Taxonomy

The Diversity of Hornets in the Genus Vespa (Hymenoptera: Vespidae; Vespinae), Their Importance and Interceptions in the United States

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Abstract

Hornets in the genus Vespa (Vespidae, Vespinae) are social wasps. They are primarily predators of other insects, and some species are known to attack and feed on honeybees (Apis mellifera L.), which makes them a serious threat to apiculture. Hornet species identification can be sometimes difficult because of the amount of intraspecific color and size variation. This has resulted in many species-level synonyms, scattered literature, and taxonomic keys only useful for local populations. We present a key to the world species, information on each species, as well as those intercepted at United States Ports of Entry during the last decade. Images of all the species and some of the subspecies previously described are also included.

Key words: invasive species, quarantine significance, pest, diversity, social wasp

Hornets in the genus Vespa are large, predatory, eusocial wasps native to Europe and Asia. They prey on a wide diversity of insects, but several species are predatory on honeybees. Vespa nests can be physically large, with over 1,000 workers, but usually with hundreds of workers (Archer 2008). Nests can be aerial, attached to tree branches or in shrubs, in crevices, under eaves or underground depending on the species. Depending on the latitude, nests can be either annual, started by a new queen every spring, or perennial, where young queens take over from old ones (Matsura and Yamane 1990). Colonies in warm tropical climates tend to be perennial.

These wasps exhibit a range of color patterns that vary geographically. Previous authors have named numerous subspecies based solely on color patterns, but Vespa color patterns tend to grade from one region to the next (Nguyen et al. 2006), Perrard et al. (2014). These subspecies were all synonymized by Carpenter and Kojima (1997).

Beggs et al. (2011) assessed the distribution, abundance, impact, and management of invasive species of Vespidae worldwide. In the case of the hornets, several Vespa species have been introduced outside their native ranges, including V. crabro Linnaeus, 1758 (Hymenoptera: Vespidae) from Europe into the United States (Bequaert 1932, Shaw and Weidhaas 1956); V. velutina Lepeletier, 1836 (Hymenoptera: Vespidae) from Asia into Europe (Monceau et al. 2014); and V. tropica Linnaeus, 1758 (Hymenoptera: Vespidae) from continental Asia into the island of Guam (Anonymous 2016). There are also records of other species collected outside their ranges without becoming established (see Kimsey and Carpenter 2012 for North America).
Some of the introduced *Vespa* species have shown to be environmental stressors as predators of already declining populations of native insects, spiders, and honeybees (Shah and Shah 1991, Abrol 1994, Choi et al. 2011, among others). They can also be competitors for food and nesting sites of native wasps (Cini et al. 2018), vectors of parasites or diseases that can affect honey bees and native wasps (Choi et al. 2011), and impact human safety because of their aggressiveness and fatal reactions to their venom (Nguyen et al. 2010, Kularatne et al. 2014).

The invasion of *V. velutina* into Europe typifies these problems. These hornets prey on the domestic honey bee (*Apis mellifera* (Hymenoptera: Apidae)), disrupt the ecological role of honeybees as pollinators (Villemant et al. 2006a, b; Monceau et al. 2014), have potentially altered local biodiversity (Fedele et al. 2019), and are potentially deadly to people allergic to their stings.

In Europe, the native hornet, *V. crabro*, is protected in some regions, such as in Germany (Federal Species Protection Ordinance-WArtschV/Federal Nature Conservation Act-BNatSchG). The introduced *V. velutina* may compete for food resources with *V. crabro*, which is a more generalist predator (Shaw and Weidhaas 1956, Baracchi et al. 2010). According to Monceau et al. (2014), some beekeepers have reported increased *V. crabro* predation on honeybees since the introduction of *V. velutina* in Europe.

This species was introduced into New York State in the mid-1800s (de Saussure 1898). Since then, it has since spread throughout eastern North America (Kimsey & Carpenter 2012). *Vespa tropica* was first found on Guam in 2016 (Anonymous 2016). Since then, it has become so widespread on the island it is no longer under quarantine, even though problems have arisen because it is aggressive and may nest close to human settlements.

Studies by Blanchard et al. (2008) and Yañez et al. (2012) had shown the potential transmission of the Israeli Acute Paralysis Virus (IAPV), one of the causes of Colony Collapse Disorder in honeybees (Baracchi et al. 2010). According to Monceau et al. (2014), some beekeepers have reported increased *V. crabro* predation on honeybees since the introduction of *V. velutina* in Europe.

Materials and Methods

We performed an Ad hoc/ unlimited search for interceptions of species of Vespineae (*Vespa* and *Vespula* Thomson) at Ports of Entry (PE) to the United States using the USDA-APHIS, Plant Protection and Quarantine (PPQ) databases AQUAS (Agricultural Quarantine Activity Systems) and ARM (Agricultural Risk Management System) going back to 2010. After the search, the data were processed, filtered and the total of interceptions for hornets (genus *Vespa*) was determined for the years 2010 to 2018. In addition, some information from interception records, such as origin and means of transportation, is given in the results and the discussion.

Taxonomic keys provided below were constructed in part based on previous keys by Archer (1989, 2012). A revised, fully illustrated key was needed to clarify and simplify diagnostic characters used in previous keys. In addition to the keys, we provide, for the first time, high-resolution images of these features.

Specimens used for the images were from the American Museum of Natural History (AMNH, New York, NY (C. Lebeau) and from the Bohart Museum of Entomology (BME), University of California, Davis (S. Heydon). Images were captured and edited using a Nikon SMZ18 System with a Nikon DS-fi2 camera, the stacking software, Helicon Focus 6.0, and Photoshop Elements 12.

Type repositories are given in parentheses at the end of species entries in synonym lists. These include BASEL = Naturhistorisches Museum, Basel, Switzerland; BERLIN = Museum für Naturkunde, Berlin, Germany; BUDAPEST = Zoological Department, Hungarian Natural History Museum, Budapest, Hungary; CALCUTTA = Zoological Survey of India, Calcutta; CAMBRIDGE = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; COPEHAGEN = Statens Naturhistoriske Museum, Copenhagen, Denmark; FUKUOKA = Kitakyushu Museum of Natural History and Human History, Fukuoka, Japan; GENOA = Museo Civico di Storia Naturale di Genova, Genoa, Italy; KAGOSHIMA = Reimeikangoshima History Museum, Kagoshima, Japan; KUNMING = Kunming Natural History Museum of Zoology, Kunming, Yunnan, China; LEIDEN = Rijksmuseum van Natuurlijke Historie (now called the Nederlands Centrum voor Biodiversiteit Naturalis), Leiden, Netherlands; LOGAN = The American Entomological Institute, Logan, Utah, USA; LONDON-LS = Linnaeae Society, London, England; LONDON-NHM = The Natural History Museum, London, England; MUNCHEN = Zoologische Staatssammlung München, Munich, Germany; OXFORD = Hope Entomological Collections, Oxford University Museum, Oxford, England; PARIS = Museum National d’Histoire Naturelle, Laboratoire d’Entomologie, Paris, France; SAPPORO = Entomological Institute, Hokkaido University, Sapporo, Japan; ST. PETERSBURG = Zoological Museum of the Zoological Institute, Saint Petersburg, Russia; TAICHUNG = Taiwan Agricultural Research Institute, Taichung, Taiwan; TOKYO = National Museum of Nature and Science, Tokyo, Japan; TURIN = Museo Regionale di Scienze Naturali, Turin, Italy; UPPSALA = Uppsala universitet Evolutionssmuseum, Uppsala, Sweden; VENICE = Museo di Storia Naturale di Venezia Venice, Italy; VIENNA = Naturhistorisches Museum, Vienna, Austria; WASHINGTON = Smithsonian National Museum of Natural History, Washington, DC, United States.

Genus *Vespa* Linnaeus

*Vespa* Linnaeus, 1758: 343. Type species: ‘*Vespa crabro* Fab’. (= *Vespa crabro* Linnaeus, 1758); designated by Latreille, 1810: 438.

Macrovespa Dalla Torre, 1904: 64 (subgenus of *Vespa* Linnaeus). Type species *Vespa crabro* Linnaeus, 1758. Designated by Bequaert, 1930: 64.


Diagnosis. The subfamily Vespinae can be distinguished from other Vespidae by the hind wings lacking an anal lobe (Fig. 1a); forewing recurrent veins ending in the same submarginal cell (Fig. 1b), marginal cell narrowly pointed along costal vein (not extending away from it) (Fig. 1b); pronotal lobe separated from tegula by a distance equal or less than its length (Fig. 1c); tarsal claws simple, not bifid (Fig. 1d), without parategula (Fig. 1e), and metasoma sessile with first tergum truncate (Fig. 1f).
(Fig. 2a), head vertex with the distance from the posterior ocellus to the posterior margin of vertex more than twice the distance between the posterior ocelli and the compound eye (Fig. 2b), the basal metasomal segment is anteriorly rounded (Fig. 1f), and the length of the forewing prestigma is three times or more the length of the pterostigma (Fig. 1b).

Keys to the Queens and Workers of the Species of Vespa of the World

1. Posterior ocelli about as close to compound eye as to each other (Fig. 2c) ........................................... binghami du Buysson
- Posterior ocelli closer to each other than to compound eye (Fig. 2d)..........................................................2
2 Apical margin of clypeus with medial tooth between laterally produced margins (Fig. 2e) ........................................analis Fabricius

- Apical margin of clypeus without medial tooth between laterally produced margins (Fig. 2f) ........................................3

3 Gena more than 1.7x medial width of compound eye in side view (Fig. 3a), interocellar distance much less than the distance from ocelli to vertex .................................................................4

- Gena less than 1.7x medial width of compound eye (Fig. 3b), interocellar distance as long or almost as long as the distance from ocelli to the vertex .................................................................5

4 Metasomal terga 3–6 black, or at most with narrow apical band on tergum 3 (Fig. 3c) ..............................soror du Buysson

- Metasomal segments 3–6 with orange apical band, tergum 6 mostly orange (as in Fig. 3d) ..................mandarinia Smith

5 Punctures on sides of tergum 2 large, separated by less than one puncture width (Fig. 4a); pronotal carina barely interrupted by pronotal fovea (Fig. 4c) .................................................................6

- Punctures on sides of metasomal tergum 2 small, separated by more than one puncture diameter (Fig. 4b); pronotal carina widely interrupted by pronotal fovea (Fig. 4d) ......................7

6 Clypeus mostly black (Fig. 4c); metasomal terga mostly black or at most with yellow apical band on tergum 1 (Fig. 5a) ...................................................................................................................fervida Smith

- Clypeus yellow (Fig. 4f); metasomal terga 1–5 often with apical yellow band (Fig. 5b) ................................luctuosa de Saussure

7 Pretegular carina complete (Fig. 7a); clypeus medially with coarse or large punctures, separated by one puncture diameter or less (Fig. 6c) .................................................................8

- Pretegular carina incomplete (Fig. 7b); middle of clypeus with small punctures separated more than one puncture diameter (Fig. 6d) ..................................................................................16

8 Apical margin of clypeus produced into two acute triangular projections (Fig. 8a) ........................................9

- Apical margin of clypeus produced into two broadly rounded projections (Fig. 8b) .........................................11

9 Vertex black (Fig. 8c) and first three metasomal terga primarily orange-yellow (Fig. 7a) ......................philippinensis de Saussure

- Vertex orange (Fig. 8d) or light brown, if black then orange-yellow coloration restricted to first two metasomal terga (Fig. 7c), or first three metasomal terga black, with at most narrow distal orange-yellow band (Fig. 7d) .......................10

10 Metasomal terga never entirely black; metasomal tergum 2 with broad orange-yellow band extending one-third or more across tergum (Fig. 7c and d) .......................ducalis Smith

- Metasomal terga all black (Fig. 7f), or metasomal tergum 2 orange-yellow (Fig. 7e), or tergum 2 black with narrow, distal orange-yellow band that extends much less than one-third of tergal width (Fig. 7b) ........................................tropica (Linnaeus)

11 Metasomal terga 2, 5 and 6 reddish brown or dark brown; tergum 3 and usually tergum 4 mostly yellow, with basal reddish brown band extending medially and two small, lateral reddish brown spots (Fig. 9a and b) ..............................orientalis Linnaeus

- Metasomal terga coloration not as above ........................................12

12 Metasomal segment 1 0.5x as long as or longer than width in dorsal view (Fig. 9c) ........................................13

- Metasomal segment 1 less than 0.5x as long as wide in dorsal view (Fig. 9d) ....................................................14

13 Scutellar punctures small and separated two puncture diameters (Fig. 10a); metasomal tergum 2 mostly black (Fig. 10c) .................................................................mocsaryana du Buysson

- Scutellar punctures large and contiguous or separated by 1 puncture diameter or less (Fig. 10b); metasomal tergum 2 usually reddish brown (Fig. 10d), or if metasomal tergum is mostly black then the vertex is also black ..........affinis (Linnaeus)

14 Clypeus strongly bulging medially, strongly convex in side view (Fig. 11a) ........................................fumida van der Vecht

- Clypeus not bulging medially, flat or gently curved in side view (Fig. 11b) .............................................................15

15 Metasomal segments 3–5 mostly yellow (Fig. 11c); vertex orange-yellow to red ......................................crabro Linnaeus

- Metasomal segments 3–5 mostly dark brown or black, some segments with narrow distal yellow band (Fig. 11d); vertex reddish to dark brown .................dybowskii Andre

16 Clypeus (Fig. 12a) and metanotum with dark markings .................................................................multimaculata Perez

- Clypeus and metanotum without black markings (Fig. 12b and d) .................................................................17

17 Clypeus yellow with black markings (Fig. 12a), or if without markings then metanotum entirely yellow (as in Fig. 12c and d) .................................................................bellica de Saussure

- Clypeus yellow to brown, without black markings (Fig. 12b); metanotum coloration variable (Fig. 12d and e) ......................18

18 Scutellum and metanotum entirely or primarily yellow (Fig. 12d) and vertex black ............................................bicolor Fabricius

- Scutellum and metanotum not primarily yellow (Fig. 12e), or if primarily yellow then vertex only partly black ..........19

19 Scutal punctures small, separated by 2–3 puncture diameters (Fig. 13a); metasomal terga 2–5 entirely black ....basalis Smith

- Scutal punctures large, separated by 1 puncture diameter or less (Fig. 13b); metasomal terga 2–5 not entirely black ...........20

20 Clypeal punctuation uniformly distributed ........simillima Smith

- Clypeal punctuation irregularly distributed, with impunctate areas .................................................................21

21 Side of prothorax close to spiracle smooth (Fig. 13c); vertex not black; mesothorax and propodeum with same coloration; terga 2 and 5 black or mostly black ..........vivax Smith

- Side of prothorax close to spiracle rugose (Fig. 13d); without above color combination .................................velutina Lepeletier

World Species of Vespa

Vespa affinis (Linnaeus) Figs. 4d, 9c, 10b, 10d, and 14

Apis affinis Linnaeus, 1767; 417. Holotype female; 'in Calidis regionibus' (UPPSALA).

Vespa affinis Fabricius, 1775; 287. Syntype females; China (COPENHAGEN). Nec Vespa affinis (Linnaeus, 1764).

Vespa unifasciata Olivier, 1792: 677. Type unknown; 'Indes regionibus' (UPPSALA).

Vespa alduini Guérin-Méneville. Nec Vespa alduini Olivier, 1792.

Vespa affinis (Linnaeus, 1764). (COPENHAGEN). Nec Vespa affinis (Linnaeus, 1764).

Vespa orientalis Gmelin, 1790. (repository unknown). Nec Vespa orientalis Geoffroy, 1785, and Vespa orientalis Olivier, 1792.


Vespa nigripennis Bissel, 1785. Type unknown; 'Indes regionibus' (GENOVA).

Vespa nigripennis de Saussure, 1854: 156. Type unknown; Philippines (repository unknown). Nec Vespa nigripennis Degeer, 1773.

Vespa cincta var. picea du Buysson, 1905 (1904): 537, Lectotype female (designated by van der Vecht, 1959: 214); Papua New Guinea, 'Tupuselia or Kapakapa' (van der Vecht does not indicate which locality) (GENOVA).

Vespa formosana Sonan, 1927: 125. Lectotype female (designated by Kojima et al. 2011: 45); Taiwan: Taihoku (TAICHUNG).


Distribution. India, Sri Lanka, Bangladesh, China, Hong Kong, Taiwan, Japan (Ryukyu Is.), Myanmar, Thailand, Laos, Vietnam, Malaysia, Singapore, Indonesia, Papua New Guinea, Philippines, and introduced into Australia, New Zealand, United States.

Discussion. This is one of the smaller bodied hornets, and is common in subtropical and tropical Asia. They are generalist scavengers,
Figs. 9–12. Vespa morphology. (a, b) Dorsal view of metasoma. (c, d) Dorsal view of basal metasomal terga. Fig. 10. (a, b) Dorsal view of scutum. (c, d) Dorsal view of metasoma. Fig. 11. (a, b) Lateral view of head. (c, d) Dorsal view of metasoma. Fig. 12. (a, b) Front view of clypeus. (c–f) Dorsal view of metanotum. Figs. 9a, 9b, V. orientalis. Figs. 9c, 10b, d, V. affinis. Fig. 9d, V. crabro. Figs. 10a, 10c, 11b, 11c, V. mocsaryana. Fig. 11a, V. fumida. Fig. 11d. V. dybowskii. Figs. 12a, 12f, V. multimaculata. Figs. 12b, d, e, V. bicolor. Fig. 12c, V. luctuosa.
feeding on nectar, fruit, tree sap, carrion, and insects, including honeybees. *Vespa affinis* nests are usually built high in trees, but can also be found in shrubs, and on and in buildings (Archer 1997).

**Vespa analis** Fabricius

*Vespa insularis* Dalla Torre, 1894, Cat. Hym. 9: 147. Replacement name for *Vespa japonica* Smith.

**Vespa tridentata** Cameron, 1903: 278. Lectotype female (designated by Kojima, 1997: 20); Japan (LONDON-NHM).  
*Vespa migrans* du Buysson, 1903: 175. Holotype male; China: ‘Yunnan, Tsé-kou’ (PARIS).  
*Vespa parallela* var. *biroi* du Buysson, 1905 (1904): 513. Lectotype female (designated by van der Vecht 1957); Singapore (PARIS).  
*Vespa analis* var. *tenebrosa* du Buysson, 1905 (1904): 516. Lectotype female (designated by van der Vecht, 1957: 14); Indonesia: Java, Goban (PARIS).  
*Vespa analis* var. (or subsp.) *barbouri* Bequaert, 1939: 40. Holotype female; India: Sikkim, Teesta Valley (CAMBRIDGE).  
*Vespa analis* var. (or subsp.) *kuangsiana* Bequaert, 1939: 42. Holotype female; China: ‘Kwangsi’, (CAMBRIDGE).  

**Distribution.** India, Nepal, China, Hong Kong, Taiwan, Korea, Japan, Russia, Myanmar, Thailand, Laos, Vietnam, Malaysia, Malaya, Singapore, Indonesia.

**Discussion.** This is one of the most widely distributed species of *Vespa*. Its native range includes tropical Asia and extends north into Japan, Russia, and Korea. Nests are typically built in trees 2–3 m above the ground (Archer 1998b).

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**Vespa basalis** Smith

Figs. 13a and 17


*Vespa obliterata* Smith, 1852: 47. Holotype female; ‘Northern India’ (LONDON-NHM).


**Distribution.** Pakistan; India, Nepal, China, Taiwan, Myanmar, Thailand, Laos, Vietnam, Indonesia: Sumatra.

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**Vespa analis** “analis”

Figs. 15 and 16. *Vespa analis* color forms. (a) Lateral view. (b) Dorsal view. (c) Front view of face.

**Vespa analis** “insularis”

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**Distribution.** India, Nepal, China, Hong Kong, Taiwan, Korea, Japan, Russia, Myanmar, Thailand, Laos, Vietnam, Malaysia, Malaya, Singapore, Indonesia.

**Discussion.** This is one of the most widely distributed species of *Vespa*. Its native range includes tropical Asia and extends north into Japan, Russia, and Korea. Nests are typically built in trees 2–3 m above the ground (Archer 1998b).
Discussion. *Vespa basalis* occurs in forested regions between 500 m and 1,500 m (Archer 1999). Nests are built on tree branches, in shrubs, on buildings, in rock crevices, and even in the ground. The mostly dark brown to black metasoma is one of the more distinctive features of *V. basalis*.

**Vespa bellica**os de Saussure

*Fig. 18*  
*Vespa bellica**os de Saussure, 1854: 146. Lectotype female (designated by van der Vecht, 1959: 216); ‘Java’ [error; Sumatra or Borneo] (TURIN).

**Vespa bicolor** Fabricius

*Figs. 2f, 8b, 12b, 12d, 12e, 19, and 20*  
*Vespa bicolor* Fabricius, 1787: 288. Syntypes, sex not stated; China (COPENHAGEN).

**Vespa lutea** Coquebert, 1804: 94. Type unknown; ‘Massiliae lecta, in navi ex India’ (repository unknown).


**Distribution.** Indonesia: Sumatra, Borneo (Kalimantan, Sarawak).

**Discussion.** This species appears to be associated with lowland tropical forests in Borneo and Sumatra (Archer 1999). It is unlikely that it would become invasive in other regions. It has very distinctive black and yellow banding on the thorax and metasoma. It is not known where *V. bellica**os* build their nests.

**Vespa bicolor** Fabricius

*Figs. 2f, 8b, 12b, 12d, 12e, 19, and 20*  
*Vespa bicolor* Fabricius, 1787: 288. Syntypes, sex not stated; China (COPENHAGEN).

**Vespa lutea** Coquebert, 1804: 94. Type unknown; ‘Massiliae lecta, in navi ex India’ (repository unknown).


**Distribution.** India, Bhutan, Nepal, China, Hong Kong, Myanmar, Thailand, Laos, Cambodia, Vietnam. Introduced into Taiwan.
Discussion. This species of *Vespa* has a very distinctively marked black and yellow thorax, with a largely yellow metasoma. It preys on honeybees, and one species of *Dendrobium* orchid exploits this behavior. These orchids produce chemicals that mimic alarm pheromones of Asian (*Apis cerana*) and European (*Apis mellifera*) honeybees to attract the hornets to pollinate their flowers (Brodman et al. 2009).

**Vespa binghami** du Buysson

Figs. 2c and 21


**Vespa bicolor** “citriventris”

19. *Vespa bicolor* “citriventris”

**Vespa bicolor** “bicolor”

20. *Vespa bicolor* “bicolor”

**Distribution.** India, Myanmar, Thailand, Laos, China, Russia, Korea.

Discussion. This is a high altitude species, found between 200 m and 2,000 m (Archer 1999). Zhang (1989) reported the presence of *Vespa binghami* in Miocene deposits in Shandong, China, but this identification needs to be verified.

**Vespa crabro** Linnaeus

Figs. 1, 2a, 2b, 3b, 3d, 9d, 11b, 11c, and 22–26


*Vespa vexator* Harris, 1776: 128. Holotype female; ‘English’ (destroyed).

*Vespa crabro major* Retzius (*in Degeer*), 1783: 63; Type unknown (repository unknown).
**Vespa pratensis** Geoffroy (in Fourcroy), 1785: 437; Type unknown; France: ‘in Agro Parisiensii’ (repository unknown).

**Vespa crabro germana** Christ, 1791: 215. Type unknown (destroyed).

**Vespa crabroniformis** Smith, 1852: 40. Syntype female, male; ‘North China’ (LONDON-NHM).

**Vespa crabro var. borealis** Radoszkowski, 1863: 128. Syntype female, male; Russia: ‘Pargolova i Osinova Roshchi’ (repository unknown). Nec **Vespa borealis** Kirby, 1837, **Vespa borealis** Zetterstedt, 1840, and **Vespa borealis** Smith, 1843.


**Vespa oberthuri** du Buysson, 1902: 140; Syntype females; China: ‘Chine: Se-Tchouen, Sio-Lou’ (PARIS).

**Vespa flavofasciata** Cameron, 1903: 280. Lectotype female (designated by Kojima, 1997: 21); Japan: ‘Nügata (Shinanogawa)’ (LONDON-NHM).

**Vespa crabro var. tartarea** du Buysson, 1905 (1904): 506. Syntype females; Japan: ‘Yokohama ... Columbia’ (BUDAPEST).

**Vespa crabro var. altaica** Pérez, 1910: 5. Holotype Female; Russia: Altaï (PARIS).


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**21. Vespa binghami**

**22. Vespa crabro “crabro”**

*Figs. 21 and 22.* Vespa color forms, (a) Lateral view. (b) Dorsal view. (c) Front view of face. Fig. 21. *Vespa binghami*. Fig. 22. *Vespa crabro*. 

*Vespa pratensis* Geoffroy (in Fourcroy), 1785: 437; Type unknown; France: ‘in Agro Parisiensii’ (repository unknown).

*Vespa crabro germana* Christ, 1791: 215. Type unknown (destroyed).

*Vespa crabroniformis* Smith, 1852: 40. Syntype female, male; ‘North China’ (LONDON-NHM).


*Vespa oberthuri* du Buysson, 1902: 140; Syntype females; China: ‘Chine: Se-Tchouen, Sio-Lou’ (PARIS).

*Vespa flavofasciata* Cameron, 1903: 280. Lectotype female (designated by Kojima, 1997: 21); Japan: ‘Nügata (Shinanogawa)’ (LONDON-NHM).

*Vespa crabro var. tartarea* du Buysson, 1905 (1904): 506. Syntype females; Japan: ‘Yokohama ... Columbia’ (BUDAPEST).

*Vespa crabro var. altaica* Pérez, 1910: 5. Holotype Female; Russia: Altaï (PARIS).


Vespa crabro vulgata Birula, 1925: 55. Syntype female, male: west Europe (St. Petersburg).

Vespa crabro meridionalis Birula, 1925: 55. Syntype females: Transcaucasia, north Persia, western part of Transcaspian region (ST. PETERSBURG).


Vespa crabro var. xirulai Bequaert, 1931: 105. Replacement name for Vespa crabro chinensis Birula.

Vespa crabro var. gribodai Bequaert, 1931: 105. Replacement name for Vespa crabro var. anglica Gribodo.

**Distribution.** Eurasia, Algeria. Introduced into eastern North America, and Guatemala.

**Discussion.** Vespa crabro usually nests in sheltered aboveground sites, such as tree hollows, wall voids, beehives, and outhouses (Archer 1993). However, nests have been found in subterranean
sites as well. This species adapts well to urban and suburban settings. It is widespread in Eurasia, and now eastern North America. The species was first reported in the United States in New York in the 1800s. More recently, the species was recorded from a single worker collected in Guatemala City, Guatemala. It was found in the Entomological Collection of the Universidad del Valle de Guatemala (Landolt et al. 2010). There is no evidence that the species is established in Guatemala. Nests are built in cavities in trees or buildings.

**Vespa ducalis** Smith
Figs. 7c, 7d, 8d, 13b, 27, and 28


**Vespa ducalis** var. **pulchra** du Buysson, 1905 (1904): 519. Lectotype female (designated by van der Vecht, 1959: 224); Japan: Yokohama (PARIS).


Vespa tropica pseudosoror van der Vecht, 1959: 224. Holotype female; Vietnam: Annam, Tourane, 1,000 m (PARIS).

**Distribution.** India, Sikkim, Nepal, Myanmar, Thailand; Laos, Vietnam, China, Hong Kong, Hainan; Taiwan; Russia: Korea; Japan, including Ryukyu Is.

**Discussion.** This species of *Vespa* is quite different from the others. It preys on nests of other paper wasps, feeding the paper wasp pupae and larvae to their larvae. Their colonies are small with an average of 50 individuals, and nests are built underground, in tree hollows, and even in attics (Archer 1991).

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27. *Vespa ducalis* “ducalis”

*Vespa ducalis* color forms. (a) Lateral view. (b) Dorsal view. (c) Front view of face.

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28. *Vespa ducalis* “pseudosoror”

*Vespa dybowskii* ‘Rad. in litt’. André, 1884: 582. Holotype female; Russia: ‘Sibérie’ (PARIS?).

*Vespa dybowskii*; Dalla Torre, 1904: 65. Misspelling of *Vespa dybowskii* André.


*Vespa dybowskii mutata* Ma, 1937: 30. Holotype male; China: ‘Hangchow’ (HANGZHOU, destroyed?).

**Distribution.** Myanmar, China (Tibet, Zhejiang), Russia (Siberia, Primorsky), Korea, Japan.

**Discussion.** This species is relatively rare in collections. It is a nest parasite of *Vespa crabro* and *V. similima*. *Vespa dybowskii* queens take over the nests of these species and use the host workers to raise their own brood (Martin et al. 2008).
Vespa fervida Smith


Distribution. Indonesia (Sulawesi, Salayar, Buton).

Discussion. This species has a very limited distribution on Sulawesi and nearby islands in Indonesia. They build nests in forested areas, and around human habitations, nests have been found under leaves and on fences. It is a small-bodied, dark-colored Vespa. Overall, its biology is poorly known (Matsuura and Yamane 1984, Archer 1999).

Vespa fumida van der Vecht


Distribution. Indonesia (Sulawesi, Salayar, Buton).

Discussion. Vespa fumida is found at high altitudes between 600 m and 3,000 m across northeastern India into China (Archer 1999). Otherwise, little is known about its biology.

Vespa luctuosa de Saussure

Vespa luctuosa de Saussure, 1854: 143. Holotype male; Philippines (LONDON-NHM).

Vespa luctuosa de Saussure, 1854: 143. Holotype male; Philippines (LONDON-NHM).

Vespa luctuosa de Saussure, 1854: 143. Holotype male; Philippines (LONDON-NHM).

Vespa luctuosa de Saussure, 1854: 143. Holotype male; Philippines (LONDON-NHM).

Vespa luctuosa de Saussure, 1854: 143. Holotype male; Philippines (LONDON-NHM).

Distribution. Philippines.

Discussion. This species has been found nesting in forested regions between 200 and 1,500 m elevation. The nests are built on tree branches, sometimes as high as 20 m above the ground (Archer 1999).

Vespa mandarinia Smith
Figs. 33–35


Vespa magnifica Smith, 1852: 45. Syntype females; Nepal ‘Nepaul’ (LONDON-NHM, OXFORD).


Vespa mandarina; Dalla Torre, 1894: 149. Misspelling of Vespa mandarinia Smith.

Vespa magnifica var. nobilis Sonan, 1929: 140. Holotype female; Taiwan: ‘Musha’ (TAICHUNG).

Vespa magnifica sonani Matsumura, 1930: 1. Lectotype female (designated by Kojima, 1997: 22); Taiwan: ‘Sina’ (SAPPORO).

Distribution. India, Sri Lanka, Bhutan, Nepal, Myanmar, Thailand, Laos, Vietnam, Malaysia, Malaya, China, Hong Kong, Taiwan, eastern Russia, Korea, Japan (including Ryukyus).

Vespa fumida

Figs. 31 and 32. Vespa color forms, (a) Lateral view. (b) Dorsal view. (c) Front view of face. Fig. 31. Vespa fumida. Fig. 32. V. luctuosa.
Discussion. This species occurs in hilly regions. It nests in the ground, starting with mammal burrows or decayed root cavities, enlarging them as the colony develops (Archer 1995, 2008). This is another species of *Vespa* that preys on honeybees. Zhang (1989) reported the presence of *Vespa magnifica* in Miocene deposits in Shandong, China. This identification needs to be verified. This species has also been introduced into the Pacific Northwest, where nests have been found recently (Anonymous 2020).

**Vespa mocsaryana** du Buysson


**Distribution**. India: Meghalaya, Sikkim, Assam; China: Sichuan, Anhui, Fujian, Hong Kong; Myanmar; Thailand; Laos; Vietnam; Malaysia: Peninsular Malaysia; Indonesia: Sumatra.

**Discussion**. Not much is known about the biology of this species. It occurs in montane forests in southern Asia. Nests have been found in a shrub and on a ceiling (Archer 2008).

**Vespa multimaculata** Pérez

*Vespa multimaculata* Pérez, 1910: 14. Lectotype female (designated by van der Vecht 1957); Brunei (PARIS).

*Vespa luctuosa* var. *malayana* Bequaert, 1934: 4. Replacement name for *Vespa annulata* Smith.


**Distribution**. Thailand; Laos; Malaysia: Peninsular Malaysia, Sarawak, Sabah; Singapore; Indonesia: Sumatra, Borneo (KALIMANTAN); Brunei.

**Discussion**. *Vespa multimaculata* is found in lowland and montane forests in Southeast Asia (Archer 1999, 2011), and is unlikely to disperse to temperate regions. Martin (1995) found nests in the ground beneath the roots of a tree.

**Vespa orientalis** Linnaeus


*Vespa turcica* Drury, 1773: 74. Type unknown; Turkey: Smyrna (destroyed?).

*Vespa quadripunctata* Forskal, 1775: 84; Type?; Egypt: Cairo, ‘Kahrae’ (COPENHAGEN?).

*Vespa crabro fusca* Christ, 1791: 216. Type unknown; Turkey: ‘Smirna’ (destroyed).

*Vespa aegyptiaca* Vallot, 1802: 170; Type unknown; Egypt (repository unknown).
**Discussion.** This is a distinctively marked reddish orange and yellow wasp. The nests are built in the ground in rodent burrows or rock crevices (Archer 1998a). Around human habitation, nests have also been found in empty beehives, under eaves or floorboards, and even in abandoned outhouses. It has been recorded from Mexico but is evidently not established (Dvořák 2006). *Vespa orientalis* are scavengers, feeding on nectar and fruit as well as insects and carrion. They also prey on honeybees and other pollinators. A study by Plotkin et al. (2010) found that this species has a novel form of photosynthesis using yellow pigments in the cuticle.

*Vespa philippinensis* de Saussure

Figs. 6a, 6c, 7a, 8a, 8c, and 41

*Vespa philippinensis* de Saussure, 1854: 148. Holotype male; Philippines (LONDON-NHM).

**Distribution.** Philippines (Leyte, Luzon, Negros, Samar).

**Discussion.** Little is known about the biology of this endemic species. A nest described by Starr (1987) from the island of Leyte was found in a cavity in the ground (Archer 1991).
Vespa similimma Smith

Fig. 42 and 43. Vespa similimma color forms. (a) Lateral view. (b) Dorsal view. (c) Front view of face.

Vespa similimma Smith
Vespa xanthoptera Cameron, 1903: 278. Holotype male; Japan: ‘Michzusawa’ (LONDON-NHM).
Vespa micado Cameron, 1903: 279. Lectotype female (designated by Kojima, 1997: 20); Japan: Nagasaki (LONDON-NHM).
Vespa mongolica var. flavata Pérez, 1910: 17. Holotype female; China (PARIS).

Distribution. China (Liaoning), southwestern Russia, Korea, Japan (including Yaku-shima Is.). Introduced into British Columbia, Canada, but not established; Taiwan?

Vespa soror du Buysson

Fig. 3a, 3c, and 44


Distribution. India, southwestern China, Hong Kong, Thailand, Laos, Vietnam.

Discussion. Little biology is known for this species. It has been found in hilly and montane sites up to 1,500 m in continental southeastern
Asia (Archer 2008). The nests are typically underground. These wasps are predators of other insects and even small vertebrates, like geckos. They will also attack nests of honeybees and other social vesps, including hornets (Lee 2009).

**Vespa tropica** (Linnaeus)
Figs. 7b, 7e, 7f, and 45–49

*Sphex tropica* Linnaeus, 1758: 571. Holotype female; ‘in Indiis’ (UPPSALA).


*Vespa crabro tenebrionis* Christ, 1791: 216. Type? (destroyed).

*Vespa deusta* Lepeletier, 1836: 506. Lectotype female (designated by van der Vecht, 1959: 226); ‘Patrie inconnue’ (TURIN).

*Vespa unicolor* Smith, 1863: 44. Holotype female; Indonesia: ‘Bouru’ (OXFORD).

*Vespa cinta* Wroughton, 1889: 35. Misspelling of *Vespa cincta* Degeer 1773.


*Vespa rubricans* Pérez, 1910: 10. Lectotype female (designated by van der Vecht 1957); ‘Lindi (Afrique orientale allemande)’ (PARIS).


*Vespa tropica trimeres* van der Vecht, 1957: 19; Holotype female; Indonesia: Sulawesi, ‘Palu, West Celebes’ (LEIDEN).


**Distribution.** Afghanistan, Pakistan, India, Sri Lanka, Bhutan, Nepal, southeastern China, Hong Kong, Myanmar, Thailand, Laos, Cambodia, Vietnam, Malaysia, Malaya, Borneo, Indonesia, Papua New Guinea (including New Britain), Philippines; exotic in Guam.

**Discussion.** This is a distinctively colored *Vespa*, with a black metasoma, except for a broad yellow to orange stripe across most of the second segment (as in *V. affinis*), although some individuals may lack this stripe. *Vespa tropica* are nest predators of other social wasps as well as other large-bodied insects, including honeybees (Archer 1991). Nests are either above ground in tree cavities or in cavities in the ground. Around human habitations, they will build nests under eaves, in shed, and attics.

*Vespa velutina* Lepeletier

**Figs. 6b, 6d, 13d, and 50–52**

*Vespa velutina* ‘De Haan’ Lepeletier, 1836: 507. Holotype female; Indonesia: ‘Java’ (TURIN?).

*Vespa auraria* Smith, 1852: 46. Syntype females; ‘Northern India’ (LONDON-NHM, OXFORD).


*Vespa fruhstorferi* Stadelmann, 1894: 89. Holotype female; Indonesia: West-Java, Gunung Gede, ‘in einer Höhe, 8000 ft’. (Berlin?).


Vespa auraria flavitarsis Ma, 1937: 31. Misspelling of Vespa flavitarsus Sonan, 1929?
Vespa velutina variana van der Vecht, 1957: 37. Holotype female; Thailand: Ban Umphang, Doi Hua Mot (LEIDEN).

Distribution. Afghanistan, Pakistan, India, Bhutan, Nepal, southern China, Hong Kong, Taiwan, Myanmar, Thailand, Laos, Vietnam, Malaysia, Malaya, Indonesia. Introduced into Korea, Japan (Tsushima I.), France, Belgium, United Kingdom, Spain, Portugal, Italy, Yemen.

Discussion. Vespa velutina has distinctive yellow tarsi and velvety appearing dark brown to black thorax and metasoma. It is native across Asia. However, V. velutina was introduced into Europe apparently with Chinese pottery in the past couple of decades (Keeling et al. 2017). Although this species preys on a variety of insects, including flies, dragonflies, and Orthoptera, it is a notorious predator of pollinators, particularly honeybees (Apis mellifera and A. cerana). Apis cerana have adapted to this hornet

Figs. 44 and 45. Vespa color forms. (a) Lateral view. (b) Dorsal view. (c) Front view of face. Fig. 44. V. soror. Fig. 45. V. tropica.
using avoidance behaviors and balling behaviors where they heat the hornet to death (Abrol 2006).

**Vespa vivax** Smith

*Figs. 13d and 53*


**Distribution.** India, Nepal, Myanmar, Thailand, China (Sichuan, Yunnan, Tibet), Taiwan.

**Discussion.** Little is known about this south Asian *Vespa* species. In Taiwan, nests have been found in montane regions at elevations between 1,500 and 2,500 m (Archer 1994).

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**Conclusion**

From 2010 to 2018, there have been close to 50 interceptions of *Vespa* (hornets) and *Vespula* (yellow jackets (*Vespula*)) at US ports of entry. Little less than half of those interceptions were hornets. The *Vespa* species intercepted include *V. bellicosus*, *V. crabro*, *V. orientalis*, *V. mandarina*, and *V. tropica*. One of the interceptions of significance was an entire nest of *V. mandarina* containing live brood and pupae that was sent via express courier from Asia.

All species of *Vespa*, except *V. crabro*, which is already introduced into the eastern United States, are considered of quarantine importance by the USDA-APHIS. As part of the work of monitoring for possible introductions of hornets in the United States, one of us (AHSP) created a website, *Invasive Hornets* ([https://www.ipmimages.org/browse/projectthumb.cfm?proj=1159](https://www.ipmimages.org/browse/projectthumb.cfm?proj=1159)), which is part of a cooperation between the USDA, Animal Plant Health Inspection Service (APHIS), Plant Protection and Quarantine (PPQ) and the University of Georgia. This website contains more than 1,000...
Figs. 48 and 49. *Vespa tropica* color forms. (a) Lateral view. (b) Dorsal view. (c) Front view of face.

48. *Vespa tropica* “pulchra”  
49. *Vespa tropica* “trimeres”
50. *Vespa velutina* "auraria"

51. *Vespa velutina* "nigrithorax"

Figs. 50 and 51. *Vespa velutina* color forms. (a) Lateral view. (b) Dorsal view. (c) Front view of face.
stacked, high-quality images of all the species and most of the races of the genus *Vespa*.

It is important to have the resources for the identification and prevention of introduction of non-native species and to understand the potential effects of invasive hornets in our ecosystems. Hornets are dangerous for the beekeeping industry because they can alter pollination in agriculture and disrupt the beekeeping industry, as well as create public health and safety problems.

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**Figs. 52 and 53.** *Vespa* color forms. (a) Lateral view. (b) Dorsal view. (c) Front view of face. Fig. 53. *V. velutina*. Fig. 54. *V. vivax*.


