black, with only a faint orange or brownish streak on each side at lateral margins. Wings brown throughout, though darker at base than at tip. Head black, with only a narrow reddish line at inner orbits. (Philippine Islands) *nigriventris* n. subsp.
5. Clypeus red (margins narrowly fuscous); mesoscutum often with red markings; pronotum and scutellum almost entirely ferruginous. First and second abdominal tergites with complete orange bands. (North New Guinea) *archboldi* n. subsp.
- Clypeus black, sometimes with a few red spots 6
6. First and second abdominal tergites entirely orange-yellow. (Borneo; Celebes; North Moluccas). *rufonigrans* n. subsp.
- Bands on first and second tergites more or less reduced, at least on the second tergite divided by dark median line. 7
7. First tergite with dark band or line at posterior margin, the orange band more or less blotched with brown; band on second sternite more or less distinctly divided by a dark median line. (South Moluccas) *moluccana* n. subsp.
- Both the first and the second tergites with dark apical band, occupying the posterior half of the horizontal part of tergite 1, and the posterior third of the visible part of tergite 2, respectively; moreover both tergites with ill defined median dark band (about as wide as the apical band of tergite 1). (New Britain) *alticincta* n. subsp.

Vespa affinis indosinensis Pérez

1910. Pérez, J., Act. Soc. Linn. Bordeaux, vol. 64, p. 8, ♀ or ♂ (Cochinchina; Annam; Malaya; northern Celebes; India; type locality not designated).
1936. Bequaert, J., Treubia, vol. 15, p. 349 (in part only).

The typical series in the Pérez collection (MP) contains a female from Annam, and some workers from Indo-China and Malaya; two workers from Celebes belong to subsp. *rufonigrans*. The female from Annam is herewith designated as the lectotype, because this specimen was described in detail.

I n d o - C h i n a: Tonkin, 2 ♀ frontière de China, Ha-Giang, A. Weiss, 1901; 1 ♀ Hanoi, 1911, G. Dupouy; 2 ♀ Hoa Binh, 1927, 1934, A de Cooman; Annam, 2 ♀ prov. Phanrang, région de Ca-na, 700-800 m, 1923, leg. Poilane; Cochinchine, 1 ♀ Cap St. Jacques, 1913, leg. Fouquet; 2 ♀ Saigon, leg. Germain, 1894 (all MP).

M a l a y a: several specimens from Perak, Kelantan, Kedah, and Selangor (ex coll. H. M. Pendlebury and coll. H. T. Pagden; BM; ML; MP); 1 ♀ Penang (USNM).

In the Malayan specimens the coloration varies as follows: Head often with some red markings on front, vertex, and upper half of temples. In dark specimens the orange colour on the first tergite may be reduced to two transverse spots and a narrow apical band. Second sternite dark at base, orange at sides and posteriorly; in dark specimens with only a triangular spot in each posterior corner.

S u m a t r a: throughout the island, about 80 specimens from many

localities (see fig. 5) in MB, ML, and MP; also on several surrounding small islands: Pulu Weh in the extreme north (ML), Simalur (ML), Nias (ML), Siberut (MB, ML) and Sipora (MB), all on the west coast. There is one specimen from Enggano I. in the ML, but the species was not found there by J. K. de Jong who collected 10 specimens of *Vespa tropica* during his stay on Enggano from May to July 1936. A recent expedition of the Bogor Museum collected *V. affinis indosinensis* on the islands Legundi, Sebesi, and Sebuku in the Sunda Straits; it was apparently not rare at this extreme southern limit of its distribution area.

The coloration in the Sumatran specimens is fairly constant. Head generally black, in some specimens with distinct reddish markings on vertex and temples. As a rule the declivous part of the first abdominal tergite is black, but in a worker from Lubuk Sikaping the orange band extends over the margin of the truncation.

B a n g k a I.: 1 ♂ "Banka", leg Budding (ML); 1 ♀ Aer Mesu near Pangkalpinang, Febr. 1932, van der Vecht (ML).

***Vespa affinis nigriventris*, new subspecies**

Worker. — Head and thorax black; the red colour on the head reduced to a narrow line running along inner orbits from the clypeus to the level of the posterior ocelli. Abdomen black; first tergite with orange band on dorsal surface, this band irregular anteriorly, more or less incised in the middle and at the sides, medially with faint black line; second tergite orange, with ill-defined black area in anterior lateral angles; sternites black, except for a faint brownish streak at lateral margins of second sternite.

Wings brown, darker at base than at tip, but the apical part not yellowish brown as in subsp. *indosinensis*.

P a l a w a n: 3 ♂ Puerto Princesa, 12 Dec. 1952, Henry Townes (1 ♂ type in coll. Townes; 2 ♂ paratypes ML); 1 ♂ Inagawan, 9 Dec. 1952, Henry Townes (paratype, coll. Townes); Puerto Princesa, 1 ♀ 13 ♂ leg. Baker, and 9 ♂ Aug.-Nov. 1925, R. C. McGregor (paratypes, USNM).

Bequaert (1941) has recorded *Vespa affinis* "var. *indosinensis*" from Palawan, Samar, Dumaran, and Mindanao (Zamboanga), but I have not seen any other Philippine material than that recorded above.

***Vespa affinis rufonigrans*, new subspecies**

Female, worker, and male. — Head mainly red, but the clypeus black, sometimes with two red spots or a transverse band in anterior half, rarely also with two red spots at base. Thorax black, pronotum as a rule with a

ferruginous blotch on each side, tegulae partly ferruginous. First and second abdominal tergites orange-yellow.

Specimens with this colour pattern were recorded under typical *V. affinis* by Bequaert (1936), but they appear to differ constantly in having the thorax almost entirely black. The subsp. *indosinensis* is distinguished by the front, vertex, and temples, which are mainly black.

I have examined over 200 specimens of this form.

Type: ♀, Palu, North West Celebes, Jan. 1937 (ML); all other specimens recorded below are paratypes.

Borneo: West Borneo, 5 ♀ Singkawang, Dec. 1933, L. Coomans (MB); East Borneo, 2 ♀ 1 ♂ West Kutai, Muara Muntai, B. M. Hoeks, 2 ♀ Samarinda, Muara Kaman, Nov. 1950, A. M. R. Wegner (MB); 1 ♀ Sangkulirang, 1937, Mrs. M. E. Walsh (ML); 1 ♂ Banguay (ML); 1 ♀ "Borneo", leg. Schwaner (ML); 10 ♀ Sipangkot near Sibutu, Sulu Is. north-east of Borneo, Snellius Exp. (ML).

Celebes: common throughout the island; I have examined over a hundred specimens from various localities (see map), including a series of about 50 specimens from the type locality (MB, ML, MP).

The subspecies also occurs on several smaller islands around Celebes: Talaud Is. (18 ♀, Beo and Lirung, leg. C. Franssen, ML); Salajar Is. (3 ♀ ML); Buton (1 ♀, leg. P. N. van Kampen, ML).

North Moluccas: Halmahera, 7 ♀ 1 ♂ Kau, Galelo and Tolewang (MB, ML), 1 ♀ leg. Van Diejen (LEW); Ternate, 4 ♀ leg. Bernstein (ML), 5 ♀ May 1951, G. A. L. de Haan (MB); Tidore, 1 ♀ 1 ♂ Tjobo, Sept. 1929, Snellius Exp. (ML); Batjan, 11 ♀ and ♀, Labuha, July-Aug. 1929, W. Roepke (LEW, ML), 19 ♀ and ♀, 1 ♂, June-July 1953, A. M. R. Wegner (MB); Obi, 28 ♀ and ♀, 6 ♂, Angga, Obi Lake, Lake River, Wajaloar, and Kasowari, July-Nov. 1953, A. M. R. Wegner (MB, ML).

Some specimens from Ternate show a tendency to develop a transverse dark line or band on the first abdominal tergite at some distance from the posterior margin. In a few specimens from Batjan there is a small dark spot in the middle of this tergite. Three large specimens from Obi Lake have the pronotum partly orange brown.

Misool: 18 ♀ 1 ♂ Solal, Haitlal, Fakal, Waigama, and Misaron, Sept.-Oct. 1948, M. A. Lieftinck (MB, ML).

Clypeus often with four spots, sometimes almost entirely red. Pronotum on each side with red spot of variable size. Mesoscutum and scutellum black, the latter in one large specimen (probably a female) with two reddish blotches.

Most specimens have traces of a dark median line on tergite 1 or on ter-

gites 1 and 2, tergite 1 sometimes also with dark transverse line at short distance from apical margin (distinct in 7 specimens).

In the only male the clypeus is entirely black.

Salawati: 3 ♀ leg. Bernstein (ML); 1 ♂ Solol on north coast, 5 Aug. 1948, M. A. Lieftinck (ML). The workers have the clypeus black with two spots or a transverse band on anterior third red; in the male the clypeus is almost entirely red.

Waigeu: 1 ♀ 2-3 Aug. 1948, M. A. Lieftinck (ML).

New Guinea: 13 ♀ and ♂, Sorong, June-July 1948, M. A. Lieftinck (ML); 12 ♀, Sorong and Doom I. 1), March-April 1952, L. D. Brongersma and W. J. Roosdorp (ML); 1 ♀ Serui, Japen I., May 1952, W. J. Roosdorp (ML).

The specimens from Sorong and Doom I. are more or less transitional to the subspecies *archboldi*. Clypeus rarely entirely black (one specimen), in most specimens almost entirely reddish. Pronotum with large red spots; mesoscutum and scutellum black, the latter in some large specimens (probably females) with faint red blotches; first abdominal tergite sometimes with dark median spot, rarely with dark transverse line or band.

The worker from Japen Island is a typical *rufonigrans* (clypeus, area between and below antennae, and the thorax black, only the pronotum with vague reddish markings).

The collection of the Paris Museum contains two teneral workers from Dorey (now Manukwari), collected in June 1877 by Raffray and Maindron; the following note is attached to one of them: "nymphes sortis du petit nid de *Vespa cincta* (à la galerie) lequel se trouvait dans un grand nid, sur un arbre, le grand nid abandonné").

***Vespa affinis alduini* Guérin**

1831. Guérin-Méneville, F. E., Voyage Coquille, Zoologie, vol. 2, pt. 2, div. 1, pl. 9 fig. 6 (*Vespa alduini*; Buru I., type Mus. Genova).

1838. Guérin-Méneville, F. E., do., p. 264 (*Vespa bimaculata*).

1936. Bequaert, J., Treubia, vol. 15, pp. 346, 351 (*V. affinis* var. *alduini*, in part only).

The name *alduini* has been used for specimens from several islands in the Moluccas, but I prefer to restrict it to the form occurring in Buru.

First abdominal tergite black, or at most with slight traces of orange markings. Band on second abdominal tergite reduced to two large, irregular, orange-yellow spots which are sometimes entirely separated, but more often are coalescent in the middle; the spots are usually blotched with brown. Head and thorax black; front, vertex and temples with some dull reddish markings.

1) A small island near Sorong.

Buru I.: 24 ♀ 1 ♂ leg. Denin (MB, ML); 1 ♀ 2 ♀ Station 1, Febr.-March 1921, 1 ♀ Station 9, May 1921, L. J. Toxopeus (MA, ML); 1 ♀ Leksula, 4 July 1929, W. Roepke (LEW).

***Vespa affinis moluccana*, new subspecies**

Female, worker, and male. — Head and thorax as in *V. affinis rufonigrans*; first abdominal tergite with dark band at posterior margin, the orange band more or less blotched with brown, but as a rule distinctly produced on the anterior, vertical, face of the tergite; the band on the second tergite more or less distinctly divided by a dark median line, but less strongly reduced than in subsp. *alduini*.

This form is transitional between *rufonigrans* and *alduini*, and forms part of a series which reaches its extreme degree of melanism in subsp. *picea* Buyss.

Type: ♀, Saparua I. near Amboina, 22 Oct. 1949, M. A. Lieftinck (ML).

South Moluccas: Ceram, 7 ♀ Wahai, 1 ♀ Toluarong, leg. Denin (MB); Amboina, 1 ♀ Hunut, March 1941, 2 ♀ Soja, 1 ♀ Sei Waitumu, April 1941, E. Lindquist (MB), 1 ♀ Laha, Oct. 1949, M. A. Lieftinck (ML), 8 ♀ "Ambon", leg. Hoedt (ML); Saparua (see above); Haruku, 5 ♀ 3-7 May 1930, Snellius Exp. (ML); 2 ♀ Amboina, identified by du Buysson as *V. cincta* var. *alduini* (MP).

Kei Is.: 1 ♀ Latuhalat, April 1922, H. C. Siebers (MB).

Aru Is.: 2 ♀ or ♀, leg. Rosenberg (ML).

New Guinea: 2 ♀ Kambrau at Arguni Bay, Aug. 1941, E. Lindquist (MB), 2 ♀ Mandiwa at Arguni Bay, July 1952, L. D. Brongersma and J. R. Schuiling (ML); 1 ♀ 1 ♂ Kaimana, June 1941, E. Lindquist (MB).

***Vespa affinis picea* Buysson**

1905. Buysson, R. du, Ann. Soc. ent. Fr., vol. 73 (1904), p. 537, ♀ (*V. cincta* var. *picea*, Tupuseleia, Yule I., Kapa-Kapa, New Guinea; type in Mus. Genova).
1911. Cameron, P., Nova Guinea, vol. IX, Zool., Livr. II, p. 186 (*V. cincta* race *picea*).
1936. Bequaert, J., Treubia, vol. 15, p. 346, 351 (*V. affinis* var. *picea*; cotype in MP examined).

South New Guinea: 1 ♀ River Patawai, west of Aindua, 1 ♀ River Aindua, July 1941, E. Lindquist (MB); 4 ♀ "Neu-Guinea" (ML); 1 ♀ Noordrivier (North River), Sept. 1909, Lorentz Exp., from MA (ML); 1 ♀ Tupuseleia, leg. Loria, July 1892 (MP).

***Vespa affinis archboldi*, new subspecies**

Female and worker. — Head dull reddish, the clypeus more or less distinctly fuscous at anterior margin, near the mandibles and in the middle

of the base. Thorax black, pronotum and scutellum almost entirely dull reddish, mesoscutum on each side with reddish line or blotch, rarely entirely dark; meso- and metapleura and propodeum partly dull reddish. Dorsal face of thorax with brownish tomentum. First and second abdominal tergites entirely orange-brown.

Type: 1 ♀ Hollandia, July 1938, L. J. Toxopeus, Archbold Exp. (ML).

North New Guinea: 3 ♀ 3 ♂ Hollandia, July 1938, L. J. Toxopeus, 1 ♀ 2 ♂ Bernhard Camp, July-Nov. 1938, J. Olthof (Archbold Expedition; MB, ML); 18 ♂ Hollandia, Dec. 1936, W. Stüber, ex coll. v. d. Vecht (ML); 2 ♂ Joka at Sentani Lake, Oct. 1954, L. D. Brongersma & L. B. Holthuis (ML); 2 ♂ Prauwenbivak, Nov.-Dec. 1920, W. C. van Heurn (MB, ML).

***Vespa affinis alticincta*, new subspecies**

1901. Cameron, P., Proc. Zool. Soc. Lond. 1901, vol. I, p. 241 (*Vespa affinis*, New Britain).

Female, worker, and male. — Head dull reddish, clypeus black, the following parts more or less extensively fuscous: temples along base of mandibles, inter-antennal area along upper margin of clypeus, the space around and behind the ocelli, and the occiput. Clypeus in the only available female with some vague reddish spots at base and apex. Thorax black, tegulae brownish, darker on inner side. The orange-brown areas on tergites 1 and 2 reduced to four spots which are separated by a dark cross, consisting of a dark median band on both tergites, and a transverse one at the posterior margin of the first abdominal tergite, the latter more distinctly defined than the former; the second tergite has a similar transverse band at the posterior margin, occupying at least the posterior third of the visible part of the tergite; first tergite fuscous at the base of the declivous part; first and second sternites fuscous with vague orange-brown blotches (the markings perhaps more distinct in fresh specimens).

Type: ♀, New Britain, Dr. A. Willey (BM, reg. 1 March 1898).

New Britain: locality uncertain, perhaps in the northern peninsula, 1 ♀ 9 ♂ 4 ♂ (paratypes), collected together with the type by Dr. A. Willey during his stay in New Britain in 1896-7 (BM, ML).

***Vespa velutina* Lepeletier (fig. 6)**

1836. Lepeletier, A. de, Hist. nat. Ins. Hym., vol. 1, p. 507, ♀ (*Vespa velutina*; Java, from de Haan, coll. Serville).

1905. Buysson, R. du, Ann. Soc. ent. Fr., vol. 73 (1904), pp. 492, 495, 548 (*V. velutina* and var. *ardens*, also *V. auraria* and varieties).

The Leiden Museum possesses five specimens collected in Java by C. G. C. Reinwardt, the founder and first Director (1817-22) of the Botanic Gardens at Buitenzorg (now Bogor). One of these bears a label in de Haan's handwriting: "*velutina* n.sp." Since Lepeletier described the species as "*velutina* de Haan" ("Java. Donnée par M. de Haan. Cabinet de M. Serville"), I suppose that the species was described from one or more specimens which originally formed part of this series. I do not know whether the typical material is still in existence; I could not find it in Paris, nor in the Spinola collection in Turin which contains some of the Hymenoptera collected by Serville.

Vespa velutina is widely distributed in the Oriental region. So far I have been able to distinguish ten subspecies, but probably there exist a few more in continental Asia. Only two of the subspecies discussed below have been described as varieties of *V. velutina* (*ardens* Buyss. and *celebensis* Pérez); one was described as a variety of *V. auraria* Smith (*nigrithorax* Buyss.) and another as a variety of *V. mongolica* André (*divergens* Pérez); the remaining five appear to be new.

The following forms, probably belonging to *V. velutina* Lep., have not yet been studied by me:

V. auraria Smith, 1852 (Northern India).

V. auraria var. *citriventris* Buysson, 1905 (Sikkim, Darjiling and Yunnan). — Perhaps a subspecies of *Vespa bicolor* Fabricius?

V. velutina var. *mediozonalis* Pérez, 1910 (Sikkim). — The type and only specimen of this form is a worker with a rather unusual colour pattern; it is probably specifically different from *V. velutina*.

Key to the Indo-Malayan subspecies of *Vespa velutina* Lep.

1. Second abdominal tergite yellow or light brown, black at base and sometimes with a dark transverse line in the middle; if more extensively blackish (in some females and males of the Malayan subsp. *divergens*) the third and following abdominal tergites are almost entirely brown. Head yellow or brown, mesoscutum very rarely entirely black 2
- Second abdominal tergite black with yellow or orange band at apical margin 3
2. Vertex, pronotum, mesoscutum (except for dark margins), scutellum, and large spots on postscutellum and propodeum pale brown; posterior (non-declivous) part of first abdominal tergite brown with dark transverse line before the middle, and narrow, bright yellow line at apical margin. (Malaya) *divergens* Pérez
- Vertex, pronotum, a large mark of variable shape on mesoscutum, scutellum, and a spot on each side of postscutellum bright yellow. Abdomen ferruginous yellow, except for the declivous part of the first tergite, and a more or less distinct transverse line on the horizontal part of this tergite, which are black; the narrow dark bands at the bases of the second and third tergites are usually more or less hidden. (Sumba Island) *sumbana* n. subsp.
3. Head and pronotum mainly orange-yellow or pale brown; if the ocellar area is

- black, the dark colour does not extend to the back of the head; upper part of temples not black 4
- Upper half of head mainly black; pronotum black with or without yellow or brown margins (in females of subsp. *velutina* from Java often more extensively yellow or brown). Femora I as a rule dark brown or black. 8
4. Mesoscutum yellow with a longitudinal black band on each side (at a short distance from tegulae) and a narrower one in the middle. 5
- Mesoscutum more extensively black 6
5. First and second abdominal tergites with equally narrow, yellow, apical bands; third tergite black with narrow apical band which is widened at the sides; fourth tergite orange-yellow with transverse, rectangular, median, black spot which occupies about one third of the width of the tergite and leaves the apical margin orange-yellow; following tergites orange-yellow or partly infuscated. (Lombok, and Sumbawa?) *ardens* Buysson
- Band on second abdominal tergite irregularly widened from the middle to the sides, distinctly wider than that on the first tergite; third tergite orange-yellow with median triangular black spot, following tergites orange-yellow. (Flores, Komodo) *floresiana* n. subsp.
6. Apical bands of tergites 2 and 3 equally narrow. (Java; Bali) see subsp. *velutina* Lep.
- Apical band of tergite 3 much wider than that of tergite 2 7
7. Femora I black, more or less brownish at apex. Scutellum yellowish-brown. Mesoscutum black, as a rule with brownish spot near anterior margin of scutellum, often with two median brownish lines. Abdominal tergites 1 and 2 with narrow apical bands, 3 and 4 entirely orange-yellow, except for basal black band, which is produced backwards in the middle, 5 and 6 brown to black; sternites 2 and 3 with broad apical band which is widely and deeply emarginate, or interrupted, in the middle. (Siam; Indo-China) *variana* n. subsp.
- Femora I brownish yellow, slightly darker at base. Scutellum black, a narrow band at posterior margin, connected with two lateral spots of variable size, brownish. Mesoscutum black, sometimes with traces of median lines in anterior half. Abdominal tergites 1 and 2 with narrow apical bands, 3 with wider band (incised anteriorly on each side), 4-6 entirely brownish yellow; sternites 2 and 3 with broad yellow apical bands, their median third brownish, sternites 4-5 with brownish apical band (incised anteriorly on each side), sternite 6 brown. (Timor) *timorensis* n. subsp.
8. Third abdominal tergite with broad apical yellowish-brown band, the dark base as a rule hardly visible *celebensis* Pérez
- Apical band of third tergite at least in the middle narrow, not distinctly wider than the band of the first tergite 9
9. Third abdominal tergite black in the middle, orange-yellow at the sides, the dark part usually less than one third of the width of the tergite; tergites 4-6 often partly black; vertex and thorax black, except for some inconspicuous lines on pronotum and scutellum. Wings with fuscous tinge. (Sumatra) *karnyi* n. subsp.
- Third abdominal tergite more extensively black 10
10. Abdominal tergites 1-5 black with narrow yellow line at apical margin; tergites 4 and 5 also yellow at the sides, on 5 the black colour reduced to median line or spot, tergite 6 yellowish brown, darker at sides. Extension of pale colour on head and thorax somewhat variable: specimens from East Java and Bali are as a rule more brightly coloured than those from West Java. Wings with yellowish tinge. (Java; Bali) *velutina* Lep.
- Tergite 3 brownish in front of apical narrow band, not deep black as in *velutina*. Visible part of tergite 4 entirely orange-yellow; tergites 5 and 6 yellowish brown. Thorax entirely black. (Continental Asia) *nigrithorax* Buys.

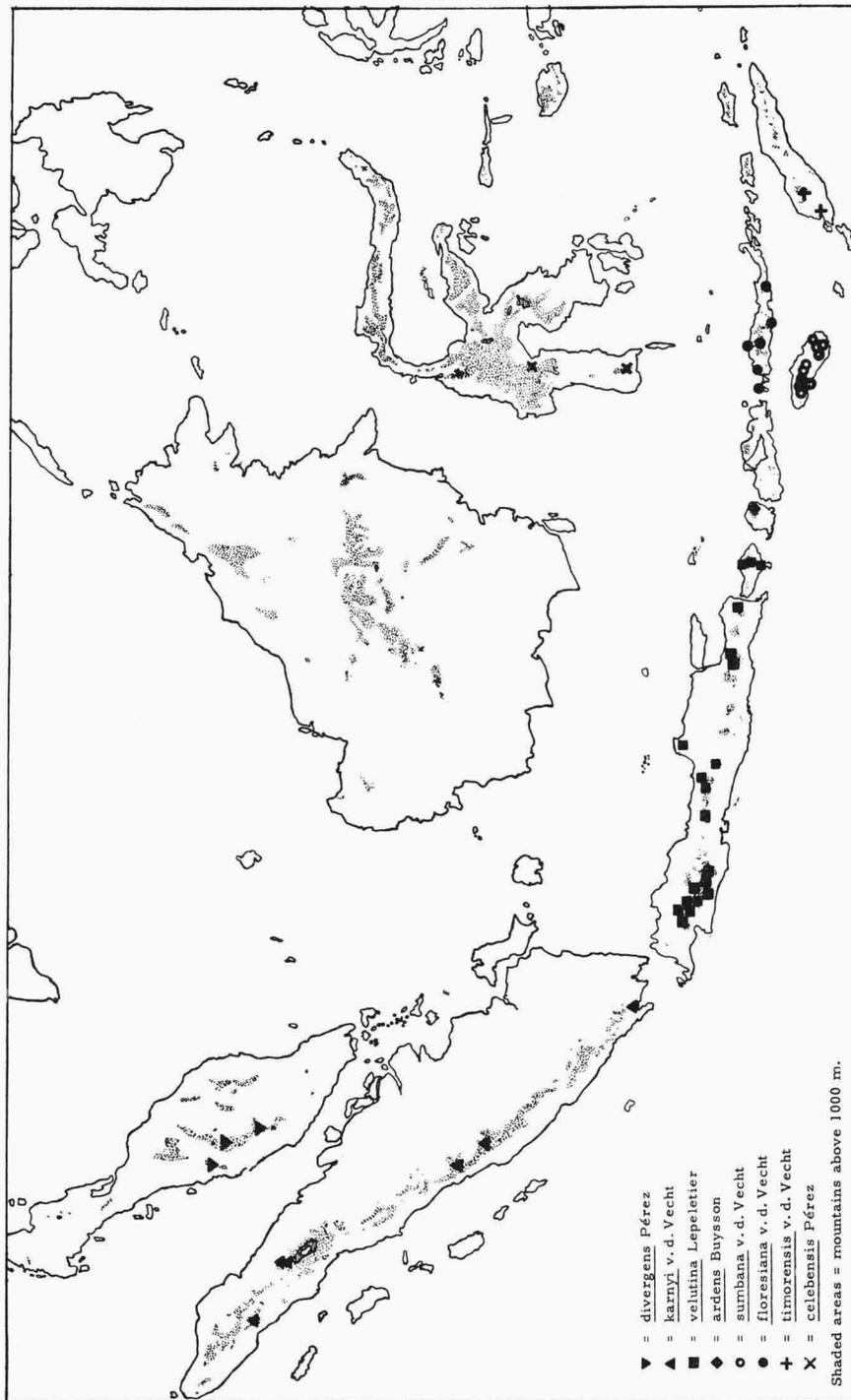


Fig. 6. The distribution of the Indo-Malayan subspecies of *Vespa velutina* Lepelletier.

Vespa velutina nigrithorax Buysson

- ! 1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 553 (*V. auraria*, var. *nigrithorax*; N. India; China, etc., type locality not given).
 ! 1910. Pérez, J., Actes Soc. Linn. Bordeaux, vol. 64, p. 13 ♀♂ (*V. velutina*, var. *megei*, "Kouei-Tchéou", Central China) (new syn.).

The series on which du Buysson based the description of this variety contained besides specimens from several localities in continental Asia (India and China) some material from Sumatra (D. Tolong, leg. Modigliani; Mt. Singgalang, leg. Beccari) and South Celebes (Bua Kraëng, 3000', leg. Fruhstorfer, and Bantimurung, C. Ribbe). I regard these latter specimens as belonging to different subspecies, and restrict the name '*nigrithorax*' to a form occurring in continental Asia. The lectotype, chosen from du Buysson's material in the Paris Museum, is a female from Darjiling, leg. Harmand, no. 2854-90.

In the collection Pérez (MP) this form is represented by the typical series of the var. *megei*, consisting of 3 ♀ and 1 ♂ from Kouy-Tchéou.

China: 1 ♀ Ningpo, leg. Felder (ML); 1 ♀ 1 ♂ Suifu, Szechuen, 1928, leg. D. C. Graham (ML); 1 ♂ Chusan, Chekiang, leg. O. Piel (ML); 1 ♂ Soochow, leg. N. Gist Gee (ML); 2 ♀ Kuanchien, Szechuen, 1600-2200', 27-29 July 1934, leg. D. C. Graham (ML); 2 ♀ Fulin, 3000-7000', 18-21 Aug. 1928, leg. D. C. Graham (ML); 1 ♂ Mt. Omei, 4400', Shin Kai Si, Szechuen, July-Aug. 1923, D. C. Graham (ML); series, "Kouy Tchéou, Se Tchouen", 1913, leg. P. Cavalerie (MP); furthermore the collection of the Paris museum contains specimens from Mou-Pin (leg. David, 1870), Kiangsi and Se-Tchouen (leg. David, 1875), Foochow, and Kouy-Yang.

A few specimens from Formosa are more brightly coloured and probably represent a separate race.

India: 5 ♀ Padong, Bhutan, 1913, leg. L. Durel, ex coll. R. Oberthür (MP, ML); a series from Bhutan, leg. R. Oberthür (MP); 1 ♂ Sikkim (coll. Pérez, MP).

Vespa velutina variana, new subspecies

This form resembles subsp. *ardens* Buyss. and *floresiana* n. subsp., but the mesoscutum is darker, and the fifth and sixth abdominal tergites are mainly dark brown to black.

North Siam: 5 ♀ Doi Hua Mot, 3000', Aug. 1934, H. M. Smith, from USNM (received as "*V. auraria* Smith") (type and paratypes, ML); 1 ♂ Khim Tan Mts., 4000', May 1933, H. M. Smith (paratype, ML).

Indo-China: 3 ♀ Laos, région de Xieng-Khouang, Tranninh, 1920, leg. R. Miéville (MP); 1 ♀ 4 ♂ Tonkin, rég. de Hoa-Binh, 1927-1936, leg. A. de Cooman (MP).

The collection Pérez (MP) contains a worker labelled "Sikkim et Assam" and identified as var. *ardens*, under which name it was discussed by Pérez (1910, l.c., p. 11).

***Vespa velutina divergens* Pérez**

! 1910. Pérez, J., Act. Soc. Linn. Bordeaux, vol. 64, p. 16, ♀ (*V. mongolica* var. *divergens*; Perak, Malaya).

1931. Dover, C., Jl. Fed. Mal. St. Mus., vol. 16, p. 259 (*V. auraria* Smith; Pahang and Perak).

The type is a worker from Perak, without further indications, in the collection Pérez (MP); it is probably the only specimen seen by this author.

Dover identified this form as *V. auraria* Smith, which was described in 1852 from Northern India, but if *auraria* is a race of *V. velutina*, it will certainly prove to be different from *divergens*, which appears to be restricted to the mountain forests of the Malay Peninsula.

Malaya: Larut Hills, Cameron Highlands and Fraser's Hill, 4200-6000', several specimens in ML (3 ♀, 11 ♂, 2 ♂) and BM.

***Vespa velutina karnyi*, new subspecies**

1931. Meade-Waldo, G., Jl. Fed. Mal. St. Mus., vol. 8, p. 220 (*V. velutina* var. *nigrithorax* Buyss., Korintji, Sumatra, 4000-7300').

The Sumatran subspecies of *V. velutina* is remarkably different from the Malayan *divergens* and resembles more closely the typical form occurring in Java. It is easily distinguished from the latter by the colour of the third abdominal tergite and by the darker wings.

Female, worker, and male. — Head and thorax slightly darker than in the Java form; the following parts orange yellow: clypeus, mandibles (cutting edge dark), underside of antennae, a spot between antennae (truncate above, about halfway between antennae and anterior ocellus), the eye-emargination (this mark separated from spot on interantennal shield, and produced downward along inner orbit to clypeus), lower half of temples, narrow lines along transverse carina and at posterior margin of pronotum (often hardly visible), a narrow line at posterior margin of scutellum.

First abdominal tergite with yellow line at apical margin, second tergite with yellow band at sides, narrowed towards the middle and here over a considerable distance either extremely narrow or absent; third tergite orange-yellow, the middle third black with very narrow orange line at posterior margin; fourth and following tergites black, their apical margins very narrowly brownish. Sternites black, apical margins testaceous, second and third sternites with brownish yellow spots at apical margin.

Legs as in subsp. *velutina* Lep.

Wings with a rather strong fuscous tinge, distinctly darker than in the subsp. *velutina*.

Type: ♀, Bandar Baru, Deli, 9 Oct. 1925, Fulmek and Karny (ML). All other specimens recorded below are paratypes.

S u m a t r a: Apparently not rare, occurring throughout the island in mountain forests. Atjeh: a series from Mt. Kemiri (top, 3200 m), Laut Tiga Sagi and Mt. Leuser, 2000-2700 m, Leuser Exp. 1937, C. G. G. J. van Steenis and A. Hoogerwerf (MB, ML); Deli: 2 ♀ Mt. Sibajak, 1800 m, Oct. 1929, W. M. Docters van Leeuwen (MB); 1 ♀ Brastagi, 1400 m, Nov. 1950, M. A. Lieftinck (MB); West coast: 1 ♀ 2 ♀ Alahan Pandjang, Sept. 1877, Sumatra Exp. (ML), 1 ♀ 1 ♂ Korinchi Peak, May 1914, leg. H. M. Pendlebury (BM), 1 ♀ do., Aug. 1915, E. Jacobson (ML); Lampong Districts: a series from Mt. Tanggamus, 1600 m to top (2100 m), 1934 and 1940, L. J. Toxopeus and M. A. Lieftinck (MB, ML).

Vespa velutina velutina Lepeletier

1836. Lepeletier, A. de, Hist. Nat. Ins. Hym., vol. I, p. 507. ♀ (*Vespa velutina*; Java).

The extension of the yellow colour on head and thorax is somewhat variable. The females are often more brightly coloured than the workers, having orange-yellow spots on pronotum and scutellum; in the workers the pronotum has at most a narrow yellow margin, and the scutellum is nearly always black.

J a v a: a common species in the mountain areas throughout the island, occurring in forests as well as in plantations above 1000 m; numerous specimens in ML (34 ♀, 51 ♀, 9 ♂), MB, and LEW. Occasionally specimens have been collected at a much lower level: 1 ♀ Bogor, 250 m, May 1935, van der Vecht (ML); 1 ♀ Radjamandala, 400 m, May 1936, F. C. Drescher (MB); 3 ♀ Salatiga (height not noted, but probably ± 500 m), 1910-1912, W. Roepke (LEW).

B a l i: 2 ♀ Batu Meringgit, Oct. 1928, leg. Franck (MB); 1 ♀ 1 ♀ Gitgit, 550 m, June 1939, van der Vecht; 1 ♀ Kintamani, 1500 m, May 1935, leg. R. Awibowo (ML); 14 ♀ 2 ♂ Baturiti, 1000 m, Aug. 1941, leg. Kalis, ex coll. v. d. Vecht (ML); 1 ♀ Den Pasar, 50 m, June 1935, leg. R. Awibowo (ML).

Generally the Balinese specimens agree well with those from Java, but the worker from Kintamani has large orange spots on the pronotum, and an almost entirely orange scutellum (blackish in the middle); the female from Den Pasar cannot be distinguished from subsp. *ardens* and is perhaps an immigrant from Lombok.

Vespa velutina ardens Buysson

! 1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 550, ♀♂ and ♂
(*V. velutina* var. *ardens*; Lombok and Sumbawa).

L o m b o k: 3 ♀ Sapit, 2000', leg. Fruhstorfer (LEW, ML). These specimens belong to the series from which this race was described by du Buysson, and which is represented by 1 ♀, 4 ♂ and 1 ♂ in the Paris Museum.

Vespa velutina floresiana, new subspecies

Head and thorax as in subsp. *ardens*, but the abdomen more extensively yellow (compare the key).

Type: ♀, Labuan Badjo, Flores, June 1937, J. K. de Jong (ML). The specimens recorded below are paratypes.

F l o r e s: 2 ♀ Labuan Badjo, June 1937, J. K. de Jong (MB, USNM); 1 ♀ Wolasambi, 1950, leg. Miss H. C. Vos, ex coll. v. d. Vecht (ML).

The Swiss Sumba-Expedition (1949) collected this race at Rana Mese (1300 m), Reo, Ende, and Moni.

K o m o d o: 1 ♀ 1 ♂ June-July 1937, J. K. de Jong (MB, ML).

Vespa velutina sumbana, new subspecies

Female, worker, and male. — Abdomen almost entirely orange-yellow (distinctly brighter than in the Malayan *divergens* Pérez), but declivous part of first tergite mainly dark, and the posterior part with a more or less distinct transverse dark line. Head and thorax as in subsp. *ardens*; ocellar area often more or less fuscous; scutellum orange-yellow, rarely with dark spot in the middle of the base; postscutellum black with brownish yellow spot on each side.

Type: ♀ Kananggar, E. Sumba, 700 m, May 1925, K. W. Dammerman (ML). The specimens recorded below are paratypes.

S u m b a: 1 ♂ Mau Marru, 450 m, May 1925, K. W. Dammerman (ML); 1 ♀ Waingapu, 1947, leg. Veterinary Officer (ML); 4 ♀, 97 ♂, 2 ♂, several localities, Swiss Sumba Exp. 1949 (MBA, MB, ML).

Vespa velutina timorensis, new subspecies

As is usual in the Vespidae that have different subspecies in these islands, the Timor race is considerably darker than that of Sumba. It resembles *celebensis*, but is distinguished by the pale colour of vertex and pronotum.

In both these subspecies the band on tergite 1 occupies about one third of the horizontal part of the tergite, that on tergite 2 about one fourth of the visible part; anteriorly, the bands are brownish and much less sharply defined

than in *velutina* s.str. and *ardens*. Moreover, the bands in these latter forms are distinctly narrower.

Type: ♀ Mollo, 1350 m, Timor, June 1935, Bühler & Meyer (MBA). The specimens recorded below are paratypes.

Timor: 5 ♀ Mollo, 1350 m, June 1935, Bühler & Meyer (MBA, ML); 14 ♀ ♀, Kupang, May 1940, collected by Veterinary Officer from hollow in *Eucalyptus* tree (MB, ML, USNM; these specimens have been preserved in liquid and are slightly discoloured); 2 ♀ Nenas, Mutia Mts., Sept. 1947, leg. W. P. de Roever (ML).

Vespa velutina celebensis Pérez

! 1910. Pérez, J., Actes Soc. Linn. Bordeaux, vol. 64, p. 12 (*V. velutina* var. *celebensis*; Bua-Kraëng, Celebes).

Celebes: South Celebes, 1 ♀ Bua Kraëng, 5000', H. Fruhstorfer, 1896 (type in coll. Pérez, MP), 2 ♀ 1 ♂, same label (MP, in typical series of *V. auraria* var. *nigrithorax* Buysson); 1 ♀ Palopo, Todjambu, 1000 m, July 1936, 7 ♀ Mt. Lompobatang, 1600 m, July 1936, L. J. Toxopeus (MB, ML); 1 ♀ Mt. Lompobatang, 1200 m, Nov. 1941, local collector, leg. H. Lucht (ML).

The absence of this insect from the collections made by F. Dupont in several mountain localities in Minahasa, North Celebes, is noteworthy.

Vespa bicolor Fabricius

1787. Fabricius, J. C., Mant. Insect., vol. I, p. 288 (*V. bicolor*; China, leg. Pflug).
 1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 488, 496, 544, ♀♂♂, pl. 7 fig. 2 (Japan; China; Indo-China; Assam).
 1937. Maa, Tsing-chao, Entom. and Phytopath., Hangchow, vol. 5, p. 32 (Hangchow, China); p. 41 (figs. of male genitalia and apical sternite).

This inhabitant of India, China, and Japan appears to extend southward along the mountain range of Indo-China. I have examined specimens from the following localities:

Bhutan: 2 ♀ 3 ♀ 2 ♂ Padong, 1913, L. Durel, leg. R. Oberthür (ML, MP).

China: 2 ♀ 4 ♀ "China", leg. Heine (ML); 1 ♀ Amoy, leg. Budding (ML); 1 ♀ Foochow, July 1925, C. C. Woo, from USNM (ML); 1 ♀ Si-Gi-Pin, 6-7000', Szechuen, 1934, D. C. Graham, from USNM (ML); series from Kiangsi, leg. David, 1875, and North Peking, David, 1865 (MP); 1 ♀ with old label "*Vespa bicolor* Fab. China, 160-45", ex coll. Lepeletier, 1845 (MP).

Tonkin: 4 ♀ région de Hoa-Binh, 1926-1934, A. de Cooman (MP).

Annam: 1 ♀ prov. de Quang-Tri, rég. de Vinh-Linh, 1922, leg. Jabouille

(MP); 1 ♀ Col des Nuages près Tourane, 1923, leg. Mme Poilane; 2 ♀ prov. de Phan-rang, région de Ca-na, 700-900 m, 1923, leg. Poilane (MP).

Vespa mocsaryana Buysson

1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), pp. 490, 495, 537, ♀♂♂ (*V. mocsaryana*; Malaya; Sikkim; Assam; Tenasserim).

This little known species can be distinguished from the allied *V. velutina* by the coarser puncturation of the basal half of the clypeus. The first abdominal tergite is relatively longer, and less sharply truncate anteriorly. This latter character also separates *mocsaryana* from the *luctuosa*-group, and so does the less distinctly grooved scutellum.

Indo-China: 1 ♀ (?), 2 ♀, Tonkin, région de Hoa-Binh, 1926-1930, A. de Cooman (MP).

Malaya: Kedah, Catchment Area near Jitra and Kedah Peak (3900'); Selangor, Ulu Klang and Kuala Lumpur, altogether 8 ♀ and 5 ♂, collected by H. M. Pendlebury (BM, ML).

Sumatra: Indragiri, 1 ♀ Berapit, April 1939, leg. P. Buwalda (ML).

In the Sumatran specimen the second abdominal tergite is entirely black; in the Malayan specimens which I have seen there is a — sometimes partly reduced — narrow, yellow, apical band. Probably this difference is not important, for du Buysson, who saw only continental specimens, stated: “le 1er tergite et parfois le 2e étroitement et régulièrement lisérés de jaune pâle”.

Group of **Vespa luctuosa** Saussure (fig. 7)

In a paper on the colour forms of *Vespa luctuosa* Saussure, Bequaert (1934) distinguished four different “varieties” besides the typical form of this species. *Vespa fervida* Smith from Celebes was regarded as closely allied, but specifically different.

I have not followed this arrangement for the following reasons: (1) the “varieties” *multimaculata* Pérez (= *malayana* Beq.) and *bellicosa* Saussure occur both in Borneo and Sumatra, where they are constant and do not hybridize, thus forming a good example of a “sibling species”; (2) typical *luctuosa* from the Philippine Islands differs from these forms by the denser and coarser puncturation of the abdominal tergites, and in the shape of the seventh abdominal segment and the genitalia of the male, showing a greater resemblance in these respects with *V. fervida* from Celebes; (3) the Bornean specimens of *V. multimaculata* differ slightly in coloration from those collected in Malaya and Sumatra.

Consequently, it seems more correct to regard *V. luctuosa* sensu Bequaert

together with *V. fervida* Smith as a species group or a superspecies, consisting of the following species and subspecies:

- 1a. *V. multimaculata multimaculata* Pérez, Borneo.
- b. *V. multimaculata pendleburyi*, n. subsp., Malaya, Sumatra.
2. *V. bellicosa* Saussure, Sumatra, Borneo.

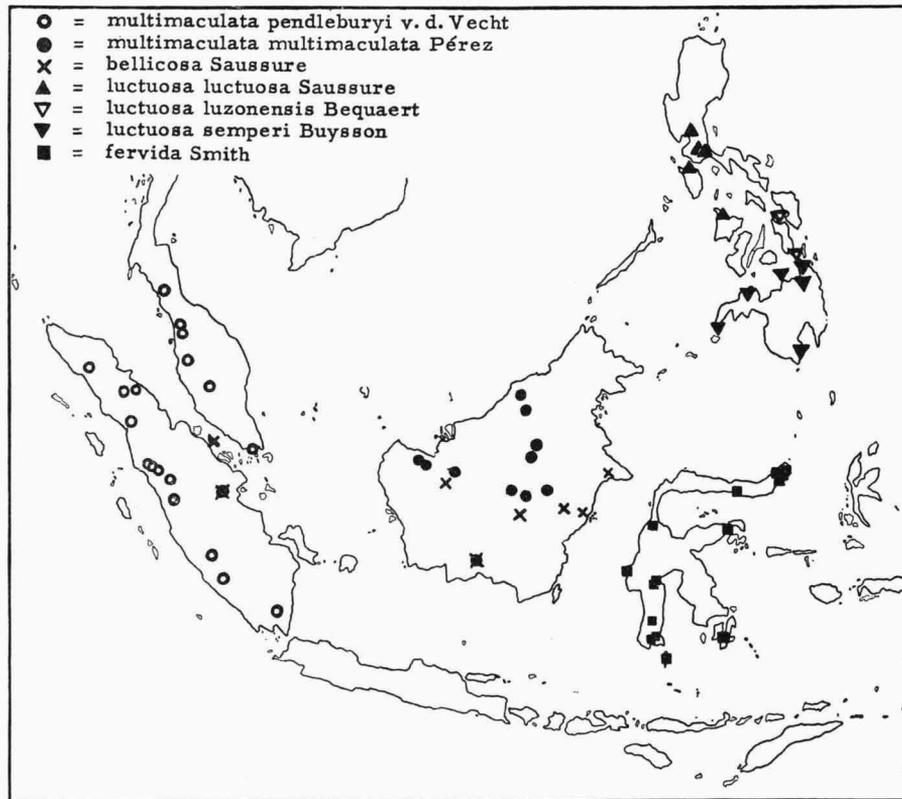


Fig. 7. The distribution of the species and subspecies of the *Vespa luctuosa*-group.

- 3a. *V. luctuosa luctuosa* Saussure, Northern Philippine Islands.
- b. *V. luctuosa luzonensis* Bequaert. Status and distribution of this form require further study.
- c. *V. luctuosa semperi* Buysson, Mindanao; Camiguin.
4. *V. fervida* Smith, Celebes, Salajar Is., Buton.

***Vespa multimaculata multimaculata* Pérez**

1858. Smith, F., Jl. Proc. Linn. Soc. Lond. Zool., vol. 2, p. 116 (*V. annulata* ♀, Sarawak, Borneo; Malaya; leg. Wallace; nec *V. annulata* Rossi 1790).

1905. Buysson, R. du, Ann. Soc. Ent. France, vol. 73 (1904), p. 542 (*V. bellicosa*, var. *annulata*; Borneo) (excl. other records, v.d.V.).
1906. Cameron, P., Jl. Straits Br. Roy. As. Soc., vol. 46, p. 122 (*Vespa annulata*; Santubong, Matang and Kuching in Sarawak, Borneo; "if not a distinct species a well marked race of *bellicosa*").
- ! 1910. Pérez, J., Act. Soc. Linn. Bordeaux, vol. 64, p. 14 (*V. multimaculata*; "Brunei, Java"; type in MP) (Brunei is in North Borneo! v.d.V.).
1934. Bequaert, J., Bull. Mus. roy. Hist. nat. Belg., vol. 10, no. 28, p. 3, 4 (*V. luctuosa* var. *malayana*, new name for *V. annulata* Smith, nec Rossi; Borneo) (n. syn.).

When Bequaert renamed Smith's *annulata*, he overlooked that this species had been described by Pérez as *V. multimaculata*, probably because Pérez compared his insect with *V. velutina* and incorrectly gave Java as the type locality. However, the type in the collection Pérez (MP) bears a label "Brunei, Borneo".

Abdominal bands, as seen from above, narrow (width of second band about one sixth of the length of the visible part of the tergite) and regular, very slightly narrowed towards the middle, where they are incised anteriorly, rather suddenly widened on the sides of the tergites.

B o r n e o: 1 ♀ Brunei (type in coll. Pérez, MP), 1 ♀ "Borneo", leg. S. Müller (ML). 1 ♂ "Borneo, 55-70" on small, round, blue label, probably collected by Wallace and syntype of *V. annulata* Smith (BM). 1 ♀ Mt. Kenepai, Jan. 1894, leg. Dr. Hallier, 3 ♀ Liang Kubung, west side, April 1894, Dr. Büttikofer, 2 ♀ ? S. Dengoy, Sept. 1894, all collected by Nieuwenhuis's Borneo Exp. (ML); 1 ♀ Central E. Borneo, leg. Siebers, Sept. 1925 (MB); 3 ♀ Pemanten-Sampit, S. Borneo, July 1953, M. A. Lieftinck (MB); 1 ♀ "Borneo", leg. R. Oberthür, 1898 (MP).

***Vespa multimaculata pendleburyi*, new subspecies**

1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 542 (*V. bellicosa*, var. *annulata* Smith; Sumatra; Himalaya) (the latter record needs confirmation! v.d.V.).
1914. Schulthess, A. von, Zool. Jahrb. Syst., vol. 37, p. 261 (*V. bellicosa* var. *annulata*; Malaya).
1934. Bequaert, J., Bull. Mus. roy. Hist. nat. Belg., vol. 10, no. 28, p. 3, 4 (*V. luctuosa*, var. *malayana*, new name for *V. annulata* Smith nec Rossi; Sumatra) (excl. other records).

Female, worker, and male. — Very closely allied to *V. multimaculata* from Borneo, but the abdominal bands are less regular and distinctly wider, though more or less narrowed towards the middle where they are incised anteriorly. At a short distance from the middle, the band on the second tergite covers about one fourth of the tergite against one sixth in *V. multimaculata* from Borneo.

Type: ♀, Catchment Area near Jitra, Kedah, N. Malaya, 11 April 1928, H. M. Pendlebury (ML). The specimens recorded below are paratypes.

Peninsular Siam: 1 ♀ Khow Sai Dow, Trong, W. L. Abbott leg., USNM (ML); 4 ♀ from this locality recorded by Bequaert, 1934).

Malaya: Kedah, 1 ♂ Catchment Area near Jitra, April 1928, H. M. Pendlebury (BM), 1 ♂ Kedah Peak, 3000-3500', March 1928, H. M. Pendlebury (ML); Perak, 1 ♂ Larut Hills, Febr. 1932, at light, H. M. Pendlebury (ML); Selangor, 3 ♂ Bukit Kutu, 3500', 18-20 April 1926, at light, H. M. Pendlebury (BM), 1 ♀ do., 25 Sept. 1932, H. M. Pendlebury (ML); Singapore, 1 ♀ leg. C. F. Baker (ML).

Sumatra: 1 ♀ 2 ♀ "Sumatra", leg. S. Müller (ML); Atjeh, 1 ♀ Pendeng, 400 m, Febr.-March 1937, Loeser-Exp., A. Hoogerwerf (MB); Deli, 1 ♀ Tandjong Morawa, leg. Dr. B. Hagen (ML), 1 ♀ Bandar Baru, Oct. 1925, H. Karny (MB), 1 ♀ 2 ♀ do., Febr. 1940, J. C. van der Meer Mohr, with note: "Batak name = oewiel-oewiel (pron. oo-weel); Tapanuli, Pagarapisang (no specimens seen, recorded as "Pangheran Pisang, leg. Modigliani" by du Buysson); Westcoast: 2 ♀ 3 ♀ Lubuk Sikaping, 1923-27, leg. L. Hundeshagen (MB, ML); 1 ♀ 1 ♀ Tanangtal, Ophir, 1915, leg. A. de Kock (E. Jacobson, nrs. 8506, 8507) (ML); 1 ♀ Muara Sako, Oct. 1915, E. Jacobson, no. 8508 (ML); 1 ♀ Pajakombo, H. Rouyer (ML); 1 ♀ Datar, May 1877, Sumatra Exp. (ML); Indragiri, 4 ♀ Berapit, 2 ♀ Pangkalan Kasai, 1 ♀ Muara Padjanki, April 1939, P. Buwalda (MB, ML); Benkulen, 2 ♀ Muara Tenam, 4 ♀ Tandjong Sakti, 3 ♀ Bukit Item, May-July 1935, leg. Mrs. Walsh (ML); Palembang, 1 ♀ Surulangun, Aug. 1878, Sumatra Exp. (ML); Lampong (2 ♀ from Gunungsugih recorded by Bequaert, 1934).

A female from Pagarapisang, leg. Modigliani, 1890-91, in the Paris Museum, was misidentified by du Buysson as *V. bellicosa*; a female labelled "Himalaya, Dr. S. Martin, leg. Mus. de Munich, 1903" in the same Museum (see du Buysson, l.c., p. 542) was probably collected in Sumatra.

***Vespa bellicosa* Saussure**

- 1853-4. Saussure, H. de, Ét. fam. Vesp., vol. 2, p. 146, ♀, pl. 14, fig. 10 (*V. bellicosa*; "Java, coll. Spinola et coll. Smith").
1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 488, 489, 540, ♀ ♀ ♂, pl. 5, fig. 7 (*V. bellicosa*; Bengkalis; Sumatra; Borneo) [erroneously recorded from Singapore, v.d.V.].
1906. Cameron, P., Jl. Straits Branch Roy. As. Soc., vol. 46, p. 122 ("*V. bellicosa* Smith" (recte: Saussure!); recorded from Pulo Burong, Borneo).
1934. Bequaert, J., Bull. Mus. roy. Hist. nat. Belg., vol. 10, no. 28, p. 4 (*V. luctuosa*, var. *bellicosa*; Sumatra; Borneo; also recorded from Mindanao and Zamboanga, Philippine Islands, and the Moluccas).

The recorded locality "Java" is another instance of the frequent occurrence of incorrect locality labels in old collections, for the species does not occur

in this island. Neither has it been found in the Moluccas, from where it was recorded by Bequaert (specimens in the Museums of Paris and Berlin). If this form occurred in the eastern half of Indonesia, it would certainly have been represented in the extensive collections made there in recent years by Franssen, Lieftinck, Wegner and others. The record "Singapore" (du Buysson, 1905, and cited by Bequaert, 1934) is based on a misidentified male of *V. analis tyrannica* Smith in the BM. The occurrence in the Philippine Islands (Bequaert, 1934) needs confirmation.

Provisionally I regard *V. bellicosa* as a distinct species, although the females and workers appear to differ from *V. multimaculata* in coloration only. It will be of interest to study the male of this form.

S u m a t r a: Bengkalis, 5 ♀ leg. Maindron, 1885 (MP); Indragiri, 1 ♀ Pangkalan Kasai, 5 ♀ Berapit, 2 ♀ Kuala Lau, April-June 1939, P. Buwalda (MB, ML).

V. bellicosa was recorded by du Buysson from "Pangheran-Pisang" (= Pagaranpisang), but the only specimen from this locality in the Paris Museum is undoubtedly a female of *V. multimaculata pendleburyi*.

B o r n e o: 3 ♀ "Borneo", leg. S. Müller (ML); West Borneo, 13 ♀ Sintang, leg. Borneo Exp. 1894 (ML); East Borneo, 2 ♀ Muara Muntai, West Kutai, Sept. 1938, leg. B. M. Hoeks (MB), 1 ♀ Maluwi, 1 ♀ Sangkulirang, 1938, Mrs. M. E. Walsh (ML), 1 ♀ Muara Kaman, Nov. 1950, A. M. R. Wegner (MB); South Borneo, 1 ♀ Pemanten-Sampit, July 1953, M. A. Lieftinck (MB); 6 ♀ "Borneo" (MP).

It is of interest to note that at three different localities: Berapit and Pangkalan Kasai in Sumatra, and Pemanten-Sampit in South Borneo, this species was collected together with *V. multimaculata* Pérez.

Vespa luctuosa Saussure

In this species the females and the workers differ distinctly in size, measuring 24-27 mm, and 20-22 mm, respectively. They are also much darker, and whereas the workers and males can easily be separated in three subspecies by differences in the coloration of thorax and abdomen, the females of these forms have undoubtedly often been confused, and some authors even have identified them as *fervida* Smith.

The workers differ as follows:

1. Abdominal tergite 6 yellow (tergites 1-5 with yellow bands). (Mindanao; Camiguin) *semperi* Buysson
- Abdominal tergite 6 black 2
2. Propodeum black; tergites 1-4 or 1-5 with narrow yellow apical bands; the width of the second band about one sixth of the length of the tergite; the third and fourth bands slightly wider than the others. (Northern Philippine Islands) *luctuosa* Saussure

- Propodeum extensively marked with yellow; tergites 1-4 with rather wide apical bands; the width of the second band about one fourth of the length of the tergite; the following bands even wider, the visible parts of the black base of tergites 3 and 4 much narrower than the bands. (Some islands between Luzon and Mindanao)

luzonensis Bequaert

***Vespa luctuosa luctuosa* Saussure**

- 1853-4. Saussure, H. de, Ét. fam. Vesp., vol. 2, p. 143, ♂ (*V. luctuosa*; Philippine Is., type in BM).
 1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 619 (unidentified species).
 1919. Williams, F. X., Bull. Hawaii Sugar Pl. Ass., Ent. Ser., vol. 14, p. 164 (*V. luctuosa*, notes on nest and prey).
 1934. Bequaert, J., Bull. Mus. roy. Hist. nat. Belg., vol. 10, no. 28, p. 3 (*V. luctuosa*, forme typique).
 1941. Bequaert, J., Phil. Jl. Sci., vol. 75, p. 66 (*V. luctuosa*, var. *luctuosa*).

Luzon: 4 ♀ Mt. Banahao (USNM; ML) (first tergite black or with very narrow apical band which is indistinct in the middle, second and following tergites without apical bands); 6 ♀ Los Baños (ML; USNM) (tergites 1-4 with yellow band at apex, those on 1 and 2 narrower than on 3 and 4; following tergites dark brown, in some specimens with apical band on tergite 5 or with traces of such a band; sternite 2 with widely interrupted apical band, 3 with complete band, the following sternites entirely dark); 1 ♂ Los Baños (ML), 1 ♂ do., March 1953, Townes family (coll. Townes) (coloration of abdomen as in the workers, tergite 5 and sternite 4 with traces of apical band); 1 ♀ Mt. Makiling, leg. Baker (USNM).

Mindoro: 2 ♀ San Teodoro, Aug. 1952, Townes family (coll. Townes) (coloration as in the workers from Luzon, but apical band on tergite 5 more distinct, though narrower than on tergites 3 and 4).

Panay: 1 ♀ 1 ♀ N.W. Panay, leg. Baker (USNM) (abdomen of ♀ entirely black; ♀ with tergites 5 and 6 black).

Bequaert (1941) has recorded this form from Luzon, Mindoro, Negros, Samar, Ticao, and Mindanao, but some of these records appear to need confirmation (see under subsp. *semperi*).

***Vespa luctuosa luzonensis* Bequaert**

1934. Bequaert, J., Bull. Mus. roy. Hist. nat. Belg., vol. 10, no. 28, p. 5 (*Vespa luctuosa* var. *luzonensis*; type ♀, Luzon, leg. Jagor, Mus. Berlin).
 1941. Bequaert, J., Phil. Jl. Sci., vol. 75, p. 67 (*V. luctuosa* var. *luzonensis*).

This form was based on a single worker from Luzon, and a long series of specimens from "Philippine Islands", without precise locality (Mus. Berlin).

A worker from Biliran, leg. Baker (USNM) agrees in all respects with

one from the typical series, which was kindly sent to me by Dr. G. Steinbach, Zoologisches Museum, Berlin. A female with the same label, however, also in the USNM, differs from *luctuosa* female from Luzon only in having a rather distinct band at apex of tergite 1, and rudiments of apical bands in the middle of tergites 2 and 3.

The British Museum possesses a ♂ from Panaon (small island between Leyte and Mindanao), "12.15 Böttcher", which agrees well with Bequaert's description. It has the head as in typical *luctuosa*, but the eye-emargination partly black (line at inner orbit ends at middle of upper side); the thorax, however, is more extensively marked with yellow than in a male from Luzon: pronotum with short band along transverse carina, on each side with short branch along posterior margin; a spot on mesopleura below tegulae, two lateral spots on scutellum, connected by a narrow band along posterior margin, postscutellum, a spot on metapleura extending on side of propodeum, and an irregular spot in centre of propodeum; also the tegulae yellowish. Abdomen black, with rather wide bands on tergites 1-4 and sternites 1-3. Legs yellow, coxae, trochanters and femora partly dark.

The distribution of this form requires further investigation. It seems possible that the type is incorrectly labelled and that *luzonensis* does not occur in Luzon!

***Vespa luctuosa semperi* Buysson**

1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 542, ♀ (*V. bellicosa*, var. *semperi*; 2 ♀ Comigu¹), Philippine Is., leg. Semper 1867, types in Mus. Vienna; also Lubang and Luzon²)).
1934. Bequaert, J., Bull. Mus. roy. Hist. nat. Belg., vol. 10, no. 28, p. 4 (*V. luctuosa* var. *semperi*; 1 ♀ Calian, Mindanao).
1941. Bequaert, J., Phil. Jl. Sci., vol. 75, p. 67 (*V. luctuosa*, var. *semperi*; Calian, Kolambugan, and Zamboanga in Mindanao).

Upon my request, Dr. M. Beier of the "Naturhistorisches Museum" in Vienna kindly sent me the two typical specimens for examination. Both are workers and bear two labels, one "Semper, Comigu, 1867", and one written by du Buysson: "*Vespa bellicosa* Sauss., var. *semperi* Buyss., type ♀, R. du Buysson det. 1903". One of these specimens now bears a label "lectotype" with my name.

Furthermore I have seen 3 ♀ from Surigao (1 ♀ ML), 1 ♀ from Butuan, and 1 ♀ from Dapitan, all collected by Baker (USNM).

The worker of *V. luctuosa semperi* is distinguished by the coloration of the abdomen; the tergites 1-5 bear pale yellow apical bands, tergite 6 is

1) Perhaps Camiguin, a small island on north coast of Mindanao.

2) Tayabas, given as a separate island, is on Luzon.

almost entirely yellow. The bands on tergites 1 and 2 narrow, as in typical *luctuosa*, the three following bands wider, their anterior margins irregular, the band on tergite 5 much narrowed laterally; tergite 6 yellow with the sides blackish at the base. Sternites 2-4 with yellow apical band, 5 and 6 with vague yellowish streaks at apical margins. Legs slightly brighter than in typical *luctuosa*.

This is a distinct subspecies, representing *V. luctuosa* in Mindanao and one or more small neighbouring islands. Bequaert has also recorded typical *luctuosa* from some localities in Mindanao, but I suspect that these records have been based on females. As in the other subspecies, the female is apparently much darker than the worker. I have seen only one female from Mindanao (Surigao, leg. Baker, USNM), and this specimen resembles *Vespa fervida* in having the clypeus black with a transverse yellow band at the anterior margin. However, the mandibles are extensively yellow (in *fervida* at most with yellow mark at the base) and the mid and hind tibiae have a pale brown line on the outer side.

Du Buysson recorded *semperi* also from Luzon and Lubang, but some of his specimens from these localities, kindly sent to me by Prof. G. Ceballos, proved to be typical *luctuosa*.

Also the only specimen with a label "*semperi* det. du Buysson" in the Paris Museum, a worker from "Philippines, leg. M. von Bruner" proved to be typical *luctuosa*.

Vespa fervida Smith

1859. Smith, F., Jl. Proc. Linn. Soc. Zool., vol. 3, p. 23, ♀ (*V. fervida*; Celebes).

1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 543, ♀ and ♂ (*V. fervida*; Celebes and Timor).

This species, the most melanistic of the group, is distinguished by its large size (length of female to end of second tergite 22-25 mm, against 18-22 mm in the other species of the *luctuosa*-group), the coarse puncturation and the dense black tomentum which gives the body a dull appearance. In the female the abdomen is entirely black and rather densely covered with long, black bristles; the workers have a narrow yellow band at apex of first tergite, in some specimens also on the third tergite, and the abdomen has only the normal pubescence. Mandibles black or with small yellow mark at base.

Celebes: apparently rather common throughout the island. North Celebes: 2 ♀ Tomohon, leg. Berends ten Kate (ML); 1 ♀ Tonsea Lama, 13 Febr. 1920 (MB); 1 ♀ Tonsea Lama, 1 ♀ 1 ♂ Mt. Bugason, 300 m, 1 ♀ 1 ♂ Mapanget, 100 m, 1 ♀ 4 ♂ Kelabat, 500 m, 1 ♀ Sonder, 500 m,

3 ♂ Marinsow, 100 m, all July-Aug. 1941, leg. F. Dupont (ML); 5 ♀ Mapanget, May 1949, C. J. H. Franssen (ML); 1 ♀ Gurupahi, May 1917, W. Kaudern (ML); 1 ♀ Gorontalo, 2 ♀ Tulabollo, leg. Rosenberg (ML); 2 ♀ Toli-toli, leg. H. Fruhstorfer (MP), 1 ♀ same locality and collector, collection Pérez (MP). Central Celebes: 1 ♀ Kulawi, Nov. 1918, W. Kaudern (ML); Luwuk, 1 ♀ Aug. 1919, W. Kaudern (ML) and 1 ♀ May 1941, H. and E. Vonk (MB); 1 ♀ Palu, Dec. 1936 (ML); 1 ♀ on board "Snellius" near Mamudju on west coast, 5 Aug. 1929, H. Boschma, Snellius Exp. (ML); 2 ♀ Rantepao, 1936, 1938 (MB, ML); 1 ♀ Todjambu, 1000 m, July 1936, L. J. Toxopeus (ML). S. Celebes: 1 ♀ Udjunglamuru, May 1948, in secondary forest, van der Vecht (ML); 1 ♀ Tanette, 450 m, and 1 ♀ Manipi, 700 m, Jan. 1950, C. J. H. Franssen (ML).

Salajar Is.: 2 ♀ July 1935, leg. Sapari (ML). — Clypeus almost entirely black.

Buton: 1 ♀ Butonboloba, probably leg. P. N. van Kampen (ML). — Yellow markings of head and thorax more extensive than in the other workers. Lower half of temples with vertical yellow band; mesopleura with yellow mark beneath tegulae; metapleura with yellow mark below hind wing and two vague spots in lower part; propodeum with small mark in upper lateral angle, a larger, triangular spot in lower angle, and a squarish mark in the middle. Abdominal tergites 1 and 3 with narrow, yellow, apical band.

The occurrence of this species on Timor (a record of du Buysson, 1905, based on material in the BM) appears to need confirmation; I have not seen a single specimen in the various collections from this island which I have examined.

***Vespa basalis* Smith**

1852. Smith, F., Trans. Ent. Soc. Lond., new series, vol. 2, p. 46, ♀ (*V. basalis*; Nepal).

1905. Buysson, R. du, Ann. Soc. ent. France, vol. 73 (1904), p. 489, 495, 545, ♀♂♂, pl. 7 fig. 1 (*V. basalis*; Sikkim; Assam; Tenasserim; Sumatra).

1929. Dover, C., Bull. Raffles Mus., vol. 2, p. 48 (*V. basalis* (lapsus!), Khao Ram, Peninsular Siam).

Vespa basalis differs from all the preceding species by the fine puncturation, the non-emarginate sixth and seventh abdominal sternites of the male, the shape of the male antennae and genitalia, etc. The distribution deserves further study, for some old records may prove to be incorrect. *V. basalis* was recorded by Bingham from Ceylon and Malabar, but it was absent from an extensive collection of Vespidae recently made in Ceylon by Dr. F. Keiser of the Basle Museum. Rengel (Archiv f. Naturg. 82 A, H. 5, 1917, p. 120) stated to have seen 3 ♀ from Formosa, but Tsing-Chao Ma

(Ent. Phytop. Hangchow, vol. 5, 1937, pp. 29-34) did not include *V. basalis* in a list of Chinese species of *Vespa*.

A s s a m: 4 ♀ 1 ♂ 5 ♂ "Assam", leg. Staudinger (ML); 2 ♀ Carin Cheba, ex coll. Magretti (MP).

Y u n n a n: 1 ♀ Mengtse (ML).

S u m a t r a: Atjeh, 1 ♀ Atang Puter, 1200 m, April 1937, Leuser Exp., A. Hoogerwerf (ML). Deli, 1 ♀ Dolok Baros, Sept. 1939, P. A. van der Laan (ML); 1 ♀ Toba Lake, Oct. 1925, H. Karny (MB). West coast, 1 ♀ Mt. Singgalang, July 1878, leg. O. Beccari (MP). Benkulen, 1 ♂ Tandjong Sakti, May 1935, Mrs. M. E. Walsh (ML). Lampong Districts, 5 ♀ Mt. Tanggamus, 2100 m, 1 Jan. 1935, M. A. Lieftinck and L. J. Toxopeus (MB, ML).

It is remarkable that this species has not (yet) been collected in Malaya.

BIONOMICS OF ORIENTAL AND PAPUAN VESPINAE

1. Genus *Provespa* Ashmead

The three known species of this genus are nocturnal insects, which are attracted by artificial light, often in great numbers. They are characterized by the uniformly pale brown body and the enlarged ocelli, characters that are found in several other groups of nocturnal Hymenoptera, such as *Nyctomelitta* (subgenus of *Xylocopa*, Apidae), *Apoica* (Polybiinae, Vespidae), *Waterstoniella* (fig wasps, Agaonidae), certain Formicidae, Ichneumonidae, etc. The females and workers of *Provespa* differ in size, density of pubescence, and in *P. nocturna* also in the shape of the abdomen (see van der Vecht, 1936).

Very little is known about the habits of *Provespa*. The only available information on the prey of these wasps was obtained under abnormal conditions. During his stay in a Japanese prisoner-of-war camp near Palembang, Dr. C. J. H. Franssen observed several times how at night these wasps attacked the blue-bottle flies which occurred in great numbers around the latrines (oral communication). Jacobson (1935) once came across a nest in Sumatra, and remarked that the wasps were not particularly aggressive at daytime. Both this nest, and another one which he found in damaged condition, had been built above the ground.

In 1947 Mr. H. T. Pagden sent me some photographs of a nest of *Provespa*, probably *anomala* (Saussure), which had been built in a small rambutan tree (*Nephelium lappaceum*), about one meter above the ground (Puchong, Selangor, Malaya). The nest was spheroidal, with a diameter

of about 12 cm, and had a single entrance. It contained a queen and about 130 workers, but no males.

2. Genus *Vespa* Linnaeus

Our knowledge of the bionomics of the Oriental *Vespa* is mainly based on casual observations on some of the commoner species, such as *V. tropica*, *affinis*, *analisis*, and *velutina*. Unfortunately, the first mentioned two species have been confused for many years; they were recorded together under the name *Vespa cincta* by several authors, and it is often impossible to say with certainty to which of the two species the observations refer.

In the following review I have brought together various scattered notes from the literature, supplemented by some unpublished observations made by Mr. H. T. Pagden in Malaya, and by Dr. M. A. Liefstinck and myself ¹⁾ in Java.

Habitat.

In the Indo-Malayan area the most important features of the environment of the *Vespa* species, as well as of many other insects, are the type of vegetation and the height above sea-level.

Some of the Indo-Malayan species of *Vespa* are typical forest insects. They are relatively rare and very little is known about their habits. This group includes *V. basalis* in Sumatra, *V. mocsaryana* in Malaya and Sumatra, *V. multimaculata* in Malaya, Sumatra, and Borneo, and *V. bellicosa* in Sumatra and Borneo. Whereas the former two species have been found exclusively in mountain forests, the latter two live in the lowlands, occurring in primary forests and perhaps also in localities with a rich secondary plant growth.

Other species, although certainly originally forest dwellers, have become adapted to the artificial environment at present existing in the densely populated plains and lower hills of Java, and similar habitats in Malaya, Sumatra, Borneo, Celebes, and other islands. Here the lowland forests have disappeared, and the vegetation consists now mainly of crops, weeds, shade trees, and some ornamental plants. In Malaya, Sumatra, Borneo, and further eastward *V. tropica* and *V. affinis* are common inhabitants of such places, although these species are not lacking in denser and less artificial vegetation where this occurs, such as in the Moluccas and New Guinea. In Java and Bali, *V. affinis* is replaced by *V. analisis*, which is very common here below a level of about 1000 m, often nesting in gardens in towns and villages.

¹⁾ Some of my notes on the *Vespa* nests collected in West Java in 1932 were lost during the war.

The mode of occurrence of the two Javan subspecies of *V. analis* is of particular interest, because it is in striking contrast with that of the Malayan race of the same species, *V. analis nigrans*, which has not been found below a level of about 2000'. According to information received from Mr. Pagden, the Malayan specimens of this form "all come from localities which must have been either in jungle or surrounded by jungle at no great distance". In this connection it would be very interesting to know more about the habitat of *V. analis tyrannica*, a race that has been collected exclusively in Singapore Island.

A similar variation in the ecological requirements of the different races of a polytypic species can be observed in *V. velutina*. The various subspecies of this wasp occurring in Malaya (*divergens*), Sumatra (*karnyi*), Java and Bali (*velutina*), and Celebes (*celebensis*) are typical elements of the insect fauna of the mountain forest. In Java *V. velutina* inhabits also the cultivated areas above about 1000 m, such as tea- and cinchona-estates, but it rarely descends into the plains, and nests have never been found there. In some of the Lesser Sunda Islands, however, great numbers of the local forms of *V. velutina* have been collected in several lowland localities. I refer to the subspecies *floresiana* and *sumbana*, obtained by J. K. de Jong in Flores (1937), and by the Swiss Expedition (1949) in Sumba, respectively. Evidently these forms have become adapted to life in the plains, and we can only guess whether the more arid climate of these islands, the absence of competing species (both *V. affinis* and *V. analis* are lacking here), or both factors together, have been responsible for this remarkable change in habits. Unfortunately we do not know enough about the Timor subspecies to state with certainty whether it agrees in this respect with the forms of Flores and Sumba.

Food.

Like most other members of the subfamily Vespinae, the tropical species of *Vespa* are predaceous insects which feed their young on animal matter, mainly insects and spiders. Some species have been observed on dead meat and on plant juices, but it appears doubtful whether the *Vespa* species are as omnivorous as some of the smaller, holarctic, "yellow jackets" of the genera *Vespula* and *Dolichovespula*. Unlike the latter, the tropical *Vespa* have only very rarely been recorded as visitors of flowers. In fact, the only note that I have found concerning this point is that of Williams (1919) who wrote about the Philippine *V. luctuosa*: "I found the insect common in a banana grove where it fed at the elongate flowers of this plant."

Although some tropical species are not at all rare, exact observations on

their food habits are relatively scarce. According to Maxwell-Lefroy (1909, p. 214) the wasps of the genus *Vespa* "feed on caterpillars, mantids, bugs, grasshoppers, beetles and other insects and some constantly seek for fruit juice, sweets and such material." It is open to doubt, however, whether this and similar statements in other textbooks are based on actual observations on tropical species, or whether the list of victims has been copied from treatises on holarctic wasps. For this reason it appeared worth while to bring together the available information on the food of the tropical species. It was then found that the only insects recorded with certainty as prey of tropical *Vespa* are butterflies, moths, caterpillars, bees, wasps and flies. Although Maxwell-Lefroy (l.c.) states that "the number of caterpillars these wasps eat is apparently very large indeed and large nests probably exercise a considerable influence in keeping caterpillars down", I have found only one reliable record of caterpillars being taken as prey by tropical *Vespa*. Yet the most probable way in which the *Vespa* larvae become parasitized by Trigonulids seems to be by digesting leaf-eating insects, presumably caterpillars, which contain the eggs or young larvae of these parasites (see p. 70). Evidently the insect diet of *Vespa* is much more varied than it would appear from the following notes.

Butterflies and moths. — In Bengal, Rothney (1877a) noticed "*Vespa cincta*" (probably *V. tropica haematodes* Bequaert) "to be especially fond of small species of "skipper" butterflies, about the size of *H. sylvanus*; they hold these butterflies (after capture) sideways, their legs grasping firmly the roots of the two wings on the side pointing downwards, then they strip off the two wings on the other side that point upwards, and then work with their mandibles from the thorax to the apex of the abdomen squeezing out all the juices, and then when completely sucked dry they drop the body with its two remaining wings and fly away. I have watched *V. cincta* flying with "skipper" in this way, but they appear to prefer to retire to some tree or bush for the better enjoyment of their feast."

The capture of a small Pyralid moth by "*Vespa cincta*" was noted by E. E. Green (1905). The wasp "settled on a branch, supporting itself head downwards by its last pair of legs only, using the others to manipulate the insect. The wings and the legs of the moth were shredded off and the rest of the body chewed up into a pellet, which was then carried off, doubtless to feed the grubs in the nest". Dover (1921) wrote: "cases of hornets ("*Vespa cincta*") eating small moths are not very common. I have on several occasions kept an Indian Hornet and a Pyralid together in a breeding cage, and have asked several people who are keen observers if they have seen a wasp eating a moth, with absolutely negative results. On one occasion, how-

ever, I saw this wasp capture the cosmopolitan Arctiid, *Deiopeia pulchella*, denude it of its legs, wings and head, and fly off with the body, a mode of capture somewhat different from the case cited by Green”.

In Java, Hansen (1922) observed how a wasp (“tawon endas” = *Vespa* spec., probably *V. tropica tropica*) which had captured a butterfly, bit off the wings and flew away with the body of the victim.

Caterpillars. — Leefmans (1922) observed a wasp (“*Vespa cincta*”) capturing a diseased caterpillar from a *Nephelium* tree; the wasp consumed part of its prey on the spot (another part was dropped) and then flew away. The name of the caterpillar was not mentioned, but very probably it was *Tarsolepis sommeri* Hbn., a pest of *Nephelium* which is very susceptible to disease.

Bees. — In Almorah, Kumaon, Hewett (1889) observed a battle between *Vespa magnifica* and a swarm of bees which evidently intended to settle. “A wasp would suddenly come across a bee, or vice versa, and after gyrating round one another for a second or two, they closed and came tumbling down the ground; then, as it evidently happened as far as I personally saw, the wasp was the victor, and clutching his victim in his arms (sic!), he flew away with him, and on my telling the story to some of the hillmen, they said that the wasps ate the bees. The battle started about 9 P. M. and lasted till sunset.”

Driberg (1906) noted in a paper on the Ceylon honey bee: “Mr. A. P. Goonetilleke of Veyangoda has been greatly troubled with hornets raiding his hives. They kill the bees, but do not appear to care for the honey”. It is uncertain which species was involved here.

According to Fletcher, “*V. cincta* and various other large *Vespa* spp. are determined captors of honey-bees as these enter or leave the hive.” (Gravely, 1915).

Leefmans (1922) often saw “*Vespa cincta*” flying above the flowers of *Antigonon* in his garden; the wasps hunted for *Trigona*, but were not very successful.

A note by Ghosh (1924) probably refers to the race of *Vespa velutina* occurring in Burma: “At Maymyo honey bees are troubled by a wasp, locally called *padu* (apparently a variety of *Vespa auraria*). The wasps hover in front of hives, catching and killing bees as they fly out or into the hive. They are common in the rains but disappear in winter.”

The following observation was made by me in Bogor, Java, in 1932: A comb of *Apis javanica* End., covered with bees, was brought into a cage containing an inhabited nest of *Vespa analis*. Immediately the wasps became very excited, rushed out of the nest, attacked the bees and killed and con-

sumed them all within a few minutes. No other insects roused the wasps to such activity.

My colleague Dr. M. A. Lieftinck kindly supplied me with the following notes on this subject.

"On October 1, 1952, in an effort to obtain the contents of a nest of the wild honey-bee *Apis javanica* End.(?), breeding in the stem of a living forest-tree at Tjibodas (Mt. Gedeh, W. Java), workers of *Vespa velutina*, three to five at a maximum, were observed for two hours flying in close vicinity of the entrance hole of the nest. Though the sky was overcast and temperature low at this altitude (1450 m), bees and wasps were both very active. During most of the time one or two wasps were observed hovering almost motionless in the air for many minutes only a few inches away from the nest, facing the entrance. Every now and then a wasp would swerve away in rapid pursuit of an emerging bee, but in no instance the attack was seen to meet with success.

On July 25, 1953, whilst observing a colony of the stingless bee *Trigona atripes* F. Smith which nested in a hollow trunk of iron-wood (*Eusideroxylon* sp.) in a forest swamp near Pemantan, southern Borneo, I was struck by the repeated appearance of *Vespa multimaculata* approaching the trumpet-shaped chimney of the nest, evidently in an attempt to catch the little bees. The weather was dull and it drizzled most of the time. Three wasps were taken on the spot, one shortly after the other, and no other wasps were seen anywhere else in the neighbourhood".

It appears from these notes that social bees are probably a common element in the diet of various tropical species of *Vespa*. The capture of solitary bees has been noted by Dover (1921): "... once I saw *Vespa cincta* capturing the solitary bee *Megachile lanata* as it emerged from its cartridge-shaped mud nest, which it builds in the back of books, etc. on Barkuda. On another occasion... I saw one of these hornets sitting on a leaf, with its sting inserted into the thoracic region of the bee *Nomia oxybeloides* almost exactly as shown in the illustration..." (the wasp represented in the accompanying drawing is *V. tropica haematodes*).

Wasps. --- A battle between *Vespa cincta* and another social Vespid, *Polistes hebraeus*, was recorded by Cunningham (1888). Gravely (1915) received the following note from Fletcher: "Last July, when travelling by train (in India), a specimen of *Vespa cincta* flew into the carriage carrying a *Polistes hebraeus* which it had captured". Dover (1921) reported: "On Barkuda Island in the Chilka Lake I have on two occasions seen *Vespa cincta* flying along with a deed *Polistes stigma* which it carried with the front legs, and I have witnessed a similar incident near Chandipore, Orissa."

In Java and Malaya, *Vespa tropica* has been observed several times to rob the nests of other species of social Vespidae. De Ruiter (1916) described an attack of this wasp on a nest of "*Icaria spec.*" in Java. He saw how the invader opened a cell with its mandibles, carefully removed the pupa, and consumed it without being disturbed, although there were several "angry" *Icaria* wasps on the nest. Evidently these smaller wasps did not dare to attack the *Vespa*. Jacobson (1917) confirmed this observation, and remarked that *V. cincta* (here *V. tropica*) not only robs the pupae, but that it also tears pieces from the comb to consume the larvae present in the cells. H. Schroo (1917), who recorded another attack of an *Icaria* nest by *Vespa tropica*, noted that the wasps, after having consumed the pupae and larvae, bit off the empty cells, and he supposed that they used this material for their own nest. Personally, I have seen *Vespa tropica* attack the nests of *Ropalidia picta* (Sauss.) and *Parischnogaster mellyi* (Sauss.).

Recently, Mr. H. T. Pagden succeeded in making some photographs of this wasp, taken in the very act of robbing a nest of *Parapolybia varia* (Fabr.) (= *orientalis* (Sauss.)) (pl. I fig. 3).

According to Williams (1919), the Philippine *V. tropica deusta* is "a most destructive creature and a perfect bane to some of the *Stenogaster* and *Icaria* whose nests she destroys with impunity." This author describes the attack of one of these wasps on the covered nest of a small pale yellowish *Icaria*, and an attempt of another specimen to open a clay nest of "*Sceliphron intrudens*" (evidently not this species, but the Philippine subspecies of *Sc. javanum* Lep.): "The safe-breaker, stout-jawed as she was, chewed vainly for five minutes at the cement-like material before she flew off in disgust."

Flies. — Concerning *V. velutina divergens* in Malaya, Tweedie (1941, p. 60, under *V. auraria*) wrote: "The wasp is predatory, like all the social wasps, and feeds largely on flies. In Cameron Highlands it has been observed catching the Biting Stable Fly (*Stomoxys calcitrans*) on the backs of pigs and also the Blow Fly (*Chrysomya megacephala*) both agricultural pests: a redeeming feature in an otherwise unattractive character".

In 1935, I observed several specimens of *V. velutina velutina* hunting for Tachinid flies in a flax field near Pengalengan (1400 m) above Bandung, Java. These flies had developed in the caterpillars of *Heliothis obsoleta* and *Cirphis unipuncta* (Lep., Phalaenidae or Noctuidae), which a few weeks earlier had been extremely numerous, destroying most of the crop. Wasps that had succeeded in capturing a fly hung themselves with one hind leg from a thin branch of a shrub or a tree, consuming their prey which they were holding with the other legs.

Williams (1928) calls the Philippine *V. luctuosa* "a useful if clumsy enemy of obnoxious flies", after having written in an earlier paper (1919) that "a couple of these wasps made repeated clumsy and unsuccessful attempts to pounce on blue-bottle flies which were feeding at a bunch of decayed banana fruit".

Spiders. — In the forest near Tjibodas (1500 m), Mt. Gedeh, W. Java, I once saw a *V. velutina velutina* capturing a spider from a web close to the ground. The struggle lasted only a few seconds.

Other food. — According to Wroughton (1889, p. 35), "*Vespa cincta*" is attracted by sweetmeat, although other authors state that this is more especially a characteristic of *V. orientalis* Linn., which appears to be the commoner species in Northern India. Wroughton wrote: "*Cincta* is the big dark brown wasp with a broad yellow band, which may be seen in numbers about sweetmeat-sellers' shops. *Cincta* is said to loot the pupae from the nest of other Vespidae, but I confess in my mind he is always connected with a tray of "dudhpendis", "jelebis", &c., in the hands of a very dirty retail sweetmeat seller."

Near Barrackpore, Bengal, Rothney (1877a) observed "*Vespa cincta*" feeding on the juice flowing from wounds in the trunks of two date palm trees: "the trunks of these trees, just below the crown, had been cut all round in notches by the natives for the collection of the juice (Talár-Ros) in little earthenware pots (Ghurás); these pots had been taken away, but there was still sufficient juice to attract large swarms of the common Indian hornet (*Vespa cincta*), so that all the cut or bare portions of the trunks were covered by dense buzzing struggling masses of these insects."

Bartels (1938) observed great numbers of *Vespa cincta* (certainly *Vespa tropica*) on the "bleeding" stems of two tall trees (species not mentioned) in Southwest Java.

Horne (1870) stated that in the North-West Provinces of India both *V. orientalis* and *cincta* are very fond of ripe fruit, such as peaches, grapes, and apples. "The *Vespa velutina* also indulges in these luxuries, and is especially fond of the hill-apricot."

Near Padang, Sumatra, Leefmans (1922) saw great numbers of wasps ("*Vespa cincta*") feeding on the decaying meat on cattle bones.

On Mount Pantjar near Bogor, Java, W. C. van Heurn (1931) observed some wasps (later identified by M. A. Lieftinck as *V. analis analis*) flying to and from the putrifying body of a boar; he does not say, however, whether these wasps fed on the carrion itself or on the numerous fly larvae which it contained.

One week afterwards, the same spot was visited by Lieftinck, who was

surprised to find only a few scattered bones surrounding a vast number of dipterous puparia, over which were seen several low-flying *Vespa analis*, which were probably searching for remains of the carrion for food.

Colony foundation, castes and periodicity.

In some tropical Vespidae new colonies are founded by a swarm of wasps, consisting of one or more females and a number of workers, in certain genera perhaps of females only. This phenomenon has been observed especially in South American Polistinae and Polybiinae (see Richards and Richards, 1951, p. 3, etc.).

Some authors have supposed that the colonies of tropical *Vespa* are founded in the same way, but there appears to be no reliable evidence to support this view. Koningsberger (1915), in a discussion of the Javan *Vespa* species, stated that "when the nest tends to become overcrowded, a number of workers swarm out under leadership of a few queens, in order to found a new colony elsewhere", but it is very doubtful whether this communication was based on actual observations. So far I know, Koningsberger's observation that the whole swarm may sometimes be seen hanging from a branch or against a stem, has never been confirmed, and I suppose that it was either based on incorrect identification (confused with *Apis dorsata*?) or that he has seen wasps whose nest was destroyed.

Near Barrackpore, Bengal, Rothney (1877b) observed the activities of *Vespa affinis* (his "*Vespa cincta*" was almost certainly this species) on a young nest: "I have carefully watched the building of an extremely small nest of this species in a rose bush in my compound: the nest consisted of a single layer of cells, and with its paper covering, was not larger than an ordinary lemon; the hornets working at the nest were only seven in number at any one time; they obtained the material for their paper-making from some old teak beam in my verandah, at which they were continually rasping; I distinctly watched them "build" up their cells from a ground plan, watching the walls increasing through a strong glass, generally two hornets worked at the cells and two at the outside covering, the rest flying about or looking on". Bequaert (1936) remarked that this observation suggests "that *V. tropica* or *V. affinis* may perhaps start a new nest either by several fecundated females, or queens, working in unison, or by a swarm consisting of a queen and a number of workers." In my opinion, it is equally well possible that the colony consisted of a female together with the first workers which had developed in the observed nest. There is one obscure point, however, in Rothney's account: in some other species (*V. analis* and *V. velutina*) which we have observed in Java, the nest constructed by a single queen has

an envelope which, at the time of appearance of the first workers, hides the cells so completely that the further construction of the combs cannot be observed. Evidently, further observations on young nests of this species are very desirable.

During my stay in Java I have seen five or six young nests of *Vespa analis* and three of *V. velutina*, but I have never found anything to suggest that the nests were not started by a single queen. In a discussion of the nesting habits of "*Vespa cincta*" Jacobson (1922) stated that every new colony is founded by a single queen. A photograph of a young nest of *Vespa analis tenebrosa*, with the queen working on the envelope, was published by van den Bosch (1936). Concerning *Vespa luctuosa*, Williams (1928) wrote that this wasp "will occasionally commence her paper nest under the eaves of some nipa house where the environment is not too civilized; one such insect, a queen of course, built several cells from the end of the stout pedicel and laid an egg in each; the work, however, progressed slowly and, while she guarded her nest by resting on the cells for long periods, she eventually deserted this embryonic household."

In most of the Oriental species of *Vespa* the queens can be easily distinguished from the workers by their larger size. In addition, there may be more or less pronounced differences in coloration (see under *V. velutina velutina*, *V. luctuosa*, and *V. fervida*). In *Vespa tropica* and *Vespa analis*, however, there may occur so many specimens which are larger than the average worker, but smaller than most of the queens, that the castes cannot be reliably separated. So far I know, the nature of such transitional specimens has not yet been determined by dissections of samples from nests. The males appear together with the new generation of females in the final phases of a colony; they are much less frequently observed in the field and consequently are much rarer in collections.

Unlike the northern species, the tropical *Vespa* do not appear to have a seasonal periodicity. In West Java nests of *V. analis* and *velutina* can be found at any time of the year in various stages of development.

Nest construction.

The nests of the tropical *Vespa* species are very incompletely known. The following discussion is restricted to the nests of *Vespa analis*, *velutina*, *affinis* and *tropica*, with an occasional remark on the nests of *Vespa luctuosa* and *mandarinia*.

Like the Vespinae of temperate countries, the tropical species show considerable variation in the selection of the nest site. Of a few species it is definitely known that they build aerial as well as subterranean nests.

Vespa analis and *Vespa affinis* apparently always build their nests in the open, as a rule on the branches of trees or shrubs. The nest of *Vespa analis* shown on plate III was built in a hedge of *Hibiscus rosa-sinensis* L., only a few decimeters above the ground, but often the nests of this species are constructed high up in trees, like those of *Vespa affinis* pictured on plates IV and V. *Vespa velutina* also nests in shrubs or trees at varying height, but a few times nests of this species have also been observed in underground situations. Several times queens of *Vespa velutina* attempted to start a nest under the overhanging edge of the roof of the resthouse in the mountain garden "Tjibodas" on Mount Gede, West Java, but the nests were always destroyed at an early stage on account of the aggressive habits of this species. According to Williams (1919) the Philippine *Vespa luctuosa* builds large paper nests on trees and bushes.

In contrast to these species, *Vespa tropica* appears to nest preferably, perhaps exclusively, in sheltered situations, such as in hollow trees, in the attics of buildings, etc. In a short account of the habits of this wasp in Malaya, Pagden (1952) wrote: "Only on one occasion did the writer see specimens of *tropica* which were taken from a known nest, and that nest was inside the roof of a house". Later he saw a nest of *Vespa tropica* which was built underground, apparently the first recorded instance of a subterranean nest of this species.

The giant of the genus, *Vespa mandarinia* Smith, was described from Tein-tung, near Ning-po-foo, China, where it was discovered by Mr. Fortune, who wrote to Smith: "this insect constructs large globular nests in the topmost branches of trees" (Smith, 1852, p. 39). Bingham (1888) however, characterized the Burman race of this species, *Vespa magnifica* Smith, as a "huge hornet making its nest in hollow trees".

The material from which the nests are made is generally taken from the wood or the bark of dead trees and shrubs, from wooden poles, posts, etc. There is one exception to this rule, for in India *Vespa basalis* is known to attack living trees for this purpose. This was first reported by Fletcher (1920, p. 36) who had received this species from the Forestry Research Station, Dehra Dun, as doing damage by removing the bark of young *Eucalyptus stuartiana* trees growing in the Cantonment of Dehra Dun. Fletcher himself thought it rather unlikely that the hornets should strip living bark from the trees, and suspected that the trees were dead, but Beeson (1941) confirmed this observation, as follows: "*Vespa basalis* kills twigs and branches of trees by gnawing away the bark in patches and rings, removing it layer by layer until the wood is exposed; the chewed material is used in the fabrication of the nest. Among the species of trees chosen

are *Calliandra houstoniana*, *Eucalyptus* spp., *Poinciana regia*, *Schrebera swietenioides*, *Tecoma stans*. A tree is visited continuously for several weeks”.

In the early stages the nests of the tropical species appear to be very similar to the aerial nests of certain Vespinae living in temperate countries. The nest made by the queen of *Vespa analis* is pear-shaped; it consists of a single comb surrounded by a simple envelope which has an opening in the lower, narrowed end. Du Buysson (1905) published schematic figures of two such nests from Java, one with a small comb of about 7-10 cells and an incomplete envelope, and the other in a more advanced stage of development. The photograph of a young nest of *Vespa analis tenebrosa*, published by van den Bosch (1936), has already been mentioned. Young nests of *Vespa velutina* are very similar to those of *V. analis*. According to Jacobson (1922) the queen of “*V. cincta*” (probably *V. tropica*) first builds a pedicel with one cell, and then begins to work on the envelope. As the number of cells increases, new strips of paper are added to the nest wall till this is approximately spherical, often somewhat elongated below, where the entrance is situated.

After the first workers are born, a second comb is built under the first, and the envelope is enlarged by the addition of new scales on the outer side. In this respect the *Vespa* nests resemble those of the *Vespula* spp., in contrast to those of *Dolichovespula*, where the nest wall remains composed essentially of separate layers of paper (Duncan, 1939, pp. 150, 151). Unfinished scales may suggest the presence of openings in the nest wall, and some authors have indeed supposed that the interior of the nest would have several connections with the outside world. Leefmans (1912), discussing the possible presence of “ventilation channels” in the wall of a nest of *Vespa affinis*, remarked that he had never seen these openings used by the wasps, and Jacobson (1922) correctly stated that the nest wall is always closed except for a single entrance hole.

As the growing combs require more space, the inner side of the nest wall is being demolished. Except at the top, the nest wall remains a few layers thick throughout the life of the colony. If the nest is aerial, and freely suspended from a branch, the shape is approximately spherical so long as the nest contains only two combs. A nest of *V. analis* in this stage of development is shown in fig. 1 of plate II; it was 17 cm high and 14 cm wide. The first comb measured 10 cm in diameter and consisted of 148 cells, of which 95 contained pupae or had already produced workers; the second comb (43 cells) had only 2 closed cells, the others containing larvae or eggs.

In this nest the roof is already slightly thicker than the sides, showing

the beginning of a development that appears to be characteristic of the aerial nests of some, perhaps all, tropical *Vespa*. As the nest continues to grow, more and more scales are deposited on the roof or top of the nest, where the nest wall is not demolished on the inner side. In this way the top becomes more and more conical, and the nest acquires the shape of a droplet, or of a pear with the narrow end directed upward. The photographs of a nest of *Vespa analis* on plate III show this development very clearly. In some cases the conical roof of the nest is built along a branch, as in the nest of *V. affinis indosinensis* on plate IV, and in that of the same race from Penang in the Paris Museum (see du Buysson, 1905, p. 535 and pl. 13). In other nests the conical roof is entirely free, as in the nest of *V. analis analis* figured by Lieftinck (1936a) and in that of *V. affinis indosinensis* on plate V of this paper.

The photographs of the nests of *Vespa velutina* on plate VI demonstrate that this species also uses a considerable amount of building material for the construction of a roof above the first comb. The structure of this roof is shown in the smaller nest, where part of the sponge-like tissue has been removed. In the larger nest, which is held upside down, the distance from the top of the nest to the first comb was about 20 cm, and from here to the bottom of the nest 55 cm.

The only non-tropical Vespinae which are known to build similar structures appear to be the American *Dolichovespula maculata* and the allied European *D. media*. In nests of these species "sheets of paper of small extent are laid down in an overlapping fashion across the top of the nest, producing the well-known cellular cap of these nests" (Duncan, 1939, p. 147). The photographs in Duncan's paper show, however, that at least in *D. maculata* the cellular mass is much less extensive than in the tropical species discussed above.

Up to the present, the remarkable structure of the roof of the nests of tropical *Vespa* has not received much attention. Chopra (1925), describing a nest of *Vespa affinis*¹⁾ with a pronounced conical cap, noted only that the envelope consisted of a greater number of layers in its upper parts than elsewhere. But Bequaert (1936) was apparently struck by the unusual appearance of this nest and wrote in a footnote to a summary of Chopra's paper: "The figure of the nest with part of the envelope removed on one side, shows about nine tiers of cells in the lower, swollen half, while the narrower, upper half seems to be filled entirely with a sponge-like mass of

1) The species was called "*cincta*", but recently Dr. A. P. Kapur examined the wasps collected together with the nest and kindly confirmed that they belong to *affinis*.

paper layers and air-pockets. The purpose of this arrangement is not clear".

In my opinion we must regard the conical, fortified roof of the nests of these species as an adaptation to climatic factors, more particularly to the heavy tropical rains. It seems very doubtful that the large aerial nests could withstand the force of a tropical shower if the upper part of the nest wall would have remained as weak as the sides. In this connection it will be of special interest to learn more about the structure of the nests of the Palearctic races of such species as *V. affinis* and *analis*.

Sometimes *Vespa analis* builds a nest without a conical roof, but this appears to happen only when the environment prevents the construction of a cap above the first comb. A good example is the nest of the subsp. *tenebrosa*, described and figured by de Fluiter (1941). This nest was attached by a strongly thickened pedicel to the under side of the gutter at the roof of a house in Widodaren, East Java, and here all building above the base of the pedicel was physically impossible. In 1937 I saw a similarly shaped nest of the subsp. *analis* at the under side of a palm leaf in a garden near Tandjongkarang, South Sumatra.

Normally the nests have only one entrance hole. In a very early stage of the nest this hole shifts in position from the bottom of the nest to the side; usually the entrance in old nests is relatively high up on the nest wall. The nest of *Vespa affinis*, described by Chopra (1925), is said to have two "nearly circular openings on the two sides near the base".

In aerial nests new combs are usually started from the centre of the lowest comb, but I have seen one exception to this rule. In May 1932 I obtained an aerial nest of *Vespa analis* which had a very abnormal shape, the lower part being not evenly rounded, but abruptly truncate. The nest contained two normal combs, and a third one (plate II fig. 2) that was composed of five small combs, partly grown together. These had been attached, each with its own pedicel, at different points of the second comb. The cause of these irregularities became clear when I discovered that a few stones had become incorporated in the nest. Evidently the nest had at one time been damaged by these stones, thrown into it, to such an extent that the lower part of the nest, below the second comb, was lost. When the wasps had repaired the damage after this accident, the construction of new cells had apparently been so urgent that they had started at several points.

Duration of life of colonies.

Very little is known concerning the duration of life of the colonies of tropical Vespinae, but there is certainly no reliable information to support the view of Carl (1934) that the nests of these wasps are perennial. This

author found in December 1926 only a small number of non-aggressive workers in a nest with a damaged envelope of "*Vespa cincta*" (probably *V. affinis*) in the Nilgiri Hills in South India, and concluded: "Tout indiquait, dans ce nid encore, une phase de repos dans une colonie perenne, alors que la colonie des frelons des climats tempérés est annuelle et que seul des ♀ fécondées isolées hivernent." In my opinion, however, there can be little doubt that this was nothing but an ordinary annual nest in its final phase, after the emergence of the new generation of queens and males.

The nest of *Vespa affinis* from Calcutta, described and figured by Chopra (1925), reached its maximum size after about eight months; it was then 109 cm high and contained about a dozen combs. Stebbing, in his popular account of insect intruders in Indian homes (p. 148), figured a nest which contains at least 13 combs of considerable size; it was probably built by the same species, and its construction may have taken a little longer. The nest of *Vespa affinis* from Penang, described and figured by du Buysson (1905, p. 535, pl. 13), contained 12 combs, but was smaller in size than that of Chopra.

According to Horne (1870), the nest of "*Vespa velutina*" (he probably meant *V. auraria* Smith, a species of Northern India which may prove to be a subspecies of *V. velutina*) may even surpass that of *V. affinis* in size: "A nest I measured exceeded four feet in length, and, when the outer covering was broken away, showed range upon range of cells ..." The largest nest I have seen was that of *V. velutina*, shown on plate VI. It contained 11,912 cells in 11 combs, and its height was 75 cm. The age of this nest is unknown, but unless the growth rate of this species is much different from that of *V. analis*, it may be estimated at about seven to eight months. The nest yielded a considerable number of queens and males, and this may be regarded as an indication that it would probably not have existed longer than a few months more.

The nest of *Vespa analis*, shown on plate III, attained its maximum size after about seven months, when the nest contained nine combs and was nearly 80 cm high; the colony then gradually died out and the nest began to deteriorate in the course of the ninth month.

De Fluiter (1941) gave a detailed account of the contents of a nest of *Vespa analis tenebrosa*, consisting of eight combs with altogether about 3050 cells. Most of these cells were open, and contained eggs or larvae, but the majority of the cells in the two oldest combs was empty. The youngest comb was inhabited by old and fullgrown larvae, but did not contain any eggs or young larvae. The total number of closed cells was 690; they contained 145 larvae and 545 pupae or teneral wasps. Detailed examination of the last

group showed that it consisted of 3 females, 157 workers, and 385 males.

The high percentage of males, together with the presence of empty cells in the oldest combs and the absence of eggs and larvae in the youngest comb of the nest, strongly suggest that the life of this colony was gradually coming to an end.

It would appear from these observations that the colonies of *V. analis* tend to become less extensive than those of *V. affinis* and *velutina*, but further observations on this subject are much desired.

Aggressiveness and effect of sting.

The various species of *Vespa* show markedly different reactions with regard to disturbance of their nests.

Vespa analis is probably one of the least aggressive species. In Java it often builds its nests in gardens in towns or villages, but I have never heard of anybody being attacked by this species. The nest shown on plate III was built in a hedge in the garden of the Institute for Plant Diseases and Pests at Bogor, close to the ground; several people passed here daily at a distance of only two meters, but nobody was ever stung. It even proved possible to cut away some branches in order to make the nest better visible. As soon as one of my assistants, who volunteered to carry out this work, had cut a branch with a rapid snap of a pair of pruning scissors, the wasps hurried out of the entrance and ran in all directions over the envelope, angrily buzzing. After a short time the wasps quieted down and returned to the interior of the nest, and another branch could be cut by the assistant, who had meanwhile remained hidden under a cloth close to the nest. When a nest is more seriously disturbed, the wasps will undoubtedly fly out of the entrance and carry out an attack. The inhabitants of a medium-sized nest, which was placed in a large cage of wire-gauze, showed this reaction very promptly when a hand or a piece of cloth was moved rapidly over the wall of the cage. The wasps then squirted out of the entrance of the nest like bullets from a machine-gun and rattled against the gauze.

Very probably *Vespa velutina* is much sooner provoked to this kind of reaction, for in Java this species, the notorious "engang", is much feared on account of its frequent attacks on man. In tea estates this species may even become of economic importance, because considerable areas of the crop must remain unpicked until the wasp nests have been destroyed.

In 1936 Dr. C. G. G. J. van Steenis gave me some data on the aggressiveness of this species in Java. The late Dr. L. J. Toxopeus told him that an assistant of the Topographical Service had been killed by this wasp in Prigi, East Java. According to a certain Mr. de Groot a planter of an estate near

Pengalengan had met with the same fate. The report of an excursion to Mt. Patuha near Bandung in "De Tropische Natuur", vol. 19, 1930, p. 219, contains the following note: "Some Bandung tourists had been seriously stung by the notorious wasp occurring in this area (undoubtedly *Vespa velutina*!, v. d. V.) and were transported back home more dead than alive". Later, Dr. van Steenis was informed that one of these people had not survived the attack. In 1936 the wife of a high government official died from the stings of these wasps which attacked her when she visited a crater near Garut.

Fortunately the effects of the attacks of *Vespa velutina* are often less serious than in the above mentioned cases. On one of his excursions to the top of Mt. Gedeh-Pangerango, West Java, Prof. Dr. W. M. Docters van Leeuwen and his wife were stung by several specimens of *V. velutina* near Kandangbadak (2400 m), but after having suffered from high fever during a few days, they recovered completely. The newspaper "De Locomotief" of 22nd June 1934 related how two ladies were attacked by a swarm of wasps while rowing on the lake near Pengalengan. After the boat had capsized by their movements, one of the ladies managed to get rid of the wasps by swimming under water, but the other was stung by several wasps. The next morning, however, the patient was already feeling fairly well. One of the participants of an excursion to the solfatares on Mt. Salak near Bogor was stung by 15 wasps (*V. velutina*), but although only half of the wounds were treated with ammonia, the victim of the attack, a girl, did not suffer from swellings or fever (van Steenis, 1936). Dr. van Steenis himself was stung by wasps on several botanical collecting excursions, in Atjeh and the Ranau district in Sumatra, on the mountains Salak and Gedeh in West Java, in Northwest Bali and in the Anambas Islands. In most cases the attacking wasps were *V. velutina*; in the Anambas Islands he probably met with *V. affinis* (L.) or with a smaller social wasp like *Polybioides raphigastra* (Sauss).

These notes demonstrate that *V. velutina* is an extremely aggressive and dangerous insect. The effects of an attack are likely to be more serious when it is carried out by a great number of wasps, but the physical condition of the victim also appears to be of importance. It has been suggested that people with a weak heart should be especially careful in this respect.

Usually the wasps do not attack unless the nest is disturbed, but this appears to happen very easily when it is approached too closely. Entomologists will as a rule discover a nest soon enough to avoid this danger, because they are more likely to notice the peculiar type of flight of the wasps in the neighbourhood of the nest. People not paying special attention to these insects run a greater risk.

The Malayan form, *V. velutina divergens*, is probably not less aggressive than the Javan race. Tweedie (1941, p. 60, under *V. auraria*) wrote: "This is the only species of animal by which I have ever been wantonly attacked in Malaya. While hunting for specimens among fallen timber in the Cameron Highlands I must have inadvertently approached a nest (I never saw it) and was set upon and put to ignominious flight (by far the better part of valour in such circumstances) by a swarm of these wasps. They settled in numbers on my clothes and puttees which they attacked ineffectively and I was lucky to receive only one sting just below the knee. It was painful at the time and the ankle was swollen for two days but I experienced no other symptoms".

The following note by Horne (1870) on "*Vespa velutina*" probably refers to the allied species or race *auraria* Smith, an inhabitant of Northern India: "A bullet incautiously put through a nest brings down a swarm of the inhabitants, whose stings are most venomous and often dangerous to life. They will follow a party for miles through the densest jungle, and are said often to kill animals and, even, men".

Bingham (1888), discussing the occurrence of the gigantic *Vespa magnifica* (a race of *V. mandarinia*) in Burma, stated that the Burmans and Karens hold this wasp in great fear. "In investigating a nest too closely I was once stung by three of these insects in the face. The pain was something dreadful; my whole face and head swelled, nausea and violent retching followed, and it was not till twenty-four hours afterwards that the inflammation began to subside. For two months after I was stung I felt the effects, in a numbed feeling on the forehead and cheek, where the stings had entered."

In Medan, North Sumatra, I saw in 1954 a large nest of *Vespa affinis* in a tree about 4 meters from the ground above a busy road, where every day passed an almost continuous stream of various kinds of traffic, and this gave me the impression that *affinis* is not a very aggressive insect. Jacobson, however, had a most unpleasant experience with this species during a collecting excursion with W. C. van Heurn in Simalur Island, west of Sumatra. The following is a condensed translation of his account of this incident (1922): "On a small island in the bay of Sinabang we had discovered a large nest of *Vespa cincta* (actually *V. affinis*! v. d. V.) in a small tree. The island was only 40-50 square meters in size, and had a very rough surface consisting of sharp blocks of coral. I went ashore and approached the nest, after having taken care to cover my head and shoulders with a butterfly net. Standing close to the tree, in which the nest was built at a height of less than three meters, I was thinking how we could procure the

nest, when I happened to tap on the stem of the tree with my chopping-knife. This had the unexpected effect that a swarm of wasps left the nest and attacked me. Curiously enough, this attack was directed entirely on my head, whereas my bare hands did not attract the wasps. Very soon several specimens managed to get under the net and reached my face and neck. I succeeded in killing some of these by pinching them between my fingers, but yet I received 15 stings in my neck and the back of my head, and even one in the acoustic duct. I felt as if my head would burst and the fierce pain made me perform some kind of tarantella dance. Fortunately the attack came then to an end. During the first half hour the pain was unbearable, while ear and neck swelled to improbable proportions. My neck was like that of a bull and one ear grew to $1\frac{1}{2}$ times its normal size. Fortunately the swollen parts shrunk down to normal dimensions within a few days, and I did not suffer from any after-effects".

In the same paper Jacobson tells that at Padang, Sumatra, a horse was killed by a swarm of wasps which had been roused by some boys who catapulted a stone into the nest.

In Java *Vespa tropica* is not particularly aggressive, and reliable information on attacks by this species is extremely scarce. Perhaps the following note on "*Vespa cincta*" by Bristowe (1932) is referable to the subsp. *leefmansii*: "The Laos of North Siam say that to be stung by one of these makes one's hair go white. The statement that a few stings are liable to cause death is authentic, I believe..."

Enemies.

Garretsen (1923) found a wasp ("engang" = *Vespa velutina*) attacked by a fungus which was identified by Dr. Morgenthaler as *Isaria sphaecophila* Ditm., but this was rectified by van Overeem, who according to Bernard (1923) gave as the correct name: *Hirsutella saussurei* (Cooke) Sparse (= *Phaeoisaria gracilis* Vosseler & von Höhnelt). Boedijn (1938) published a picture of this fungus on "*Vespa velutina*", but his figure appears to represent a worker of *Vespa tropica*.

In June 1932 I bred a hitherto unidentified Rhipiphorid beetle from a nest of *Vespa velutina* collected near Telaga Warna, Puntjak Pass, 20 miles from Bogor, West Java. The female is entirely black; the male has brown elytra and strongly pectinate antennae. I got the impression that this is a very rare insect, for I obtained only two specimens from the six or seven nests from which I tried to breed parasites at that time.

The Trigonalid *Baraeogonalos* (= *Nippogonalos jezoensis* (Uchida) was found in somewhat greater numbers, but nevertheless this remarkable insect

is also very rare, and it was never observed in the field. In 1932 I obtained 7 specimens from a nest of *Vespa analis*, containing 1900 cells in 5 combs, and 8 specimens from a slightly smaller nest of the same species. A large nest of *V. velutina* (pl. VI fig. 2) yielded 10 specimens of this parasite, and a small one 2. All these nests had been collected near the Puntjak pass, Mt. Gedeh, West Java, at about 1200-1400 m above sea level. In *analis* nests collected in the lowlands no parasites could be found.

The remarkable life history of this Trigonid is only partly known (van der Vecht, 1933, 1934). Wasps bred from *Vespa* combs mated in the laboratory, and the females deposited great numbers of minute eggs in the margins of the leaves of various plants. Each egg is laid in a small incision, punched into the leaf tissue by the abdomen which acts as a pair of pincers, the basal spine resting on the upper surface, the tip being curved under the margin of the leaf. When nothing happens to the leaf, the eggs do not hatch, but by dissecting a caterpillar which had fed on some of these leaves, we found a few specimens of a "microtype first-instar" larva in its body, very similar to the larva of *Poecilognathus maga* Teranishi figured by Clausen (1931, 1940). Presumably the eggs hatch only in the body of an intermediate host, which must be brought to the *Vespa* nest and fed to the larvae in order to make the further development possible.

In the *Vespa* nests the Trigonid larvae were found singly as internal parasites in the wasp larvae. The parasite larva emerges after the host larva has closed the cell; it pupates in the upper half of the cell, after having separated this from the lower half by a silken partition. This lower half contains the remains of the host larva; it appears to be opened and cleaned by the *Vespa* workers soon afterwards, for we could often find the parasites by looking for open, shallow cells with a white bottom. The adult Trigonid emerges by biting a hole in the partition with her mandibles; the *Vespa* workers sometimes investigate the parasites with their antennae, but allow them to leave the nest unhindered.

The excellent defense mechanism of the Vespinae does not always protect them against being eaten by certain species of birds. Mason and Maxwell-Lefroy (1912) found that *Vespa orientalis* was taken in India by four species of birds: *Merops viridis* Linn., *M. superciliosus* Linn. ("*M. philippinus*"), *Dendrocitta rufa* (Latham) and *Caprimulgus macrurus* Horsf. In West Java a head of the notorious *Vespa velutina* was found in the stomach of *Dicrurus macrocercus javanus* Kloss (Lieftinck, 1936).

In some oriental countries man acts as an important enemy of *Vespa* by using the immature stages as food. Concerning "*Vespa auraria*" (probably a race of *V. velutina*; v. d. V.), Ghosh (1924) wrote: "When accessible, the

Shans smoke these nests at night through their single entrance holes, thus stupefying the wasps inside. The nests are then broken open and robbed of the grubs and pupae, which are eaten. Wasps building nests underground are similarly treated." According to Bristowe (1932), the grubs of "*Vespa cincta*" (Lao name: "Tua thor") are eaten in several places in Siam. The species involved is probably *Vespa tropica*, for the insect is said to nest in hollow trees and to have a broad orange stripe across its abdomen.

Also in Sumatra the larvae and pupae of some species are taken as food. In a paper on the insects consumed by the Karo-Bataks in North Sumatra, van der Meer Mohr (1941) mentions *Vespa tropica* and *luctuosa* var. *malayana*, *Provespa anomala* and *nocturna*. The immature stages of these species are cooked in water with salt, onions and peppers (*Capsicum*), or in coconut juice with sugar and other additions.

Mimicry.

The Javan *Vespa velutina* is closely mimicked by a Syrphid fly which was described by de Meijere as *Milesia simulans* (Tijdschr. v. Ent., vol. 57, 1914, p. 144). This author wrote: "An gleicher Stelle mit obiger Art (*Milesia simulans*) fing Jacobson eine Wespe (*Vespa* sp.) (without any doubt *V. velutina* Lep.; v. d. Vecht) welche der obigen Fliege in der Färbung äusserst ähnlich sieht. Obgleich, oder vielleicht gerade weil Jacobson für die Mimicry-Theorie wenig fühlt, wurde er doch durch diese Ähnlichkeit, welche, wie er mir mitteilte, bei den lebenden Tieren noch viel auffälliger ist als bei den trockenen Exemplaren, wieder sehr überrascht. Die Übereinstimmung äussert sich auch in der Beinfärbung, nur findet sich die Grenze zwischen den dunklen und hellen Partien bei der Wespe am Anfang des Tarsus, bei der Fliege am Anfang der Tibia." (l.c., p. 145). The wasp and the fly were often observed by myself in the mountain forest near Tjibodas on Mt. Gedeh, West Java. They look indeed extremely similar, and it is only when the fly settles down on a leaf that it can be at once distinguished from the *Vespa* by its different behaviour.

A very similar observation was made by Dr. Lieftinck: "Whilst I was keeping watch at the nest of *Apis javanica* (see p. 56), my attention was drawn to some individuals of a Syrphid fly hovering among the bush in close proximity of the nest and strongly recalling the wasps while on the wing. The presence of these flies was surprising as the weather was dull and only few insects were about. When settling on a leaf they were easily recognized as hover-flies. One specimen captured at the time has since been identified by Dr. F. Keiser as a male of *Korinchia simulans* (de Meij.)."

There is another Syrphid which, according to a letter from Dr. Keiser,

resembles *V. velutina velutina*, agreeing in size with the workers of this wasp. This species, *Volucella peleterii* Macq., has been collected in several localities in the mountain areas of West Java where *velutina* occurs, but I do not know whether the resemblance has ever been noticed in the field.

Bingham (1905) remarked that in Malaya "*Vespa auraria*" (actually the Malayan subsp. *divergens* of *V. velutina*) is "closely mimicked by a Syrphid fly, taken on the same day and in the same part of the jungle". Unfortunately I have not yet been able to ascertain the identity of this fly.

The very close resemblance of *Milesia vespoides* Walk. to *Vespa tropica leefmansii* was discussed by Shelford (1902). He published coloured pictures of the two insects¹), and drew attention to the fact that the bright abdominal band, though in both species equally far from the thorax, covers the entire second tergite of the wasp, but the distal half of the second tergite and the proximal half of the third in the fly. *Milesia vespoides* was originally described from Singapore, where it was collected by A. R. Wallace. The Leiden Museum possesses a specimen from Borneo; the species has been recorded from Malaya by Pendlebury (1927), and I collected a specimen at Oosthaven near Tandjongkarang in South Sumatra (March 1937; det. F. Keiser). As I have never seen it in Java, I suppose that its area of distribution does not extend beyond that of the subsp. *leefmansii* of *V. tropica*.

DISTRIBUTION OF ORIENTAL AND PAPUAN VESPINAE

The application of the polytypic species concept to the Oriental Vespinae has demonstrated that the majority of the species occurring in the Indo-Australian archipelago (including the Malay Peninsula) is also represented on the Asiatic continent. Of the 15 species discussed in the preceding pages, no less than 11 are found more or less widely distributed on the continent. Eight of these species occur in the archipelago, two have the southern limit of their area of distribution in Malaya (*Provespa barthelemyi*) or in Peninsular Siam (*Vespa mandarinia*), and one appears not to go further southward than Indo-China (*Vespa bicolor*). The four species that are restricted to the archipelago and Malaya are the members of the *luctuosa*-group. As remarked before, these species are very closely allied and may be regarded as forming one superspecies.

Evidently a discussion of the distribution of the Oriental species, in order to present a satisfactory basis for zoogeographical considerations, should take into account the entire area of distribution of these species. This, however, would go far beyond the scope of this paper, and it would require

1) The wasp was called "*Vespa cincta*".

the study of a much greater amount of continental material than I have had at my disposal. For the present we shall therefore mainly discuss the problem of the possible origin of the Vespinae of the Indo-Australian archipelago, and their distribution within this area.

The genus *Provespa* is restricted to the Oriental region, occurring from the eastern Himalayas to Sumatra and Borneo. The genus *Vespa*, as at present delimited, contains approximately 20 species, which are mainly found in eastern Asia. Only two species, *Vespa crabro* and *orientalis*, are widely distributed in the western half of the Palaearctic region. The genus is not represented in Africa south of the Sahara and in America, with the exception of *Vespa crabro* which was introduced by man into North America between 1840 and 1860. The greatest number of species as well as the greatest diversity in characters are found in the eastern Himalayas and southern China. I am strongly inclined, therefore, to regard this area as the original centre of development of the genus *Vespa*, which is undoubtedly a relatively modern group of social wasps. This leads to the conclusion, that the species occurring at present on the continent as well as in the archipelago have migrated from the former area to the latter. The few species that are restricted to the archipelago are to be regarded as descendants of an immigrant from the continent which arrived long enough ago to develop populations showing specific differences.

Considering the distribution of the Vespinae of the Indo-Australian archipelago from this point of view, we may distinguish two groups: (1) the species of supposed continental origin, and (2) the species that have obtained their specific characters by isolation within the boundaries of the archipelago.

(1) The species of supposed continental origin vary considerably in distribution and in degree of subspeciation. According to these criteria they may conveniently be divided in five categories.

a. *Vespa tropica* and *Vespa affinis*. — Both species are widely distributed in continental Asia as well as in the archipelago, the northern limit of their area of distribution running from western India through China to Japan (*tropica*) or Formosa (*affinis*). *Vespa tropica* goes further northward than *affinis* and has been collected in southern Manchuria, the Ussuri district of eastern Siberia and in Korea, whereas *affinis* does not occur beyond Central China and the Riu-kiu Islands. In the archipelago (see fig. 8) *Vespa affinis* is particularly remarkable for its absence in Java and the Lesser Sunda Islands; on the other hand it is perhaps the only species of *Vespa* that has reached New Britain, for the records of *Vespa tropica* from this locality appear to need confirmation.

Both these species have developed a considerable number of subspecies. Some of the insular forms inhabit only small areas, whereas some of the continental races are rather widely distributed. The tropical subspecies have become adapted to life in the lowlands, a factor which has undoubtedly contributed considerably to their extensive distribution in the archipelago. They are able to live in fairly open country, and do not disappear when the original vegetation is destroyed and the land is cultivated.

b. *Vespa velutina*. — This species is less widely distributed in continental Asia than the preceding two, but the continental forms have not yet been thoroughly studied, and the limits of its area of distribution are insufficiently known. In the archipelago this mountain inhabitant has spread along the chain of volcanoes of the Sunda arc (fig. 8), and has also reached South Celebes, evidently from the Lesser Sunda Islands. With regard to the various subspecies, some interesting points are (1) the difference between the races of Malaya and Sumatra, two areas which are often inhabited by the same subspecies of wasps, and (2) the adaptation to life in the lowlands in the subspecies of Sumba.

c. *Vespa analis*. — Distributed from the eastern Himalayas¹⁾ (Sikkim; Assam) through China, Manchuria, and southeastern Siberia to Japan and Formosa, southward to Malaya, Java, and Bali, but apparently absent in North and Central Sumatra and in Borneo (figs. 3 and 8).

This discontinuous distribution is hard to explain. It seems possible that the two races occurring in Java are relics of an earlier invasion of species that have not been able to maintain themselves in Sumatra and Borneo at the time when Java was separated from the rest of the Sunda shelf. Some other wasps that are endemic in Java probably belong in this same category (*Calligaster cyanopterus* Sauss., *Ropalidia copiaria* (Sauss.), etc.).

d. *Provespa anomala* and *nocturna* (fig. 2). — Since these two species have often been confused, the northern limits of their areas of distribution deserve further study. In the archipelago both species are restricted to Sumatra, Malaya and Borneo, thus neither crossing the line of Wallace, nor the Sunda Strait. The latter fact is perhaps the most remarkable, for as both species occur in cultivated lowlands, there is no apparent reason for their absence from Java. — No subspecies have been distinguished.

e. *Vespa basalis* and *mocsaryana* (fig. 9). — Two relatively rare species, distributed from the eastern Himalayas to Sumatra. *Vespa basalis* is known from Nepal, Sikkim, Assam, and Tenasserim; it has also been recorded from Peninsular Siam and from Formosa, but I have not yet seen specimens

¹⁾ Records from southern India and Bengal need confirmation.

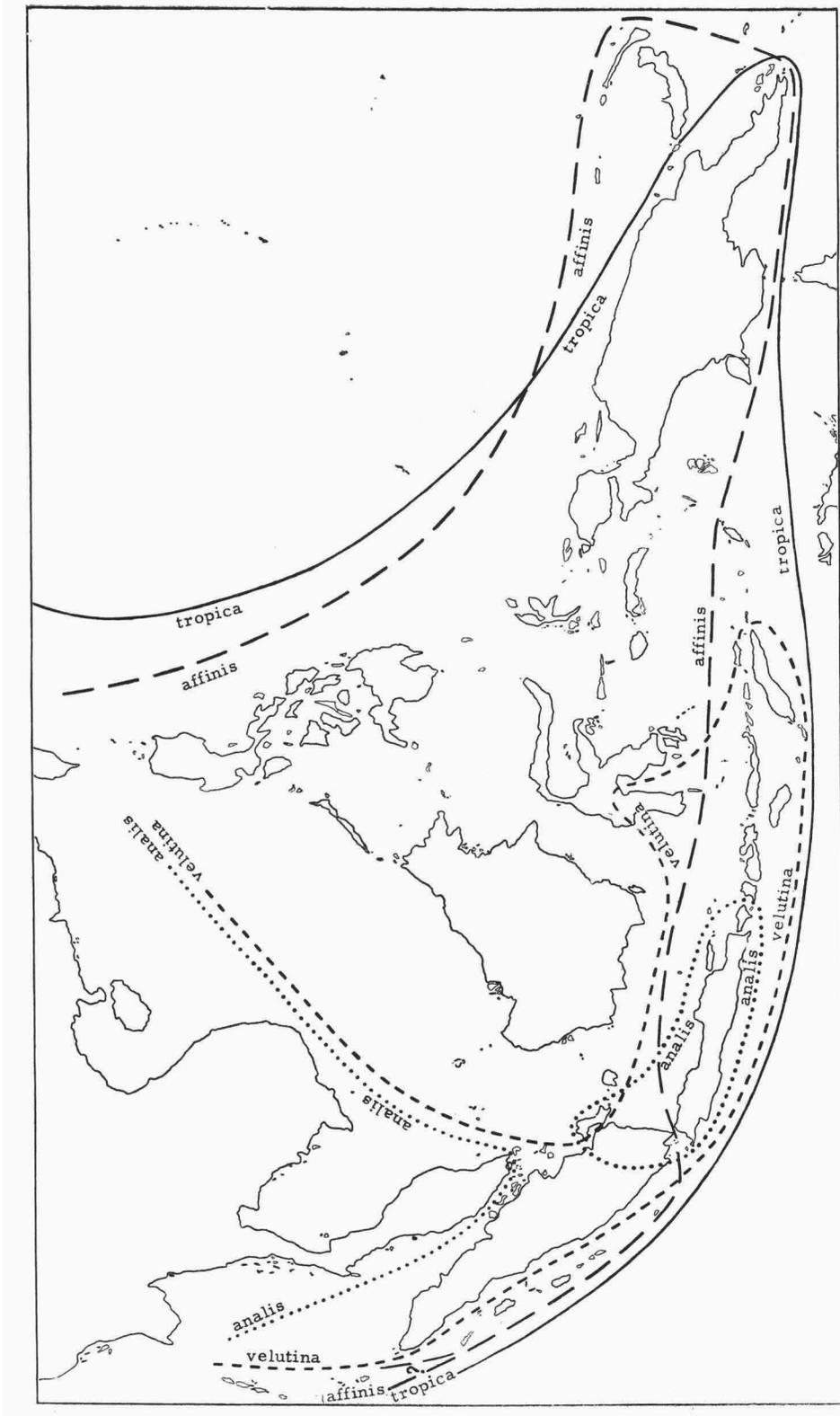


Fig. 8. The south-eastern parts of the distribution areas of *Vespa analis*, *tropica*, *affinis*, and *velutina*.

from these localities, nor from Indo-China and Malaya. *Vespa mocsaryana* occurs from Sikkim and Assam to Indo-China in the east and through Malaya to Central Sumatra in the south.

Vespa basalis appears to be restricted to mountain forests, but *mocsaryana* has been found in the lowlands of Malaya and Sumatra. No subspecies have been distinguished.

(2) The *luctuosa*-group (see figs. 7 and 9) comprises four closely allied species that live in well-forested areas in the lowlands. On the basis of morphological characters they can be separated into two pairs of species, one occurring west of the line of Wallace, on the Sunda shelf (minus Java), one living east of that line, in the Philippines and Celebes. The separation of the ancestors of these pairs has evidently been the first phase of the speciation process in this group. In a later phase isolation of the population of Celebes from that of the Philippines must have led to the differences existing between the forms of these areas, *fervida* and *luctuosa*. These differences are perhaps overrated by calling them specific, but nevertheless they appear to be greater than those existing between the three forms of *luctuosa* inhabiting various parts of the Philippine archipelago.

Similarly there has probably been a period of separation of the ancestral populations of the two species which inhabit the Sunda shelf, *bellicosa* and *multimaculata*, but here this phase was followed by an extension and partial overlapping of their areas of distribution, so that we find now these two forms as sympatric species both in Borneo and in Sumatra. The subsequent separation of Borneo from Sumatra and Malaya must be held responsible for the development of slight differences in the coloration of the *multimaculata* populations of these areas.

If we consider now the distribution of the Indo-Australian Vespinae from a geographic point of view, we may mainly refer to the accompanying maps. Taken together, they present a picture of the present state of our knowledge of the Vespinae in the various parts of the Indo-Australian archipelago.

Malaya harbours 9 species of Vespinae, the three *Provespa* species, and *Vespa analis*, *tropica*, *affinis*, *velutina*, *mocsaryana*, and *multimaculata*.

Sumatra has a very similar fauna, and most of the polytypic *Vespa* species of Malaya are represented here by the same subspecies. The differences are: *Provespa barthelemyi* is absent, *Vespa analis* and *velutina* are represented by different subspecies, and there are two species which have not been found in Malaya: *V. basalis* and *bellicosa*. Thus Sumatra appears to be even richer in species than Malaya. Nevertheless the only really characteristic

form is the Sumatran subspecies of *Vespa velutina*, which is slightly different from the Javan representative. The Sumatran population of *Vespa analis* is restricted to the southern part, and agrees so completely with the Javan specimens that it seems possible that this subspecies has migrated from Java into South Sumatra, just like certain Javan subspecies of butterflies.

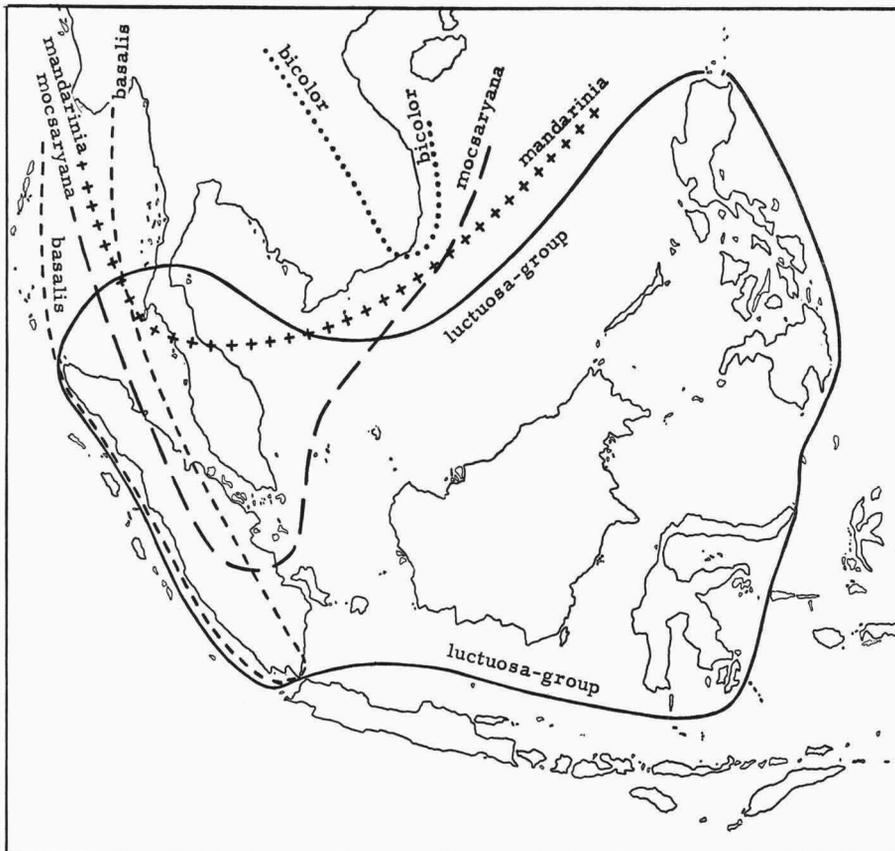


Fig. 9. The distribution area of the *Vespa luctuosa*-group, and the south-eastern parts of the distribution areas of *Vespa basalis*, *mocsaryana*, *mandarinia*, and *bicolor*.

As we might expect, the Vespine fauna of Borneo is very similar to that of Sumatra, but it is decidedly poorer. We find here *Provespa anomala* and *nocturna*, and the *Vespa* species *tropica*, *affinis*, *bellicosa* and *multimaculata*. The apparent absence of *V. analis* supports the view that this species has only recently migrated from Java into South Sumatra and Bangka Island. So far we know, the Sumatran mountain species *basalis*, *mocsaryana*

and *velutina* do not occur in Borneo, but it should be kept in mind that the Hymenoptera of the mountains of this island are very incompletely known, and that one or more of these species may yet be found. The collection of the Paris Museum contains a specimen of *V. variabilis* Buyss. with a label "Borneo" (from the collection of Sichel, see du Buysson, 1905, p. 523), but it seems doubtful whether this Chinese species does indeed occur here.

Vespa tropica is represented in Borneo by the same race as in Sumatra, but Bornean specimens of *V. affinis* cannot be distinguished from the race occurring in the eastern half of the archipelago.

Java has an exceedingly poor Vespine fauna, for only three of the ten species occurring in Sumatra are represented here. The Vespinae of this island are very well known, and it is therefore absolutely certain that this difference cannot be ascribed to insufficient collecting. Besides by being so poor, the Javan fauna is of interest because the subspecies of two of the three species, *Vespa tropica* and *velutina*, are different from those occurring in Sumatra. Evidently the narrow Sunda Strait (at its narrowest point only about 25 km wide) has been a much more effective barrier than its physical properties would indicate. This raises the question to what extent ecological factors may have played a role. It is particularly remarkable that a lowland species like *Vespa affinis*, which has such an enormous area of distribution, has been unable to become established in Java. As this can impossibly be ascribed to differences in climate or vegetation, I can explain this phenomenon only by assuming that the spread of *Vespa affinis* was halted here by the presence of the West Javan lowland race of *Vespa analis*, which we must then regard as a previously established competitor occupying the same ecological niche. This theory is supported by the fact that in Malaya, where the two species occur together, the local subspecies of *Vespa analis* appears to be a typical inhabitant of the mountains, whereas *V. affinis* is common in the plains. However, further observations in South Sumatra and other areas where the two species occur together, are very desirable.

In connection with the differences between the Vespine faunas of Sumatra and Java the species of the islands in the Sunda Strait are of particular interest. Fortunately, an expedition of the Zoological Museum, Bogor, Indonesia, collected a good number of Vespinae in various islands in 1955, and this has enabled me to prepare a map of this area showing the limits of the distribution areas of some of the critical forms (fig. 10). *Vespa affinis indosinensis* was found on the islands of Sebesi, Sebuku and Legundi, occurring here together with *Vespa analis analis* and the Javan subspecies of *Vespa tropica*. Perhaps *affinis* occurs also in the Krakatau-group, from where it has been recorded by Dammerman (1948), but it was not collected

there by Wegner. The numbers of specimens indicate that *V. analis* was the commonest species in all islands in the Sunda Strait.

Bali has the same Vespinæ as Java, but the Lesser Sunda Islands from

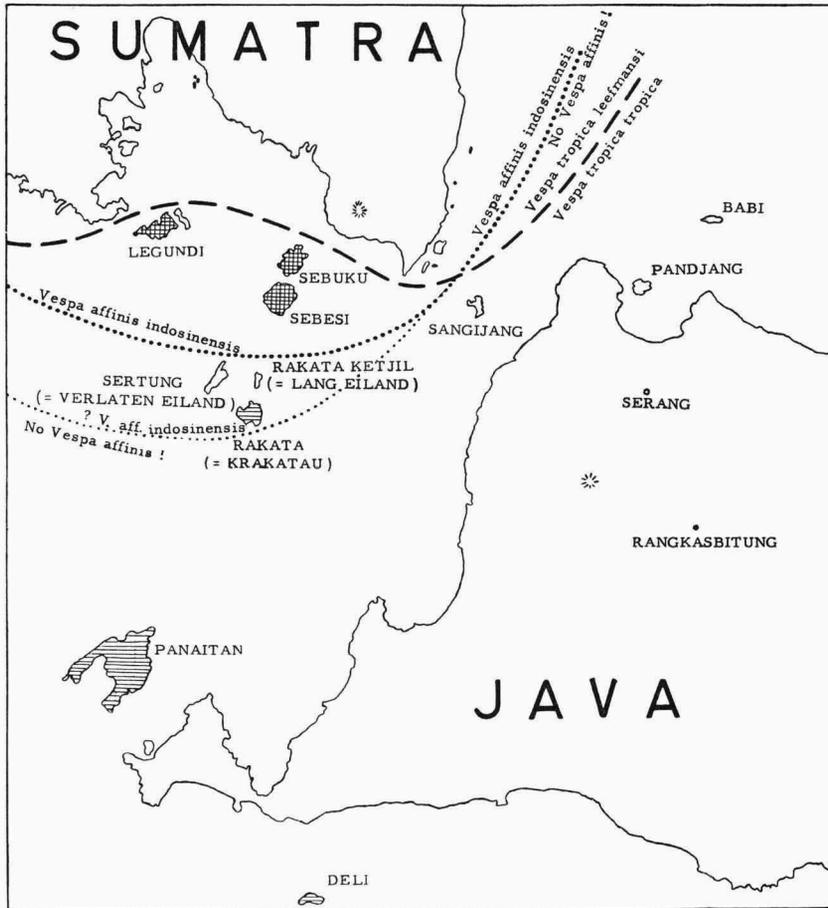


Fig. 10. *Vespa* species on the islands in the Sunda Strait. *Vespa analis analis* inhabits West Java and South Sumatra and has been collected on all islands with horizontal shading. *Vespa affinis indosinensis* inhabits Sumatra, but does not occur in Java; it has been found on all islands with vertical shading, and perhaps also on Rakata. *Vespa tropica* subsp. *leafmansii* occurs in Sumatra, subsp. *tropica* in Java; the Javan subspecies has been collected on the islands of Sangijang, Legundi, Sebuk, Sebesi, Rakata, and Panaitan.

Lombok to Timor appear to harbour only two species, *velutina* and *tropica*. The former has developed a number of subspecies in this area; the latter is represented not by the Javan subspecies, but by the race occurring in many parts of the eastern half of the archipelago. I do not know, however,

how far this form extends in western direction along the Sunda arc, for I have not yet seen *tropica* from Lombok and Sumbawa.

The Philippines agree with Java in having three species of Vespinae, but two of these are different: *V. affinis* and *luctuosa*. *Vespa affinis* appears to be common in Palawan, but remarkably enough the race occurring here shows a greater resemblance to the subsp. *indosinensis*, which occurs in Indo-China, Malaya, and Sumatra, than to *rufonigrans* which is the representative of *affinis* in Borneo, Celebes, etc. Its occurrence in other islands of the Philippine group appears to be somewhat doubtful. Both *V. luctuosa* and *tropica* have developed at least three subspecies in this area, but the distribution of these forms is insufficiently known. The published records would indicate that some islands are inhabited by more than one subspecies of *V. luctuosa* or *tropica*, but it appears somewhat dangerous to accept this conclusion without further local investigations. It has already been shown above that some of the existing confusion with regard to the subspecies of *luctuosa* must be ascribed to the fact that the differences in colour pattern between females and workers have been overlooked by previous authors.

Celebes has one species more than Java or the Philippines, for besides the widely distributed *V. affinis* and *tropica* we find here *V. fervida* which is very closely allied to the Philippine *luctuosa*, and a representative of *V. velutina* which may have reached this island from the Lesser Sunda Islands.

The islands east of Celebes are inhabited by only two species, *V. affinis* and *tropica*. Both have developed melanistic forms in this area, the former in various localities, the latter more especially in Buru.

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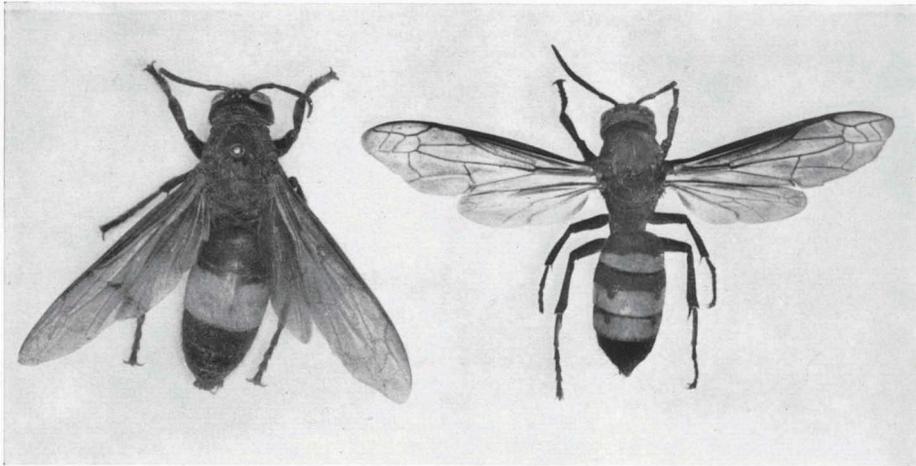


Fig. 1 (left). Type of *Sphex tropica* Linnaeus, 1758, in the collection of Queen Louisa Ulrika, Zoologiska Institutionen, Uppsala (1.2 X). — Courtesy Prof. B. Kullenberg, 1955.
 Fig. 2 (right). *Vespa tropica philippinensis* Saussure, ♀, from Mauo River, Samar, Philippine Islands (IRSNB) (1.2 X).



Fig. 3. *Vespa tropica lecfmansi* v.d. Vecht, robbing a nest of *Parapolybia varia* (Fabr.) (= *orientalis* Sauss.), Kuala Lumpur, Malaya, 8 Nov. 1953. — The nest is attached to the under side of a *Dracaena* leaf; five specimens of the lawful owner are on one side of the nest, while head and thorax of the invader are visible on the other side. — Photograph H. T. Pagden.

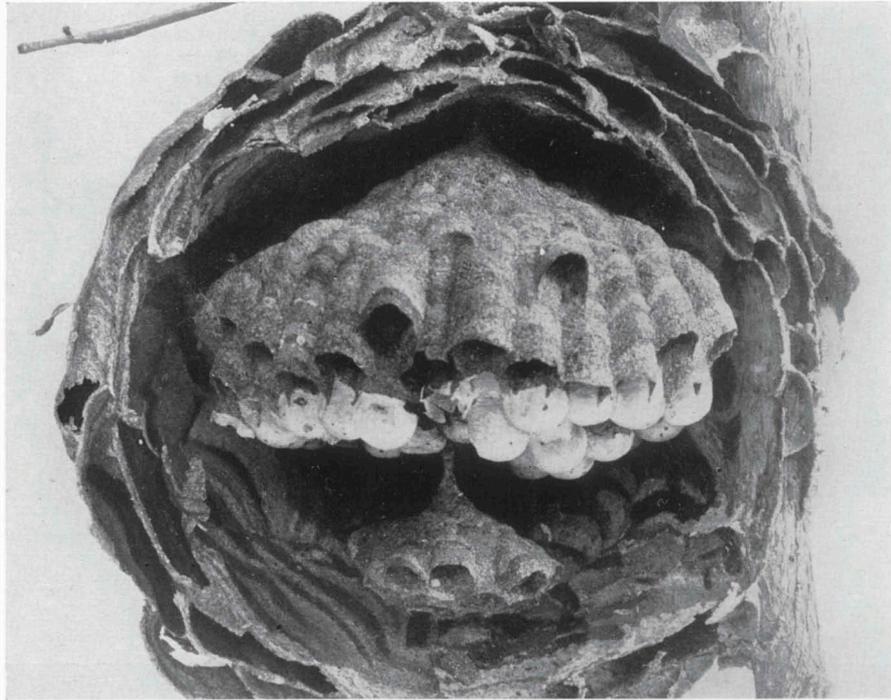


Fig. 1. Young nest of *Vespa analis analis* Fabr., Puntjak, 1200 m, West Java, 20 June 1932 (envelope partly removed). — Envelope already thicker at the top than at the sides. The conical comb is characteristic of this species.

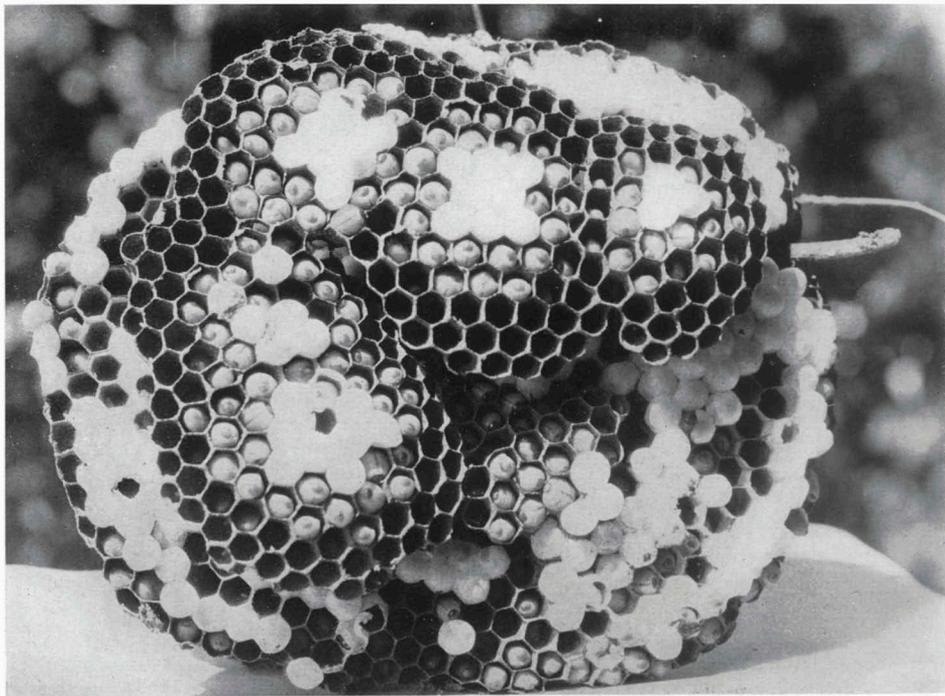


Fig. 2. Abnormal comb development in damaged nest of *Vespa analis analis* Fabr., 21 May 1932, Bogor, West Java. — New cell groups have been constructed at five different points of the lowest comb in the remaining part of the nest.



Fig. 1. Nest of *Vespa analis analis* Fabr. in hedge of *Hibiscus rosa-sinensis*, March 1937, Bogor, West Java. — The wasps have been disturbed and are running over the envelope; a few are returning to the interior through the nest entrance, on the right of the widest part of the nest.



Fig. 2. The same nest, a few months later. — A new generation of queens and males has left the nest and only a few workers remain.

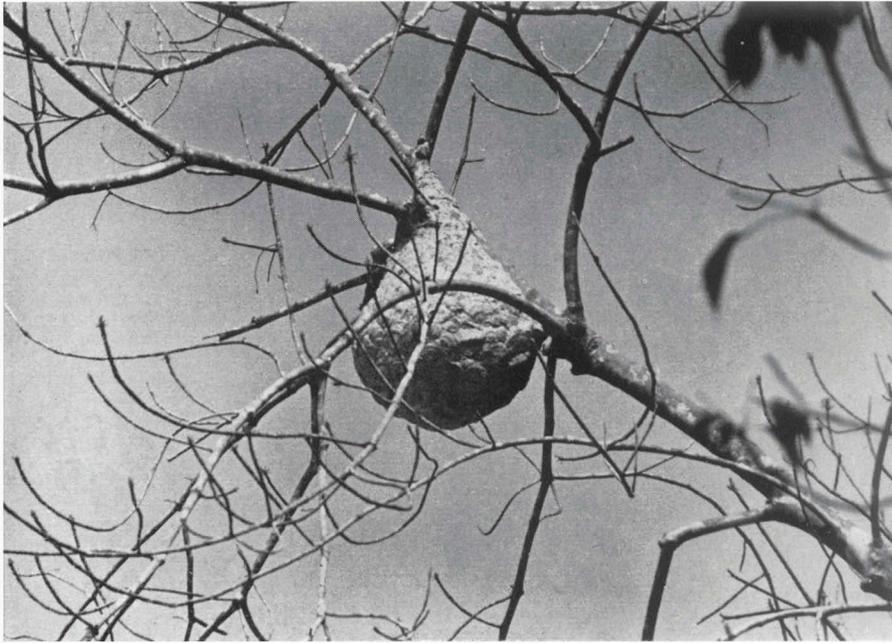


Fig. 1. Nest of *Vespa affinis indosinensis* Pérez in wintering rubber tree, Telok Bahang, Penang, Malaya, 14 Febr. 1953. — Photograph H. T. Pagden.



Fig. 2. The same nest, seen under a different angle. — Photograph H. T. Pagden.



Fig. 1. Nest of *Vespa affinis indosinensis* Pérez in wintering rubber tree, Rifle Range Road, Kuala Lumpur, 25 Jan. 1953. — Photograph H. T. Pagden.



Fig. 2. Nest of *Vespa affinis indosinensis* Pérez in rubber tree, Ampang Road, Kuala Lumpur, 25 Jan. 1953. — Photograph H. T. Pagden.

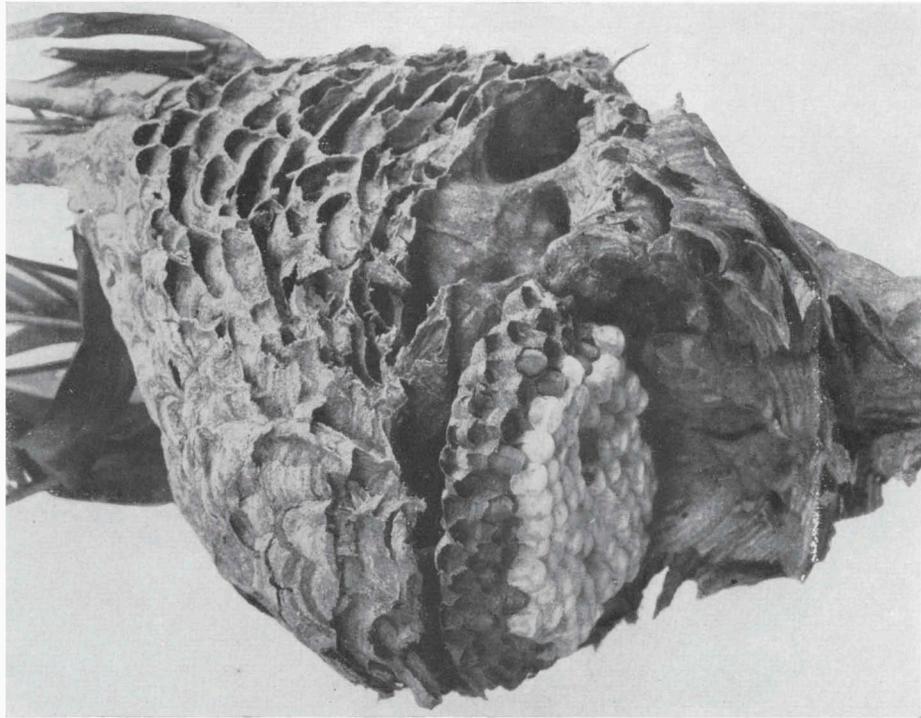


Fig. 1. Young nest of *Vespa velutina velutina* Lep. on *Cordyline fruticosa* ("handjawang"), Tjiluwung Estate, Puntjak, 1000 m, West Java. Two of the three combs and a large part of the envelope have been removed; on the right side some tissue has been cut away to show the structure of the roof of the nest.

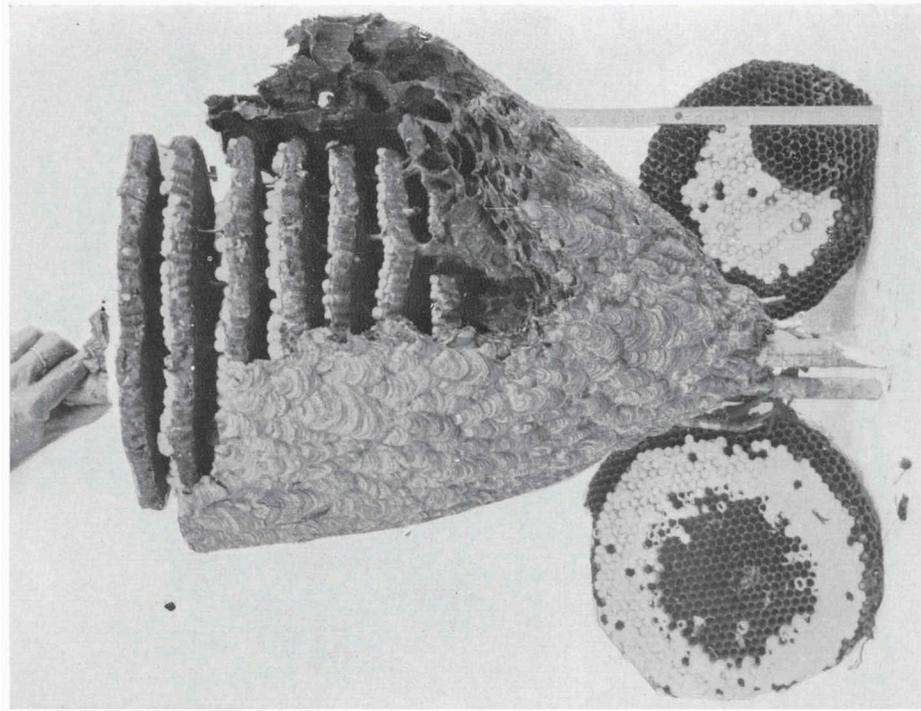


Fig. 2. Large nest of *Vespa velutina velutina* Lep., Tjiluwung Estate, Puntjak, 1200 m, West Java, May 1932. — The nest is held upside down, the envelope has been partly removed, and the three youngest combs have been placed under the nest.