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A TENTATIVE REVISION OF THE SUBGENUS PARAVESPULA
OF EASTERN ASIA (HYMENOPTERA: VESPIDAE)

By SEIKI YAMANE, ROBERT E. WAGNER and SÔICHI YAMANE

Abstract

YAMANE, SK., WAGNER, R.E., and YAMANE, S. 1980. A tentative revision of the subgenus *Paravespula* of eastern Asia (Hymenoptera: Vespidae). *Ins. matsum. n.s.* 19: 1-46, 135 figs.

The subgenus *Paravespula* of the genus *Vespula* from eastern Asia is revised. Eleven forms belonging to seven species are recognized and described. The results include some new synonyms, new combinations and changes in rank. A subdivision of the genus *Vespula* is proposed based upon morphological and behavioral characters, some of which are newly found and which may be of phylogenetic importance. Seven groups are recognized within the genus. World distributional patterns of the *Vespula* species are briefly discussed, with special emphasis on a close faunal relation between Eurasia and North America.

As an appendix a new species, *Vespula shidai* Ishikawa, Sk. Yamane et Wagner, is described from Japan, the Kuriles and Ussuri.

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1) Research Trips for Forest and Agricultural Insects in the Subcontinent of India (Hokkaidô University, University of Calcutta, and Zoological Survey of India Joint Project) [Grants-in-Aid for Overseas Scientific Survey, Ministry of Education, Japanese Government, 1978, No. 304108; 1979, No. 404307], Scientific Report No. 3.

2) Scientific Results of the Hokkaidô University Expeditions to the Himalaya, Entomology No. 36.

INTRODUCTION

The subfamily Vespinae is a compact group composed of four genera, *Provespa*, *Vespa*, *Vespula* and *Dolichovespula*. Although widely distributed over the Northern Hemisphere, it is generally supposed to be of Asiatic origin. *Provespa* and *Vespa*, which are limited to the Old World, have been extensively studied by Vecht (1957, 1959). *Vespula* and *Dolichovespula* are Holarctic in distribution, and the European and North American forms belonging to them have been well studied by Blüthgen (1961), Guiglia (1972), Bequaert (1932) and Miller (1961). Our interest, then, has recently centered on the Asiatic forms of the latter two genera in expectation of meeting interesting problems concerning the distribution and evolution of the genera. Birula (1927, 1930a, 1930b) revised the genus *Dolichovespula* and the *Vespula rufa* group (subgenus *Vespula*) of the USSR including eastern Siberia, Kamchatka and Sakhalin. Although his works contain some misconceptions about species he studied, they have provided the most detailed and reliable information available to date. Unfortunately Birula did not treat the *Vespula vulgaris* group (subgenus *Paravespula*). Recently new information has been given on some *Dolichovespula* species from Japan (Ishikawa, 1969; Sk. Yamane, 1975). Thus the subgenus *Paravespula* is the most poorly known group in eastern Asia. In the course of our studies of this group it has become evident that some forms must be shifted in their taxonomic status and some names must be synonymized. A total of eleven forms in seven species are recorded from this faunal region (eastern Siberia, Sakhalin, Japan, Korea, China, Burma, Nepal and India). Several new characters of phylogenetic importance have been found and used in our subdivision of the genus *Vespula*. Biogeographic data are still incomplete especially in China, Burma and the Himalayas, but we will give distribution maps for some forms and will briefly discuss the world distributional pattern of the genus, with special emphasis on a close faunal relation between Asia and North America. The subgenus *Paravespula* as here understood seems to contain diverse forms and might not be a monophyletic group, but it should be retained here for convenience.

The present study is chiefly based upon the materials in the collections of Entomological Institute, Hokkaidô University, and U. S. National Museum, Washington, D.C. The specimens from U.S.N.M. are asterisked.

SUBGENUS PARAVESPULA BLÜTHGEN

Type-species: *Vespa vulgaris* Linné, 1758

Subgen. *Vespula*, subgroup A, Bequaert, 1932, Entom. Amer. N.S. 12: 88.

Subgen. *Paravespula* Blüthgen, 1938, Konowia 16: 271; Guiglia, 1972, Faun. Eur. Bas. Med. 6: 106.

Recognition characters. Adult: Occipital carina distinct, reaching the base of mandible in at least the queens, except in *V. shidai* and *V. flaviceps* in which the carina becomes evanescent towards the mandibular base even in the queen. It is often weak in the worker of *V. vulgaris*, and less developed in the males of most species of the subgenus. Gastral tergites without distinct punctures even in the queen. Disk of male gastral tergite VII (last tergite) more or less depressed. Shaft of aedeagus slender; apex of aedeagus a subcircular or heart-shaped spoon, or

in *V. koreensis* like a cup opened dorsally with thin walls (the males of *V. minuta* and *V. structor* are unknown to us).

Mature larvae: As in *V. rufa* with regard to the structure of head, but distinguished therefrom by the much shorter collar processes of the spiracles in at least the species of which the larvae are known. For a closer description, see Sk. Yamane (1976).

Mature nest architecture: Light brown or buff in color and brittle, or in *V. germanica* and *V. pensylvanica* gray and pliable; envelope formed of numerous, shell-like pockets. Support for the comb except for the mainstay is usually provided by pillars (ribbon-styled supports are rarely built, Fig. 46). Nest size very large. MacDonald (1977) presents a table which lists comparative nest architectural parameters of vespine wasps. For embryo nests, see Sk. Yamane and Makino (1977). Neither embryo nor mature nest is yet known for *V. koreensis*, *V. minuta* and *V. structor*.

Biology: Generally wasps of the subgenus *Paravespula* build large nests underground in cavities, or in building wall voids. They inhabit mountainous districts as well as lowlands, but prefer warmer and lower places than do the *V. rufa* group and genus *Dolichovespula* in at least the Palearctic region. They are often abundant in urban environments, some species commonly becoming pests in both the New and Old Worlds (Akre & Davis, 1978). The colonies persist till late autumn and often overwinter in some southern localities. The number of combs in mature nests ranges from several to about 30 (especially numerous in perennial nests of *V. germanica* introduced into New Zealand; Thomas, 1960). The smaller worker cells are clearly distinguished from the larger queen cells. *Paravespula* species are general feeders, hunting live arthropods such as lepidopterous larvae, diptera and spiders, and even marine invertebrates (Fig. 2), or collecting meat from dead mammals, fish, frogs, etc. The scavenging habit is most pronounced in this subgenus. Adult wasps collect nectar from flowers with short corollas, honey dew of aphids (Fig. 1) and coccids, tree sap, sweets, or fruit juice.

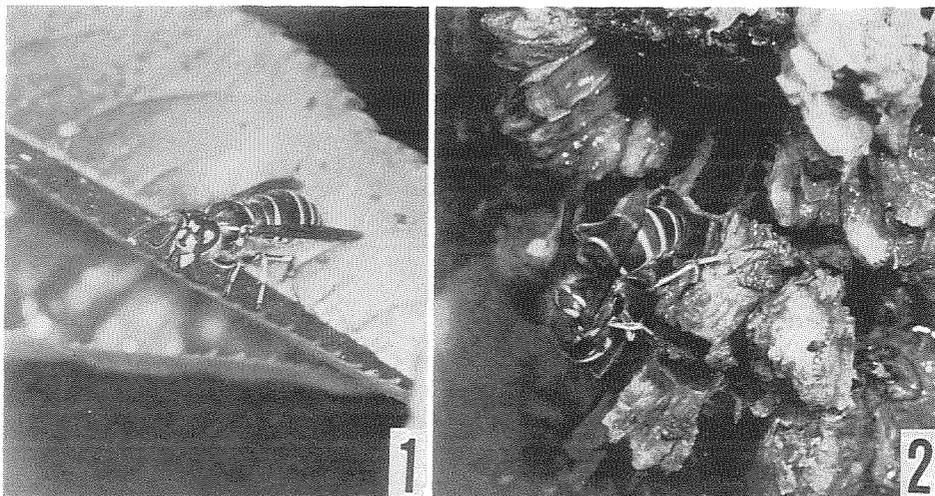


Fig. 1. A *Vespula flaviceps lewisii* queen feeding upon aphid honey dew. (Photo S. Aoki.)

Fig. 2. A *Vespula shidai* worker collecting meat from an injured barnacle. (Photo T. Sunose.)

In this regard *Paravespula* species are again general feeders, but at least in Asia where many *Vespa* species are sympatric, tree sap is usually exclusively dominated by *Vespa*. Little is known of the behavior of *V. koreensis*, *V. minuta* and *V. structor*.

Distribution. The subgenus is Holarctic with two species in Europe, seven in Asia and four in North America, comprising a total of ten species (some species extend to S.E. Asia). The *V. flaviceps* and *V. koreensis* groups (see p. 33) are found only in eastern Asia. Recently the Palearctic *V. germanica* has been accidentally introduced into New Zealand, Tasmania, South Africa, eastern North America, Chile, etc., and the Holarctic *V. vulgaris* has become established in Australia (Edwards, 1976) and on the island of Maui in the Hawaiian Is.

KEY TO THE EASTERN ASIATIC FORMS

Queens (♀)

1. Propodeum with distinct striae. First flagellar segment of antenna 0.71–0.74 as long as scape. Prebasal depression of gastral tergite I distinct (Fig. 6). Cubital vein IIa shorter than IIb (Fig. 23). A large species; $H+Th+T_1+T_2=13.5-16$ mm. *Vespa koreensis* Rad. 2
 —Propodeum without distinct striae. First flagellar segment 0.72–0.83 as long as scape (usually more than 0.77). Prebasal depression of gastral tergite I weak or absent (Fig. 4). Cubital vein IIa longer than IIb (Fig. 21). $H+Th+T_1+T_2=11.0-14.0$ mm. 3
2. Pronotum yellowish brown; posterior margin yellow. Scutellum and post-scutellum with yellowish spots. Gastral tergite II with a wide yellowish apical band which is as wide as the basal black part of the tergite (Fig. 109). *V. k. koreensis* Rad.
 —Pronotum nearly entirely black; posterior margin brownish only in the middle. Scutellum and postscutellum usually without yellowish markings. Brownish apical band on gastral tergite II very narrow (Fig. 112). *V. k. orbata* Buys.
3. Occipital carina nearly reaching the base of mandible. Body markings yellow to orange yellow. 4
 —Occipital carina visible only in upper 3/5–2/3 of the gena. Body markings white to yellowish brown. 5
4. Third mandibular tooth distinctly concave along mesal margin (Fig. 24). Clypeus with three black spots placed like the points of a triangle (Fig. 65). Genal yellow band complete, without interruption (Fig. 39). Gastral tergite I medially with a rhombic black maculation; tergites II–V each with a pair of isolated black spots (Fig. 107). *V. germanica* Fab.
 —Third mandibular tooth nearly straight along mesal margin (like Fig. 25). Clypeus with an anchor- or club-shaped black marking (Figs. 61, 62). Genal yellow band usually interrupted (Fig. 37). The base of gastral tergite I widely black; tergites II–V usually without isolated black spots (Fig. 103). (In the continental specimens the genal band without distinct interruption, and tergites with isolated black spots; Figs. 38, 104). *V. vulgaris* L.
5. White area of ocular sinus with distinctly concave medial margin. Black bar of clypeus reaching the apical margin of clypeus (Fig. 60). Body markings white. *V. shidai* Ishikawa et al.
 —White or yellow area of ocular sinus more extensive, usually not concave along mesal margin. Clypeus entirely pale-colored or with black marking rarely reaching the apical margin of clypeus (Figs. 47–50, 54–57). Body marked with white to brownish yellow. *V. flaviceps* Sm. 6
6. Body markings white. Clypeus with a black anchor-shaped marking (Figs. 54,

- 55). *V. f. lewisii* Cam.
 — Body markings at least on the gaster yellow to brownish yellow. Black or brown markings on clypeus less extensive and variable in shape (Figs. 47–50, 56, 57). 7
7. Yellow bands on gastral tergites I and II very narrow, less than 0.5 mm wide (Figs. 96, 97). Thoracic markings very whitish. *V. f. karenkona* Sonan
 — Yellow bands on gastral tergites I and II relatively wide, usually more than 0.5 mm wide (Figs. 87–91). Thoracic markings not very pale. Body markings extremely variable; frons and temple often with brownish or yellowish markings (Fig. 50). *V. f. flaviceps* Sm.
 (Because the queen of *V. minuta* is unknown, and the description of the queen of *V. structor* by Bingham (1897) is vague, we were unable to include them in the key.)

Workers (♀)

1. First flagellar segment of antenna 0.70–0.76 as long as scape. Cubital vein IIa shorter than IIb (Figs. 22, 23). Occipital carina always strong and reaching the base of mandible. 2
 — First flagellar segment of antenna 0.72–0.90 as long as scape (usually more than 0.76). Cubital vein IIa as long as or longer than IIb (Fig. 21). Occipital carina in some species weak or absent near the base of mandible. 5
2. Propodeum with distinct striae (very rarely indistinct). *V. koreensis* Rad. 3
 — Propodeum without distinct striae, medially with a short vertical carina near the base. *V. minuta* Dover. 4
3. Ground color of gastral tergites blackish brown or black (Figs. 110, 111). Vertical face of tergite I entirely blackish. Antenna blackish brown to brown.
 *V. k. koreensis* Rad.
 — Gaster tergites often lighter colored, ground color sometimes yellowish or reddish brown (Figs. 113–115). Vertical face of tergite I brown to light brown. Antenna much lighter in color. *V. k. orbata* Buys.
4. Mesoscutum anteriorly with a large, reddish diamond-shaped marking. Head entirely yellowish brown; frons above corona, ocellar area and vertex darker (Fig. 72). A broad apical band on gastral tergite III and visible part of the subsequent tergites brown (Fig. 116). Antenna brownish. *V. m. minuta* Dover
 — Mesoscutum usually entirely black, rarely anteriorly with reddish spots. Head yellow; frons above corona and ocellar area black (Fig. 73). Apical bands on gastral tergites yellow; rarely with a brownish area between the basal black area and yellow apical band (Figs. 117, 118). Antenna blackish.
 *V. m. arisana* Sonan
5. Occipital carina usually reaching the base of mandible (sometimes obsolete near the base of mandible in *V. vulgaris*). 6
 — Occipital carina not reaching the base of mandible, only visible in the upper 2/3. 8
6. Gaster tergite I without a medial black maculation; visible part of gastral tergites nearly wholly orange (Fig. 106). Clypeus yellow without distinct black marking. Corona not separated from ocular sinus by dark color (Fig. 64). Yellow markings on thorax much reduced. *V. structor* Sm.
 — Gaster tergite I very often with a medial black maculation which is a rhomboid or transverse arrow (Figs. 104–107, 108). Gaster tergites black with yellow apical bands. Clypeus with more or less distinct black marking. 7
7. Third mandibular tooth distinctly concave along the mesal margin. Genal band not interrupted by black. Clypeus without distinct anchor-shaped black marking, rarely entirely yellow (Figs. 65, 66). *V. germanica* Fab.
 — Third mandibular tooth straight or at most slightly concave along the mesal margin. Genal band with a black medial interruption. Clypeus with a distinct anchor- or club-shaped black marking (Fig. 63). *V. vulgaris* L.

8. Body black with white markings. White area of ocular sinus with deeply concave medial margin. Black bar on clypeus much developed, usually reaching the apex of clypeus (Fig. 60). Mid- and hind tarsi very often dark brown. *V. shidai* Ishikawa et al. — Black with white or yellow markings. White or yellow area of ocular sinus nearly straight or at most slightly concave on medial margin, or the yellow connected with corona. Black bar on clypeus variable in shape, but rarely reaching the apex of clypeus. Mid- and hind tarsi light brown. *V. flaviceps* Sm. 9
9. White or yellow apical bands on gastral tergites usually broad and very often irregular, especially in the southern specimens (Figs. 92–95). Tergite I nearly always with a pair of short white or yellow lines at the base of horizontal face (Figs. 93, 94). Clypeal marking poorly developed, often completely lost (Figs. 51–53). *V. f. flaviceps* Sm. — White or yellow apical bands on gastral tergites narrow and regular. Tergite I rarely with a pair of short lines at the base of horizontal face. Clypeal marking usually well developed. 10
10. Ivory-whitish or pale-yellowish apical bands on gastral tergites very narrow and regular (0.13–0.18 mm wide as measured near the middle of T₁; cf. Fig. 3B). Whitish transverse lines on scutellum and postscutellum very narrow. Propodeum usually without whitish spots. Tergite I without whitish lines at the base of horizontal face. Clypeal bar black, sometimes replaced by brown, not much developed (Figs. 58, 59). *V. f. karenkona* Sonan — White apical bands on gastral tergites slightly wider than in *karenkona*, and regular (0.18–0.35 mm as measured near the middle of T₁). White markings on scutellum and postscutellum wider. Tergite I rarely with a pair of short white lines near the base of horizontal face (Fig. 100). Propodeum sometimes with white spots. Clypeus with a distinct anchor-shaped marking (Figs. 54, 55). *V. f. lewisii* Cam.

Males (♂)

1. Propodeum with distinct striae. Thoracic punctation distinct. Apical lobe of gastral tergite VII not flat, apically deeply emarginate (Figs. 16, 18). Terminal segment of antenna curved in profile (Fig. 27). Aedeagal terminus shaped like a deep cup opened dorsally and with parallel sidewalls (Figs. 13, 14). *V. koreensis* Rad. 2
 — Propodeum without distinct striae. Thoracic punctation weak. Apical lobe of gastral tergite VII flat, apically slightly incised (Figs. 15, 17). Terminal segment of antenna slender, not curved (Fig. 28). Aedeagal terminus subcircular or spoon-shaped (Figs. 7–9). 3
2. Antenna black or blackish brown; scape below spotted with yellow. Corona with a black spot at the level of antennal socket (Fig. 85). *V. k. koreensis* Rad. — Antenna brown. Corona without black spot (Fig. 86). *V. k. orbata* Buys.
3. Aedeagal terminus inflated in lateral view with a pair of lateral wing-like processes basally as seen from below (cf. Menke & Snelling, 1978, Fig. 28 vs. 30). Third mandibular tooth distinctly concave along medial margin (based upon the American and European specimens). *V. germanica* Fab. — Aedeagal terminus flattened in lateral view (Figs. 10–12), with a pair of lateral spine-like processes basally as seen from below (Figs. 7–9). Third mandibular tooth straight along medial margin. 4
4. Ventral inner edge of gonostipes without pad (Fig. 19). Mandibular base with a triangular black spot. Body markings always yellow. *V. vulgaris* L. — Ventral inner edge of gonostipes with a pad (Fig. 20). Mandibular base without triangular spot; if the spot present body markings always white. 5
5. White area of ocular sinus with concave medial margin. Mandible basally with a triangular black spot (Fig. 82). Genitalia relatively elongate; L/W=1.03–

- 1.10 (cf. Fig. 3, A); lateral processes of aedeagal terminus longer, with nearly parallel outer sides (Fig. 8). *V. shidai* Ishikawa et al.
 — White or yellowish area of ocular sinus with straight or convex medial margin. Mandible basally without distinct black spot (Figs. 74–81). Genitalia relatively short; L/W=0.88–1.02; lateral processes of aedeagal terminus shorter, with less parallel outer sides (Fig. 7). *V. flaviceps* Sm. 6
6. Body markings white. Clypeus usually with a distinct black bar not attaining the ventral margin of clypeus. Medial margin of the white of ocular sinus usually not concave (Figs. 77, 78). *V. f. lewisii* Cam.
 — Body markings usually ivory white to yellow. Clypeal marking often much reduced. Medial margin of the yellow of ocular sinus very often convex or connected with corona (Figs. 75, 76, 81). 7
7. Body markings ivory white or pale yellow. Apical bands on gastral tergites very narrow (0.10–0.20 mm wide as measured near the middle of T₁; cf. Fig. 3, B). *V. f. karenkona* Sonan
 — Body markings usually yellow (in the northern specimens often pale yellow). Apical bands on tergites moderate in width (usually more than 0.20 mm wide as measured near the middle of T₁). *V. f. flaviceps* Sm.

ENUMERATION OF FORMS

Vespula flaviceps Smith (Figs. 4, 7, 10, 15, 17, 21, 25, 28, 133)

(= *Vespa flaviceps* Smith, *Vespa japonica* Saussure, *Vespa saussurei* Schulz, *Vespa lewisii* Cameron, *Vespa karenkona* Sonan, *Vespa quadrimaculata* Sonan)

This species has the widest range of distribution among the eastern Asiatic *Paravespula* species, and is rather common. Continental specimens of this species are often similar in coloration to those of *V. vulgaris* and *V. germanica*, while in Japan, where *V. germanica* is lacking, this species is easily distinguished from *V. vulgaris* and they dominate different habitats. There is a striking queen-worker dimorphism in color in the Taiwanese form (subsp. *karenkona*) and a weaker one in the nominate subspecies, while the Japanese form (subsp. *lewisii*) shows no such dimorphism.

Diagnosis. Queen and worker: Third mandibular tooth straight or nearly so along the mesal margin. Occipital carina distinct in upper 3/4 of gena in the queen and less developed in the worker. Relative length of scape short ($F_1/S=0.73-0.90$; usually more than 0.78). Distance between the lateral ocelli more than half the width of lateral ocellus. Cubital vein IIa as long as or longer than IIb. Thoracic punctation weak. Propodeum smooth without carina medio-basally. Prebasal depression of gastral tergite I weak. Body black with white to orange yellow markings. The marking of ocular sinus nearly straight or at times convex on the medial margin. Black bar on clypeus not well developed, at most anchor-shaped and not reaching the lower margin of clypeus, very often much reduced into a short basal bar plus two small spots located on the sides near the end of the bar, or even entirely lost. Mid- and hind tarsi pale brown.

Body length (H+Th+T₁+T₂): 11.0–14.0 mm in the queen, 7.0–10.5 mm in the worker.

Male: Occipital carina distinct only in upper 1/2 or 3/5. Antennae without tyloides; terminal segment slender, not curved. Last gastral tergite with a flat apical lobe. In structure very similar to *V. shidai* male, but different from the

latter in that the genitalia are less elongate ($L/W=0.88-1.02$; cf. Fig. 3) and the lateral processes of aedeagal terminus are shorter, with less parallel outer sides. White area of ocular sinus not concave on the medial margin. Mandible without triangular black spot at base.

Body length ($H+Th+T_1+T_2$): 7.5-9.5 mm.

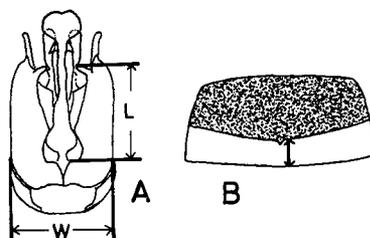


Fig. 3. Schematic drawings of male genitalia (A) and gastral tergite I (B), showing measuring parts.

Vespula flaviceps flaviceps Smith
(Figs. 29-32, 47-53, 74-76, 87-95, 119-121, 133)

Vespa flaviceps Smith, 1872, Trans. Zool. Soc. Lond. 7: 174, 191, pl. 21, figs. 11, 12; Bingham, 1897, Faun. Brit. Ind. Hym. 1: 406.

Vespa germanica var. *flaviceps*; Buysson, 1904, Ann. Ent. Soc. Fr. 73: 614-615; Liu, 1936-1937, Peking Nat. Hist. Bull. 2: 228; Wu, 1941, Cat. Ins. Sin. 6: 226.

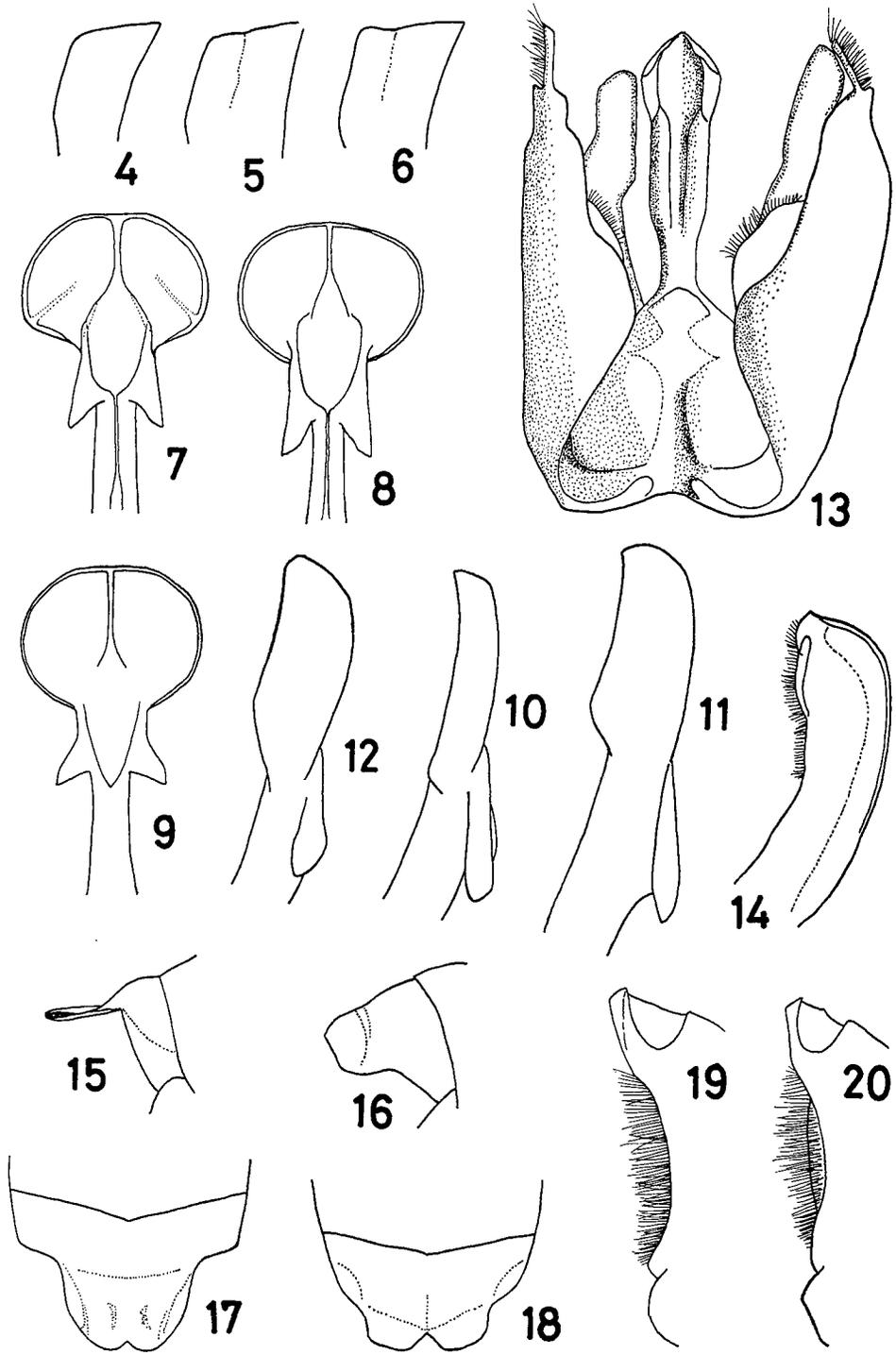
Vespa vulgaris var. *flavior* Stofa, 1933, Bull. Soc. Veneziana Storia Nat. 1: 49, syn. nov.

Vespula vulgaris flaviceps: Ma, 1937a, Ent. Phytopath. 5: 32-33.

Vespula japonica pionganensis Giordani Soika, 1976, Ann. Hist. -Nat. Mus. Natn. Hung. 68: 290, syn. nov.

Specimens examined. Many queens, workers and males from the following localities. Southern Primor'e (Anisimovka, Ussurisky region; Lake Khanka, sent by Dr. Kurzenko); Korea (Seoul, Suigen); China*: Peking (Tsin Lung Shan), Fukien (Foochow), Cheking (Hangchow), Szechuen (Yachow, Mt. Omei, Suifu, Kuanshien, Tatsienlu); India: Uttar Pradesh (Mussooree, ca. 2000 m alt.), Himachal Pradesh* (Simla).

Diagnosis. Queen: Considerably variable in color pattern. In the specimens from southern China the yellow or orange markings are more abundant than in those from northern, mountainous parts of India or northern China to southern Primor'e. In some specimens from N. W. India and southern Primor'e the body markings are much paler, approaching ivory white. Head yellowish. Frons above corona, temple and vertex black, but the black often confined to ocellar area, the rest being replaced by brown; eye loops present in the southern specimens. The yellow of ocular sinus usually connected with corona. Clypeus nearly entirely yellowish, or basally with a brown or black bar not reaching the apical margin of clypeus; this bar sometimes divided into three spots (as in *V. germanica*) or into a short basal bar plus two small spots, and in the northern specimens sometimes anchor-shaped (but always less developed than in subsp. *lewisii*). Genal band complete but in some northern specimens having a black encroachment from posterior margin causing the yellow to narrow somewhat. Antenna black except for scape below light or dark brown. Thorax black, the following parts yellow or pale yellow: posterior margin of pronotum (often widely so), triangular spot under wing base, anterior half of scutellum (the yellow posteriorly deeply incised medially), anterior margin of postscutellum, a pair of spots variable in size on propodeum. Yellow markings on scutellum and postscutellum often much reduced or lost even in southern specimens. Gaster black with yellow or orange bands



which are always deeper in color than the thoracic markings. In the specimens from Hangchow, southern China, yellowish markings sometimes extremely extensive: gastral tergite I except for a black triangular marking, apical half of tergite II (medially much narrowed), visible parts of the subsequent tergites nearly entirely; yellowish band on tergite II sometimes much reduced; tergites II-V sometimes each with a pair of brownish spots in the yellow (Figs. 90, 91). In northern specimens yellow bands less developed; tergites III-V sometimes each with a pair of oval black spots. Sternites similar to the tergites in coloration. Legs nearly entirely yellowish, but in the northern or mountainous specimens coxa, trochanter and the basal half of femur brownish.

Worker: Similar to queen except in the narrower and more parallel gastral bands. Body black, with yellowish markings (sometimes the markings are whitish and both the yellowish and whitish types are collected in the same locality). Head as in the queen; clypeal markings reduced or lost more frequently than in the queen. Thoracic markings pale; posterior band of pronotum often wide in southern specimens, but usually narrow in northern ones. Propodeum always with a pair of yellowish spots of variable size. Legs largely yellowish; coxa and trochanter partly, and femur basally sometimes blackish, especially in northern specimens. Gaster tergites each with a yellowish or whitish apical band; the bands wider and sometimes irregular in southern specimens. Tergite I very frequently with a medially interrupted transverse line at the base of the horizontal face (Figs. 93, 94). Apical bands on sternites wider than those on tergites.

Male: Males are lacking in the specimens from southern China. Many specimens from a nest dug at Mussooree, N.W. India and one specimen from Korea and one from southern Primor'e were examined. Similar to the worker in coloration. Body markings pale yellow or yellow. Clypeus with a relatively short bar or spot in the apical part; the bar rarely reaching the basal margin. Mesal margin of yellow of ocular sinus often convex or connected with corona. Genal band complete. Mandible nearly entirely yellow. Gaster bands narrow and regular.

Distribution. This form is widely distributed over the continental part of eastern Asia from southern Primor'e through China to western Burma and N. India (Fig. 133). Color pattern varies considerably, but it is difficult to divide this form into further subspecies.

USSR: Southern Primor'e; Korea; China; Burma (Tenasserim); N. India (Manipur, Assam, Sikkim, Kumaun, Binsur, Uttar Pradesh, Himachal Pradesh).

Biology. This form nests underground, and its nest architecture is essentially the same as in the Taiwanese and Japanese forms. The mature nest with envelope measures 20-25 cm in width and ca. 20 cm in height. A mature nest dug out by one of the authors, Sk. Yamane, at Mussooree (30°N, 78°E) on Nov. 3, 1978 with the help of Dr. J.M. Julka and Dr. H. Fukuda contained seven combs (two

Figs. 4-6. Profile of gastral tergite I, showing prebasal depression. 4: *V. flaviceps*; 5: *V. minuta*; 6: *V. koreensis*.

Figs. 7-12. Aedeagal terminus of male genitalia. 7, 10: *V. flaviceps*; 8, 11: *V. shidai*; 9, 12: *V. vulgaris*. (7-9: from below; 10-12: profile.)

Figs. 13 and 14. Male genitalia of *V. koreensis*. 13: dorsal view; 14: profile of aedeagal terminus.

Figs. 15-18. Last (7th) gastral tergite of male. 15, 17: *V. flaviceps*; 16, 18: *V. koreensis*. (15, 16: profile; 17, 18: dorsal view.)

Figs. 19 and 20. Ventral inner margin of gonostipes. 19: *V. vulgaris*; 20: *V. shidai*.

for new queens), ca. 7000 cells, a founding queen, ca. 2000 workers and 245 males. New queens were about to emerge.

Literature. Cameron, 1903 (*Vespa germanica*; one specimen from Assam); Ma, 1936 (*Vespa germanica flaviceps*; biology, larva), 1937b (*Vespa vulgaris flaviceps*; male genitalia).

Vespa flaviceps lewisii Cameron, stat. nov.¹⁾
(Figs. 1, 33, 43, 44–46, 54, 55, 77, 78, 99, 100, 122, 133)

Vespa japonica Saussure, 1858, Rev. Mag. Zool. 10: 261; Buysson, 1904, Ann. Soc. Ent. Fr. 73: 494, 498, 581; Matsumura, 1911, Thous. Ins. Jap. Suppl. 3: 103, Fig. 13; Matsumura, 1931, 6000 Ill. Ins. Jap., p. 13, fig. 63.

Vespa lewisii Saussure (M.S.): Smith, Trans. Ent. Soc. Lond. 1873: 198; Cameron, 1903, Entomologist 36: 280 (descript.).

Vespa saussurei Schulz, 1906, Spolia Hym. p. 231; Bequaert, 1930, Bull. Brook. Ent. Soc. 25: 67.

Vespa vulgaris var. *lewisii*: Liu, 1936–1937, Peking Nat. Hist. Bull. 11: 232; Wu, 1941, Cat. Ins. Sin. 6: 227.

Vespa lewisii: Yasumatsu, 1937, Fukuoka Hak. Zasshi 2: 71; Ishikawa, 1965, Icon. Ins. Jap. col. nat. ed. 3: 291, pl. 146, fig. 2. (*Vespa lewisii*).

Specimens examined. *Hokkaidô.* Many queens, workers and males from the following localities: Shumarinai-ko, Kitamoshiri, Asahigawa, Furano, Kôshunai, Sunayu, Obihiro, Lake Shikotsu, Lake Tôya, Nopporo, Sapporo, Jôzankei, Tomari, Bikuni, Onuma, Esashi. *Honshû.* Many queens, workers and males from the following localities: Aoni (Aomori Pref.); Morioka, Kuzakai & Getô Spa (Iwate); Inawashiro, Tadami & Adachi (Fukushima); Ageo (Saitama); Utsunomiya (Tochigi); Tôkyô; Narita (Chiba); Yawatano (Shizuoka); Nagano C., Nojiri-ko & Todai (Nagano); Takasago (Hyôgo); Wakayama; Yamaguchi. *Shikoku.* 1 ♀, Aki, Tosa, 3 v 1936 (S. Sasaki); 1 ♀, Susaki, Tosa, 21 v 1933 (Y. Sugihara); 1 ♀, Hirooka, Tosa, 7 xi 1933 (H. Okamoto); 1 ♀, same loc., 19 xi 1935 (H. Okamoto); 1 ♂, Yashima, Takamatsu, Kagawa, 19 xi 1974 (T. Sunose). *Kyûshû.* 1 ♀, Mt. Wakasugi, Fukuoka, 17 ii 1935 (S. Oishi); 1 ♀, Fukuoka, 23 ix, 1929 (K. Yasumatsu); 1 ♀, Gokayama, 29 iv 1930 (K. Yasumatsu); 1 ♀, Kumamoto, 5 iv 1907 (H. Kawamura); 2 ♀ ♀, same loc., 24 vi 1907 (H. Kawamura); 1 ♀, same loc., 25 x 1907 (H. Kawamura). *Amami Ôshima.* 1 ♀, Yakkachi, Sumiyô-mura, 18 vii 1933 (Esaki & Yasumatsu).

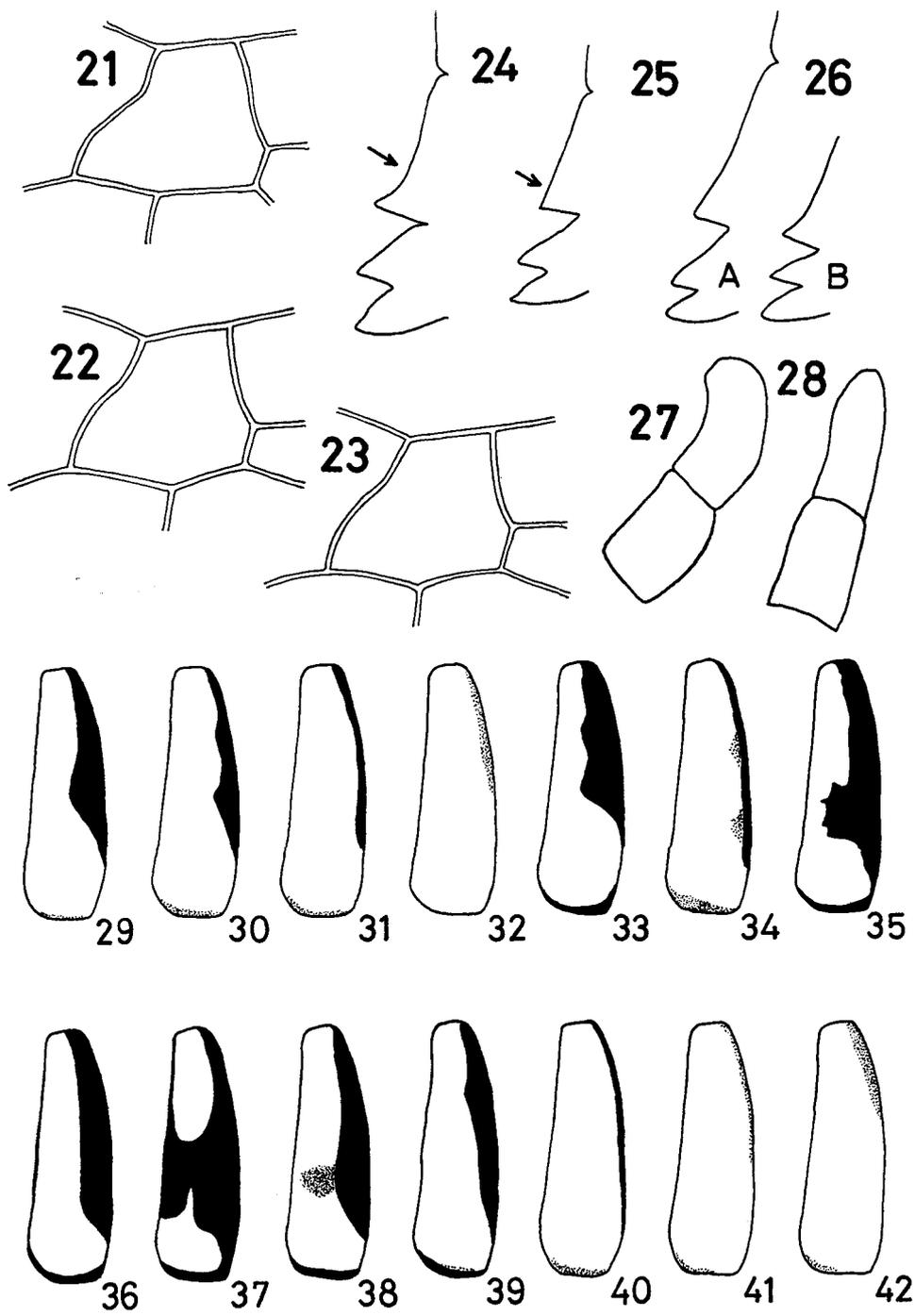
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- 1) Two distinct forms have long been confused under the name *lewisii*. This name, however, has been applied by some authors to the form which is here treated as *Vespa flaviceps lewisii*. This application is not based on the type-material, which, however, may be lost (see appendix, p. 44). Most of the authors here listed except Ishikawa (1965) might have confused the two forms.

Figs. 21–23. Cubital vein II of fore wing. 21: *V. flaviceps*; 22: *V. minuta arisana*; 23: *V. koreensis*.

Figs. 24–26. Mandible. 24: *V. germanica*; 25: *V. flaviceps*; 26: *V. koreensis* (A–♀, B–♂).

Figs. 27 and 28. Terminal segments of male antenna. 27: *V. koreensis*; 28: *V. flaviceps*.

Figs. 29–40. Genal color pattern (♀, ♂). 29–32: *V. flaviceps flaviceps*; 33: *V. f. lewisii*; 34: *V. f. karenkôna*; 35, 36: *V. shidai*; 37, 38: *V. vulgaris*; 39: *V. germanica*; 40: *V. koreensis koreensis* and *V. k. orbata*; 41: *V. minuta minuta*; 42: *V. m. arisana*.



Diagnosis. Queen & worker: Black with white markings; no distinct caste difference in color pattern. White area of ocular sinus with shallowly concave, straight or convex medial margin; the area widely separated from corona, but often narrowly in the queen. Antenna nearly entirely black. Clypeus with a distinct anchor-shaped black marking which rarely attains the apex of clypeus. White genal band complete, sometimes having a black encroachment from posterior margin. Thorax black, with the following parts white: posterior margin of pronotum narrowly, a spot under wing base, anterior margin of scutellum and postscutellum. Propodeum sometimes entirely black in the specimens from Hokkaidô, while almost always with a pair of white markings of variable size in those from southern localities. Mid- and hind tarsi usually pale brown. Gastral tergites I-V each with a narrow, white apical band; the last tergite entirely black; tergite I rarely with a pair of short white lines at base. Gastral sternites II-V each with a similar band; the last entirely black.

Male: Similar to the worker in coloration. Clypeus usually with a distinct black bar detached from the apex of clypeus. Medial margin of the white of ocular sinus not convex.

Distribution. In central and southern Honshû this form occurs in both lower and higher altitudes, but in Tôhoku (northern Honshû) and Hokkaidô it is chiefly collected in the lowlands where it may coexist with *V. shidai* which in general inhabits more mountainous areas.

Japan: Hokkaidô, Honshû, Shikoku, Kyûshû, Amami Islands.

Biology. The biology of this form has been studied mainly by Shida (1952, 1959a, 1959b, 1963) and reviewed by Iwata (1971). The following description is mainly based upon unpublished data amassed by Mr. M. Matsuura in Wakayama Pref., southern Honshû, and by Sk. Yamane in northern Japan.

In Wakayama (34°N, 135°E) the overwintered queens appear in late March to mid-April and begin to nest in late April to mid-May. The mature nests comprise 8 to 12 combs and 8000 to 12000 cells (in November). Males and new queens are usually produced from mid-October to mid-December, but in some nests they continue to emerge till March of the next year. In Morioka (39°40'N, 141°20'E), Iwate Pref., the mature nests comprise 4 to 9 combs and 1300 to 8500 cells. Workers are reared in the first 3 to 5 combs. Males and new queens are produced from late September on, but not during the winter. In Sapporo (43°N, 141°20'E), Hokkaidô, the overwintered queens first appear in early or mid-May and probably initiate a nest in late May to early June. Only a few nests have been obtained in Sapporo. They have 5 to 7 combs and 2500 to 6000 cells (in late August to early September). Males begin to emerge about the end of August or early September.

So-called nuptial flights of the males were first observed on October 10 on the crowns of trees in Morioka in 1970. The flying course was about 120 m in total length and included a maple tree, three *Pinus thunbergii* trees, bush clovers and a small building. Many males were seen visiting nearby willow trees with numerous aphids to feed upon honey dew. Some males participated in a single flight group for at least six days. During two weeks no copulation was observed; mating might have been performed on the tree crowns.

This form nests underground, in building wall voids (Fig. 44), and very rarely under the eaves (Fig. 43). Some insects are known to be parasitic on it: *Xenos vespularum* Kifune et Maeta (Stylopidae), *Metoecus paradoxus* Linné (Rhipiphoridae),

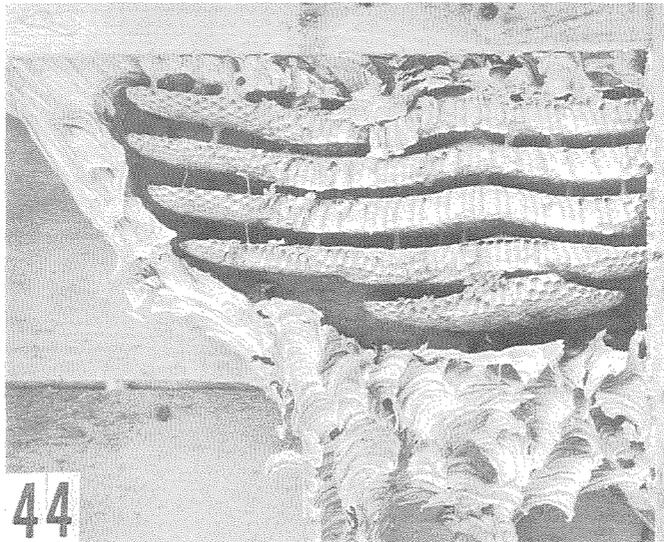


Fig. 43. Aerial nest of *V. flaviceps lewisii*.

Fig. 44. A *V. f. lewisii* nest made in building wall void. (Photo S. Makino.)

Bareogonalos jezoensis Uchida (Trigonalidae), and some diptera. Larvae of *Volucella nitobei* Matsumura (Syrphidae) are often found under the nest in soil.

Literature. Hattori & Sk. Yamane, 1975 (parasite); Iwata, 1955 (ovarian structure), 1971 (review of biology); Kifune & Maeta, 1975 (parasite); Kobayashi, 1936 (biology); Matsuura, 1966 (hibernation), 1976 (biology); Munakata & S. Yamane, 1970 (records in s. Hokkaidô); Nakayama, 1957 (hibernation); Okutani, 1950 (variation); Shida, 1952 (biology), 1959a (social structure), 1959b (life history), 1963 (prey); Sonan, 1938 (taxonomy); Suzuki, Suzuki & Takeuchi, 1961 (nest contents); Takamatsu, 1947 (reproductive organs), 1949a (postembryonic development of genitalia), 1949b (biology), 1950 (male genitalia), 1951a (distribution), 1951b (biology); S. Yamane, 1970 (adult characters); Sk. Yamane, 1969

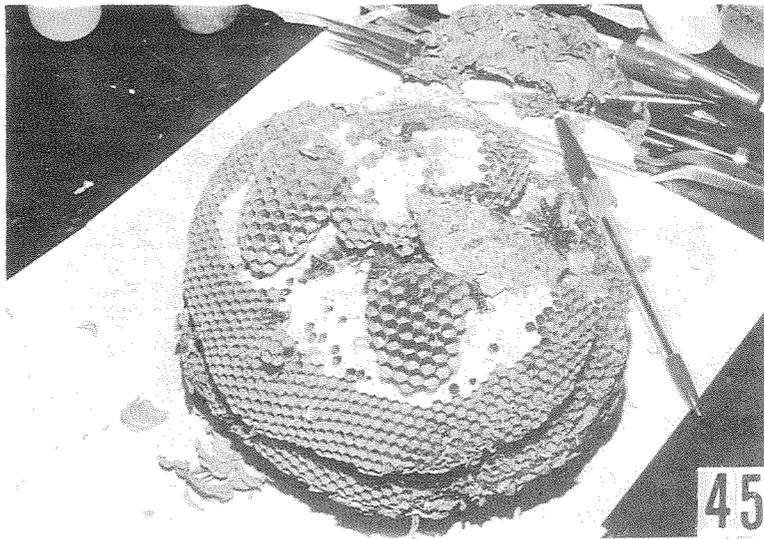


Fig. 45. Mature nest of *V. f. lewisii*.

Fig. 46. Ribbon-like supports built by *V. f. lewisii*.

(hibernation), 1976 (larva); Sk. Yamane & Kamijô, 1976 (adult characters and relation with aphids). (In most of these papers this form is referred to as *Vespula lewisi* or *V. lewisii*).

Vespula flaviceps karenkona Sonan, stat. nov.
(Figs. 34, 56-59, 79-81, 96-98, 123, 124, 133)

Vespa karenkona Sonan, 1929, Trans. Nat. Hist. Soc. Formosa 19: 148 (♂).

Vespa quadrimaculata Sonan, 1929, Trans. Nat. Hist. Soc. Formosa 19: 148-149 (♀), syn. nov.

Specimens examined. Taiwan. Many queens, workers and males from three nests dug out by S. Yamane at Kwantauchi, Nantou (24°06'N, 121°02'E; 720–1100 m alt.). These collections have shown that "*Vespa karenkona*" and "*Vespa quadrimaculata*" are conspecific and represent different castes.

Diagnosis. Queen: Black with yellow to orange yellow markings. Yellow of ocular sinus connected with corona. Eye loops absent. Clypeus yellow with a black spot of variable size in the middle; this spot sometimes extends towards the upper margin of the clypeus, thus forming a bar; there are inconspicuous, irregular brownish markings around the spot. Band of gena muddy yellow and complete. Antenna black: only scape below yellowish brown. Yellow thoracic markings reduced into the posterior margin of pronotum (medially much narrowed). Yellow anterior margin of scutellum and postscutellum very narrowly and a triangular spot under wing base (often reduced). Propodeum nearly entirely black, sometimes with a pair of small yellowish spots. Coxa, trochanter, and femur except for apical part of all legs black or blackish brown; yellow area of femur more extensive in fore leg than in mid- and hind legs; the outer parts largely yellow except for a black spot on the outer face of fore tibia. Gastral tergites I and II largely black, each with a very narrow yellow or orange apical band which is narrowed medially. Base of the subsequent tergites black; apical band wider than on the preceding tergites. The basal black area on tergite III medially and widely produced, and laterally with peninsular extensions. Tergites IV and V with a pair of small, free black spots in the yellow (Fig. 97). Sternites similar to the tergites in coloration.

Worker: Similar to the workers of the nominate and the Japanese forms, but distinct from the queen of this form. Distinguishable from the nominate form worker in the following points: Body always marked with ivory white or at most pale yellow but not with yellow, clypeus usually with a distinct black bar, and apical white bands on tergites much narrower and more regular. Distinguishable from the *lewisii* worker in the following points: Body markings more yellowish, scape below colored yellowish brown (nearly entirely black in *lewisii*), clypeal markings less developed (always distinct and anchor-shaped in *lewisii*), markings on scutellum and postscutellum and gastral bands less developed, and propodeum usually entirely black (usually with a pair of white spots in *lewisii*).

Male: Very similar to the worker in coloration, but black clypeal marking much reduced. Last tergite occasionally with a pair of whitish spots. Apical bands on sternites often much reduced and last sternite usually without whitish band. Ivory white of ocular sinus usually convex along medial margin or connected with corona. Genal band complete.

Distribution. Taiwan: Nantou (Kwantauchi, 600–2100 m alt.), Chiayi (Alishan), Hualien (1000–2300 m alt.).

Biology. This form nests underground. Its colonies are probably started in spring (in March to May) and appear to be annual, but they persist to May or June of the next year. At least part of new queens and males overwinter in the nest together with workers. Probably most new queens and males leave the nest by early Spring, but the colonies may be maintained inertly for some period by the remaining workers and males (cf. Sk. & S. Yamane, 1975). One foundress survived even in mid-March. The number of combs in mature nests ranges from 5 to 11, and the total number of cells from 5500 to 13000. A trigonalid parasite,

Bareogonalos huisumi Sk. et S. Yamane, is found from cocooned cells.

Literature. Sk. et S. Yamane, 1975 (*Vespula karenkona*; nest records, parasite); Sk. Yamane, 1976 (*V. karenkona*; larva); S. Yamane, 1977 (*V. karenkona*; biology).

Vespula shidai Ishikawa, Sk. Yamane et Wagner
(Figs. 2, 8, 11, 20, 35, 36, 60, 82, 101, 102, 125, 126, 133)

Vespula lewisii: auct. jap. pars.

Vespula A, Sk. Yamane & Kamijō, 1976, Ins. Matsum. N.S. 8: 62.

Vespula shidai Ishikawa, Sk. Yamane & Wagner, 1980, Ins. Matsum. N.S. 19: 44-46.

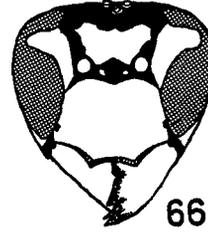
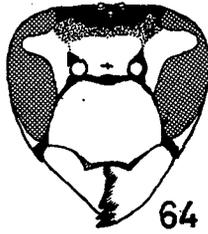
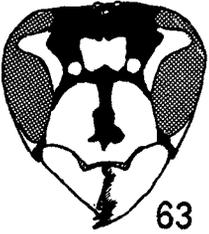
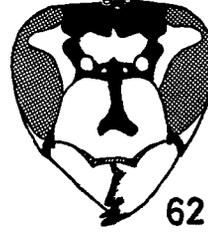
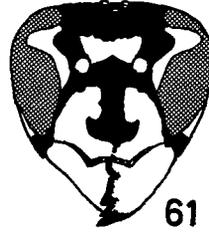
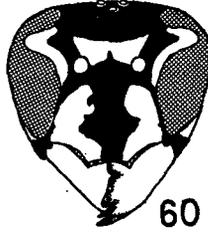
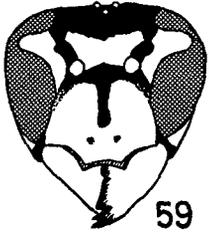
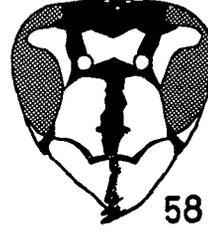
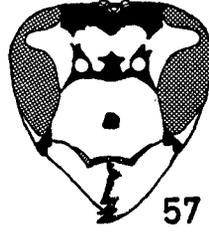
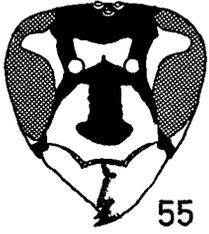
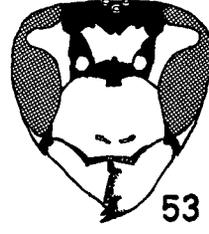
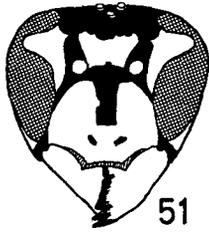
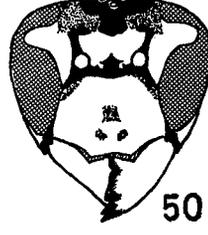
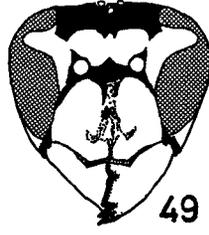
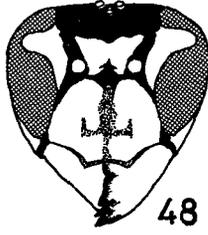
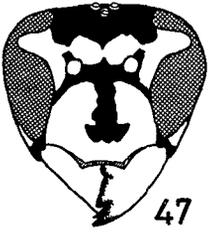
Specimens examined. USSR. 2♀♀4♂♂, southern Primor'e (sent by Dr. Kurzenko). *Chishima* (=Kuriles). 2♀♀, Nikishiro, Kunashiri Isl., 17-22 vii 1935 (T. Uchida), 1♀, Seseiki, Kunashiri Isl., 27-28 vii 1935 (T. Uchida). *Hokkaidō*. Many queens, workers and males from the following localities: Osashima, Kamiotoineppu, Asahigawa, Kamuikotan, Mt. Yūbari, Ashibetsu, Bibai, Kōshunai, Mt. Shokambetsu, Iwaobetsu, Akkeshi, Rubeshibe, Shari, Sunayu, Shirataki, Oketo, Chikabetsu, Nukabira, Tomuraushi, Shikaribetsu, Obihiro, Mt. Apoi, Tomakomai, Lake Shikotsu, Mt. Eniwa, Mt. Muine, Jōzankei, Sapporo, Mt. Teine, Otaru, Bikuni, Furubira, Tomari, Akaikawa, Ōnuma, Esashi, Hakodate. *Honshū*. 4♀♀81♂♂ from the following localities: Kuroishi, Aoni, Yamagata, Hirosaki, Zatōishi (Aomori Pref.); Goshogake Spa (Akita); Sakata, Yonezawa (Yamagata); Kitakami (Iwate); Shibata (Niigata); Ageo (Saitama); Chūzenji (Tochigi); Tōkyō; Todai, Nagano C., Fukushima (Nagano); Mts. Akaishi (Shizuoka—Nagano); Foot of Mt. Fuji (Shizuoka); Kozagawa, Hiki-shihara (Wakayama); Fukuyama (Hiroshima). *Shikoku*. 3♀♀6♂♂1♂ from Yamada, Susaki, Mt. Kuishi, Kōchi C. (Kōchi Pref.); Awa-kawashima (Tokushima). *Kyūshū*. 1♀, Kagoshima, 12 ix 1958 (K. Kamijō); 2♀♀, Takachihogawara, 7 x 1973 (H. Higuchi); 1♀, Kosugidani (ca. 1000 m alt.), Yakushima, 13 x 1976 (T. Sunose), 1♀, Ambo (ca. 200 m alt.), Yakushima Isl., 18 x 1973 (T. Kumata).

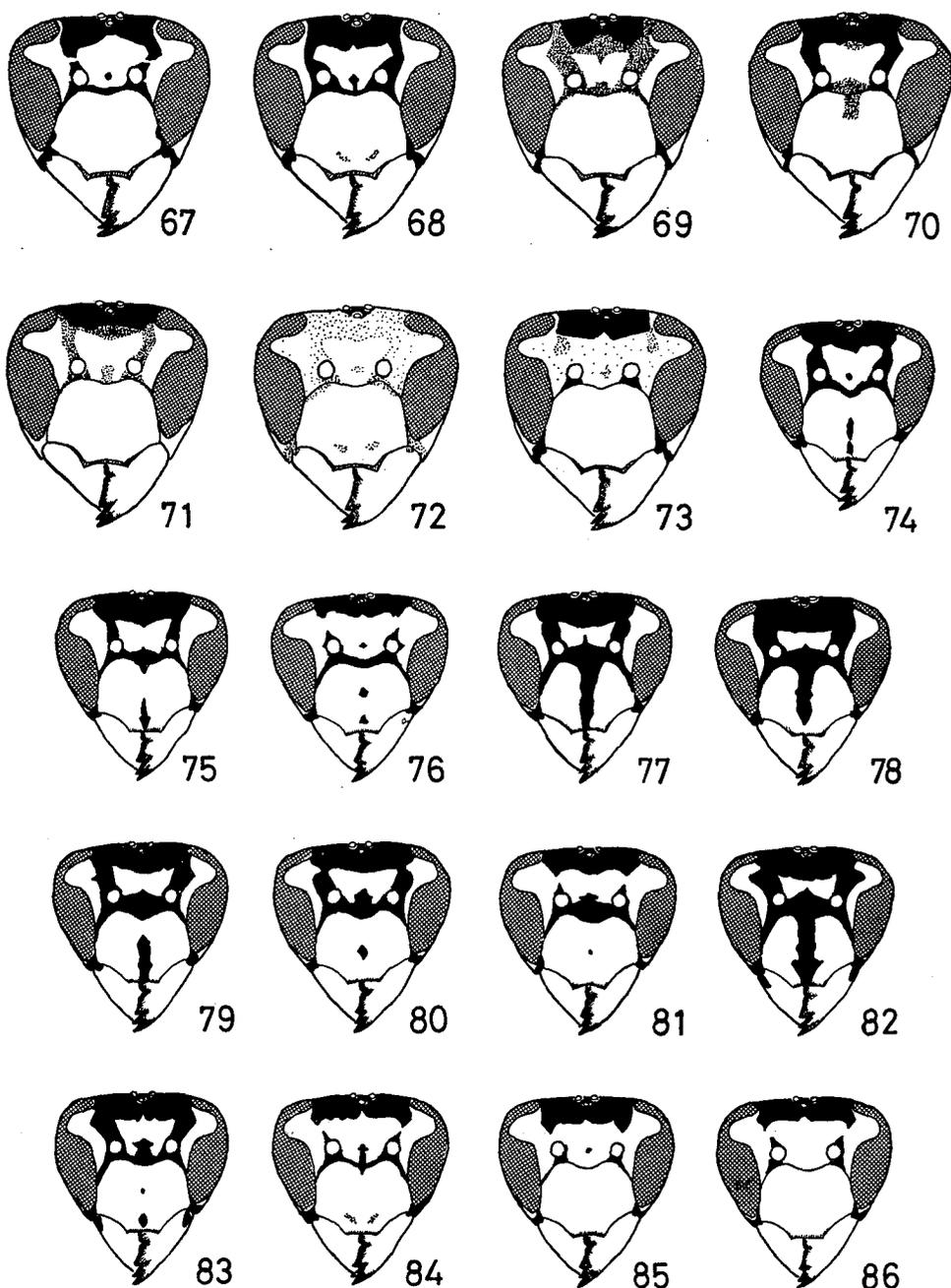
Diagnosis. Nearly identical with *V. flaviceps* in structure except in male genitalia. Queen & worker: Third mandibular tooth straight or nearly so along mesal margin. Occipital carina distinct in upper 3/4 in the queen and less developed in the worker. Relative length of scape short ($F_1/S=0.72-0.80$, usually more than 0.76). Cubital vein IIa as long as or longer than IIb. Propodeum smooth without carina medio-basally. Prebasal depression of gastral tergite I weak.

Body length (T+Th+T₁+T₂): 12.0-13.0 mm in the queen, 7.5-10.5 mm in the worker.

Very similar in coloration to *V. flaviceps lewisii* and some northern specimens of *V. f. flaviceps*, but more melanistic: White marking of ocular sinus clearly concave along medial margin, and never connected with corona. Clypeal black bar

Figs. 47-86. Facial color pattern. 47-73: ♀, ♂. 47-50: *V. flaviceps flaviceps*, ♀; 51-53: ditto, ♂; 54, 55: *V. f. lewisii*, ♀, ♂; 56, 57: *V. f. karenkona*, ♀; 58, 59: ditto, ♂; 60: *V. shidai*, ♀, ♂; 61, 62: *V. vulgaris*, ♀; 63: ditto, ♂; 64: *V. structor*, ♂; 65: *V. germanica*, ♀, ♂; 66: ditto, ♂; 67: *V. koreensis koreensis*, ♀; 68: ditto, ♂; 69: *V. k. orbata*, ♀; 70, 71: ditto, ♂; 72: *V. minuta minuta*, ♂; 73: *V. m. arisana*, ♂. 74-86: ♂. 74-76: *V. flaviceps flaviceps*; 77, 78: *V. f. lewisii*; 79-81: *V. f. karenkona*; 82: *V. shidai*; 83: *V. vulgaris*; 84, 85: *V. koreensis koreensis*; 86: *V. k. orbata*.





developed, usually anchor-shaped, very often reaching the apical margin of clypeus. Genal band often somewhat narrowed by the black especially in the middle. Propodeum usually without white spots, especially in northern specimens. Mid- and hind tarsi very often dark brown.

Male: Structurally very similar to the preceding species, but different from the latter in the genitalia somewhat elongate ($L/W=1.03-1.10$; cf. Fig. 3, A) and the lateral processes of aedeagal terminus longer, with nearly parallel outer sides (Figs. 8, 11). Coloration as in the worker. Medial margin of the white of ocular sinus deeply concave. Mandible basally with a distinct triangular black marking.

Body length ($T+Th+T_1+T_2$): 7.0–10.5 mm.

Distribution. Although the range of this species nearly coincides with that of *V. flaviceps lewisii* in Japan (Fig. 133), it is more common in Hokkaidô and the mountainous regions of Honshû. Curiously enough, it occurs also in lowlands and even near the coastal regions of southern Japan. The occurrence of this species was first noticed in Japan, but we have examined several specimens of this species from southern Primor'e (also see Eck, 1978). Some older records of "*Vespa japonica*" or "*Vespula vulgaris lewisii*" from the region of Lake Khanka and Manchuria (e.g. Buysson, 1904) may have been based upon specimens of this species.

USSR: Southern Primor'e (Anisimovka; Suputinsky Zap.); Chishima: Kunashiri Isl.; Japan: Hokkaidô, Honshû, Shikoku, Kyûshû (including Yakushima Isl.).

Biology. This species nests underground and in hollow trees, and also often in building wall voids in urban environments. In Ibaraki Pref. ($36^{\circ}50'N$, $140^{\circ}30'E$), central Honshû, mature nests comprise 5–9 combs and 3300–7000 cells in November, markedly smaller than those of *V. flaviceps lewisii* (8–12 combs and 10000–15000 cells in November) (Kojima, personal communication). In Sapporo, Hokkaidô, the overwintered queens appear in early or mid-May. The mature nests comprise 7–9 combs and 2600–15100 cells in September. *Bareogonales jezoensis* and some diptera have been found to be parasitic on this species.

Literature. Munakata & S. Yamane, 1970 (*Vespula* sp.; records in s. Hokkaidô); S. Yamane, 1970 (*Vespula* sp.; adult characters); Sk. Yamane, 1976 (*Vespula A*; larva); Sk. Yamane & Kamijô, 1976 (*Vespula A*; adult characters, relation with aphids); Sk. Yamane & Kanda, 1979 (*Vespula A*; hibernation).

Vespula vulgaris Linné

(Figs. 9, 12, 19, 37, 38, 61–63, 83, 103–105, 127, 128, 131)

Vespa vulgaris: Buysson, 1904, Ann. Soc. Ent. Fr. 73: 603–606.

Vespula vulgaris: Liu, 1936–1937, Peking Nat. Hist. Bull. 11: 231–232; Ma, 1937a, Ent. Phytopath. 5: 32; Wu, 1941, Cat. Ins. Sin. 6: 227; Ishikawa, 1965, Icon. Ins. Jap. col. nat. ed. 3: 291, pl. 146, fig. 1.

Specimens examined. *Sakhalin.* 1 ♀, Horo (Central Expt. Sta.), 20 x 1930; 1 ♀, same loc., 4 x 1930; 1 ♀, Konuma, 10 x 1932 (H. Yaku); 1 ♀, loc. not stated, 22 vii 1932 (H. Kôno, Haga & Shimizu); 1 ♀, Tarandomari, 25–27 vii 1934 (C. Watanabe & T. Inoue); 1 ♀, Taranai (Central Expt. Sta.), 19 vii 1936. *Chishima (Kuriles).* 3 ♀ ♀, Nikishiro, Kunashiri Isl., 17–22 vii 1935 (T. Uchida); 1 ♀, Yamabetsu, Kunashiri Isl., 22–25 vii 1935 (T. Uchida). *Hokkaidô.* 6 ♀ ♀ 81 ♀ ♀, from the following localities: Kami-otoineppu, Nakagawa, Osashima, Shirataki, Maruseppu, Mt. Kumaneshiri, Akan, Sunayu, Kawayu, Wakoto, Ashoro, Nukabira, Obihiro, Mt. Yûbari, Mt. Muine, Sapporo, Akaikawa, Mt. Kariba. *Honshû.* 2 ♀ ♀, Mt. Hakkôda, Aomori Pref., 13 iv 1971 (S. Aoki); 14 ♀ ♀ 71 ♀ ♀ 68 ♂ ♂, Goshogake Spa, Hachimantai, Akita Pref., 13–17 ix 1970 (Y. Maeta & Sk. Yamane); 1 ♀, Myôkô, Niigata Pref., 8 viii 1967 (H. Itami); 1 ♀, Kamikôchi, Nagano Pref., 8 vi 1925 (Y. Ota); 1 ♀, Chûzenji, Nikkô, Tochigi, 6–? vi 1911 (Matsumura).

*China**. 1♀, West of Chego-Pass, Szechuen, 13-18 vii 1923 (D.C. Graham); 1♀, 9 mi. SW of Tatsienlu (8500-13000 ft.), Szechuen, 25-27 vi 1923 (D.C. Graham).

Diagnosis. Queen & worker: Third mandibular tooth straight or at most slightly concave along mesal margin. Occipital carina reaching the mandibular base in the queen, often faint in lower 1/3 of the gena in the worker. Relative length of scape short ($F_1/S=0.78-0.84$). Cubital vein IIa as long as or slightly longer than IIb. Thoracic punctuation weak. Propodeum smooth, apically with minute striae. Prebasal depression of tergite I weak.

Body length ($H+Th+T_1+T_2$): 12-13 mm in the queen, 7.5-9.0 mm in the worker.

Black with pale and deep yellow markings. Markings on head and thorax pale and those on gaster deep. Yellow area of ocular sinus with concave medial margin and widely separated from corona. Clypeus with a distinct anchor-shaped black marking which sometimes extends downwards to the ventral margin of clypeus in the worker. Yellow genal band with a wide black interruption. Propodeum entirely black in the queen, but often with a pair of yellow spots in the worker. Gastral tergite I usually with a distinct medial black maculation with a basal stalk in the worker, while the maculation is always absent in the queen (that is, the basal black band is nearly parallel-sided) (Fig. 105 vs. 103).

In the two queen specimens from Szechuen, China, the yellow genal band is only slightly interrupted by blackish brown (Fig. 38). In one of them the margin of the yellow of ocular sinus is not concave, and the propodeum with a pair of yellow spots.

Male: Occipital carina usually absent or faint in lower 1/3 of the gena. Flagellar segments of antenna IV-XI with tyloides; last segment slender and not curved. Last gastral tergite with a flat apical lobe. Aedeagal terminus with lateral spine-like basal projections directed anteriorly. Ventral inner margin of gonostipes of uniform thickness, i.e., without pad (Fig. 19). Color pattern as in the worker except in the following points: Clypeus pale yellow, with one or two small black spots near ventral margin of clypeus. Yellow genal band not interrupted. Mandible with a triangular basal black spot. Propodeum without yellow spots. Black maculation of gastral tergite I often widely attached basally.

Body length ($H+Th+T_1+T_2$): 8.5-9.5 mm.

Distribution. This species is widely distributed in the Holarctic region, yet the color pattern is fairly stable throughout the range (Fig. 131). It was introduced to the Melbourne area in Australia (Edwards, 1976). In eastern Asia it is far less common than *V. flaviceps* and *V. shidai*. In the southern parts of China, Honshū and the southwestern parts of Hokkaidō, it usually occurs in mountains, while in the eastern parts of Hokkaidō, Chishima and Sakhalin it is not rare in plains. In at least northern Japan it associates with coniferous forests as in N. America.

USSR: Siberia (Irkutsk, Gobitza), Sakhalin; Chishima; Japan: Hokkaidō, Honshū (central and northern parts); Mongolia; China: Manchuria, Peking, Szechuen; India (northern parts).

Biology. The biology of this species has been well studied in Europe. In eastern Asia, however, little is known about its nesting habits. The following is based upon unpublished observations made by Sk. & S. Yamane in Japan. The species nests underground or in tree hollows. A mature nest from Hachimantai (40°N, 140°50'E; ca. 1000 m alt.), Honshū, comprised 9 combs and contained a

founding queen, 1142 workers, 958 males and 375 new queens (17 ix 1970). A nest from Oketo (43°40'N, 143°45'E; 400 m alt.), Hokkaidô, had five combs on 28 Aug., 1970, while males were observed to have started emerging. The nest paper is much the same as in *V. flaviceps* and *V. shidai*. A trigonalid, *Bareogonalos jezoensis*, and a syrphid, *Volucella* sp., are parasitic on this species.

Literature. Takamatsu, 1949c (*Dolichovespula norvegica saxonica*; biology); Takamatsu, 1950 (*D. n. saxonica*; male genitalia); S. Yamane, 1970 (adult characters); Munakata & S. Yamane, 1970 (records in s. Hokkaidô); Sk. Yamane, 1973 (parasite); Sk. Yamane, 1976 (larva); Sk. Yamane & Kanda, 1979 (hibernation).

Vespula structor Smith

(Figs. 64, 106)

Vespa structor Smith, 1872, Trans. Zool. Soc. 7, ser. 3: 191-192, pl. 21, fig. 12 (♂);
Bingham, 1897, Fauna Brit. Ind. Hym. 1: 404-405 (♀♂♂).

Specimens examined. *China.* 1 ♀*, Gieh Yin Temple, Mt. Omei, 10 viii 1925 (D.C. Graham). *Nepal.* 10 ♀♀, Ghora Tobela (3000-3300 m), Bagmati, 23-29 ix 1975 (S. Takagi); 1 ♀, Kyangjin Gomba-Ghora Tobela, Bagmati, 28 ix 1975 (S. Takagi); 4 ♀♀, Syn Gomba (3300-3500 m), Bagmati, 3 x 1975 (S. Takagi). *India.* 1 ♀, Simla (ca. 2000 m), U.P., 3 xi 1978 (Jap. Ind. Co. Tr.).

Diagnosis. Queen: We could not examine the queen of this species, but according to Bingham (1897) it is similar to the worker except in the following details: Gaster yellow instead of reddish yellow or orange. Basal black bands of gastral tergites I-III wider. Legs more extensively colored yellow.

Worker: Third mandibular tooth straight or at most slightly concave along mesal margin. Occipital carina reaching the base of mandible, but sometimes very weak or absent in lower 1/3 of the gena. Frontal suture very weak. Relative length of scape very short ($F_1/S=0.83-0.90$). Distance between the lateral ocelli more than half the width of lateral ocellus. Cubital vein IIa longer than IIb. Thoracic punctation very weak. Propodeum very smooth, medio-dorsally without vertical carina. Prebasal depression of tergite I weak.

Body length ($H+Th+T_1+T_2$): 7.0-9.5 mm.

Black with yellow and orange markings. Head extensively yellowish; temple black; area just above the corona brownish. Corona not sharply defined by black from the yellow of eye sinus. Genal band complete. Clypeus usually without distinct black markings. Antenna black except for the scape yellow below. Thorax black, with following parts yellow or brown: posterior margin of pronotum, pronotal tubercle (sometimes pronotum widely yellowish), a spot under wing base (often lost), a narrow short line on each side of anterior margin of scutellum. Coxae, trochanters and femora of all legs largely blackish; femora apically, tibiae and tarsi of all legs yellowish; apical half of tarsal claws brown. Gaster extensively orange. Declivous part of tergite I black; horizontal part orange. Tergites II-V basally black, but usually only orange color visible. Last tergite entirely black. Sternites more yellowish, basally black (on sternite II the black extending apically in the middle); apical broad yellow parts each containing a pair of small black spots. The last sternite nearly entirely orange yellow.

Male: No male specimen examined. According to Bingham (1897) the male is very similar to the worker in coloration; thorax nearly black, only the posterior

margin of pronotum bright yellow; gastral tergites II–V each with a pair of black elongate spots.

Distribution. This species has been known only from the Himalayas and southern China, and may be sympatric with *Vespula minuta minuta* and *V. flaviceps flaviceps*. An undetermined form close to *V. rufa* and a supposed subspecies of *V. rufa* also occur in these regions. The latter is very similar to *V. structor* in coloration, suggesting a case of the Müllerian mimicry, but we have no evidence for their coexistence.

China: Szechuen; Nepal: Bagmati; India: Binsur, Simla, Kumaun, Sikkim (up to 2500 m alt.).

Vespula germanica Fabricius
(Figs. 24, 39, 65, 66, 107, 108, 132)

Vespa germanica: Buysson, 1904, Ann. Soc. Ent. Fr. 73: 609–614.

Vespula germanica: Liu, 1936–1937, Peking Nat. Hist. Bull. 2: 226–228; Wu, 1941, Cat. Ins. Sin. 6: 225–226.

Specimens examined. USSR. 3♀♀ from southern Primor'e and Zabaikal'e (sent by Dr. Kurzenko). China. 1♀, Harusu, Manchoukuo, 12 ix 1937 (T. Inukai), 1♀, Kaigen (=Kaiyuan), Manchoukuo, 14 v 1936 (I. Okada), 1♀, same loc., 29 ix 1936 (I. Okada), 1♀, Feng-tien, Manchoukuo, 15 viii 1940 (S. Matsumura), 1♀, Anto, ix 1933 (T. Tashiro), 2♀♀, Peking, 5 ix 1939 (H. Kôno). Korea. 1♀, loc. not stated (Okamoto), 1♀, Genzan, vii 1920, 1♀, Keijo (=Seoul), vii 1920. Karakoram. 3♀♀, Shardu, viii 1975 (Maeda).

Diagnosis. Queen and worker: Third mandibular tooth concave along mesal margin. Occipital carina distinct, reaching the mandibular base. Frontal suture below the anterior ocellus invisible. Relative length of scape short ($F_1/S = 0.77-0.82$). Distance between the lateral ocelli nearly as wide as the diameter of lateral ocellus. Apical margin of clypeus concave and medially depressed. Thoracic punctation inconspicuous. Propodeum without striae, nor vertical carina. Cubital vein IIa longer than IIb. Prebasal depression of gastral tergite I not distinct.

Body length ($H+Th+T_1+T_2$): 11.5–13.5 mm in the queen, 8.0–9.5 mm in the worker.

Color pattern as in the European form. Black with yellow to orange yellow markings. Differs from *V. vulgaris* in the following points: Medial margin of the yellow of ocular sinus not concave, the yellow sometimes connected with corona. Yellow genal band not interrupted medially by black color. Clypeus with at most three small spots (one central and two lower lateral), which are sometimes much more reduced in the worker (entirely yellow, for example, in the specimens from Karakoram). Gastral tergite I always with median black maculation which is rhomboid and sometimes wider than long (the maculation absent in the queen of *V. vulgaris*). Gastral tergites II–V very often with lateral spots.

The male was not available.

Distribution. The range of this species in eastern Asia is not well known. Japan and Taiwan obviously lack this species, and the record from Sakhalin by Buysson (1904) is somewhat doubtful. It is much less abundant than *V. flaviceps* on the continent.

USSR: Southern Primor'e (Lake Khanka), Zabaikal'e, Altai; China: Manchoukuo, Peking; Korea; North India; Karakoram.

Vespula koreensis Radoszkowski
(Figs. 6, 13, 14, 16, 18, 23, 26, 27, 134)

(= *Vespa koreensis* Radoszkowski, *Vespa orbata* Buysson, *Pseudovespa birulai* Gussakovskij)

This is one of the least understood taxa within the genus *Vespula*. The original description by Radoszkowski (1887) was very inadequate, since he attempted to characterize the species by color pattern and size alone. Later Buysson (1904) examined the type-series of *V. koreensis*, 3 workers and 1 male, and redescribed the species. His redescription was not much better than the original description adding only a few minor morphological details. Although he had a male specimen he unexplainably did not examine its genitalia. Since that time the type of *V. koreensis* appears to have been lost.

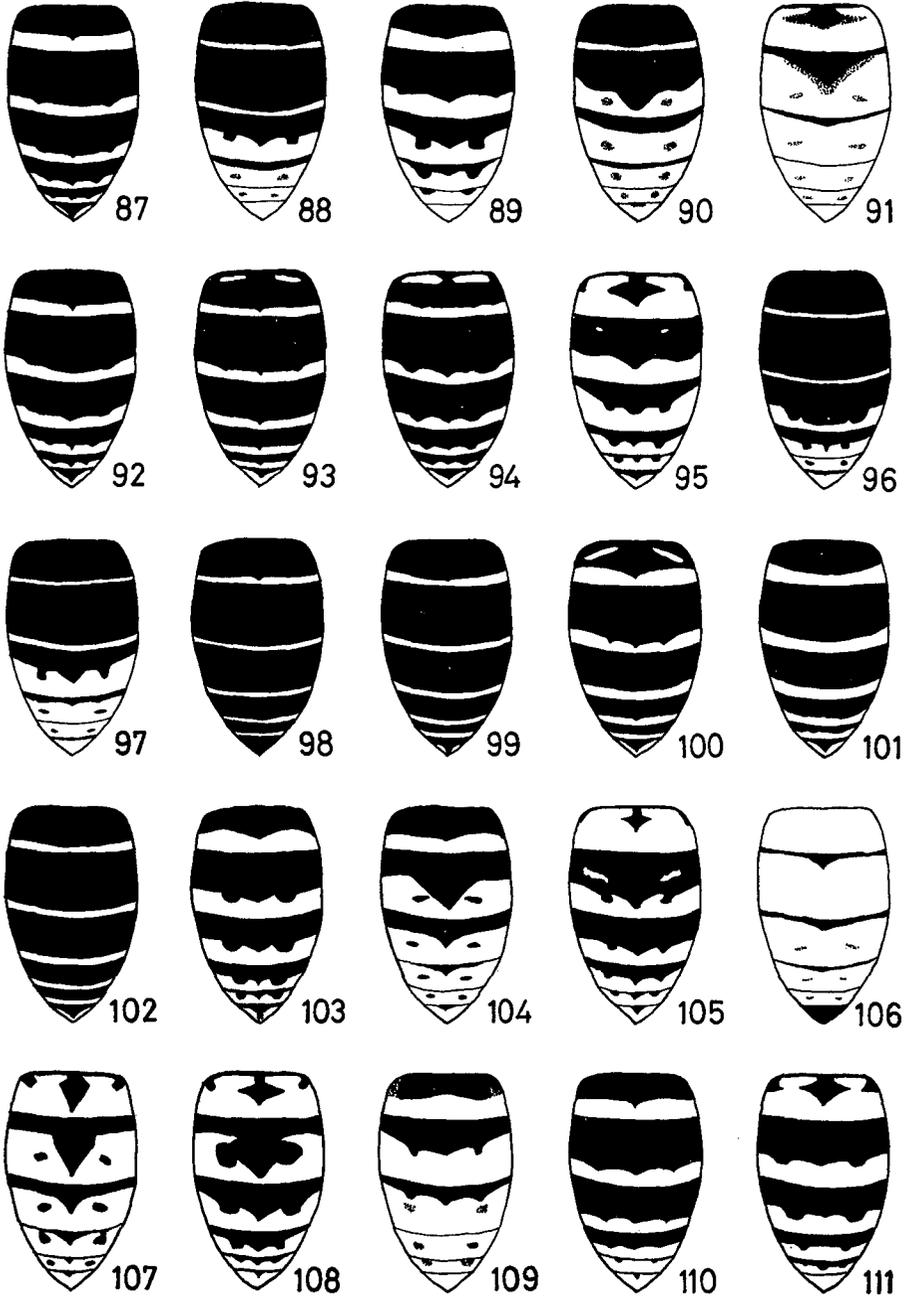
Buysson (1902) had previously described a wasp, "*Vespa orbata*", from specimens which he believed to be the workers of a true hornet species. His description of *V. orbata* included some morphological details which seem to indicate that he was in reality examining queens of a *Vespula* species. This form has also been a puzzling taxon.

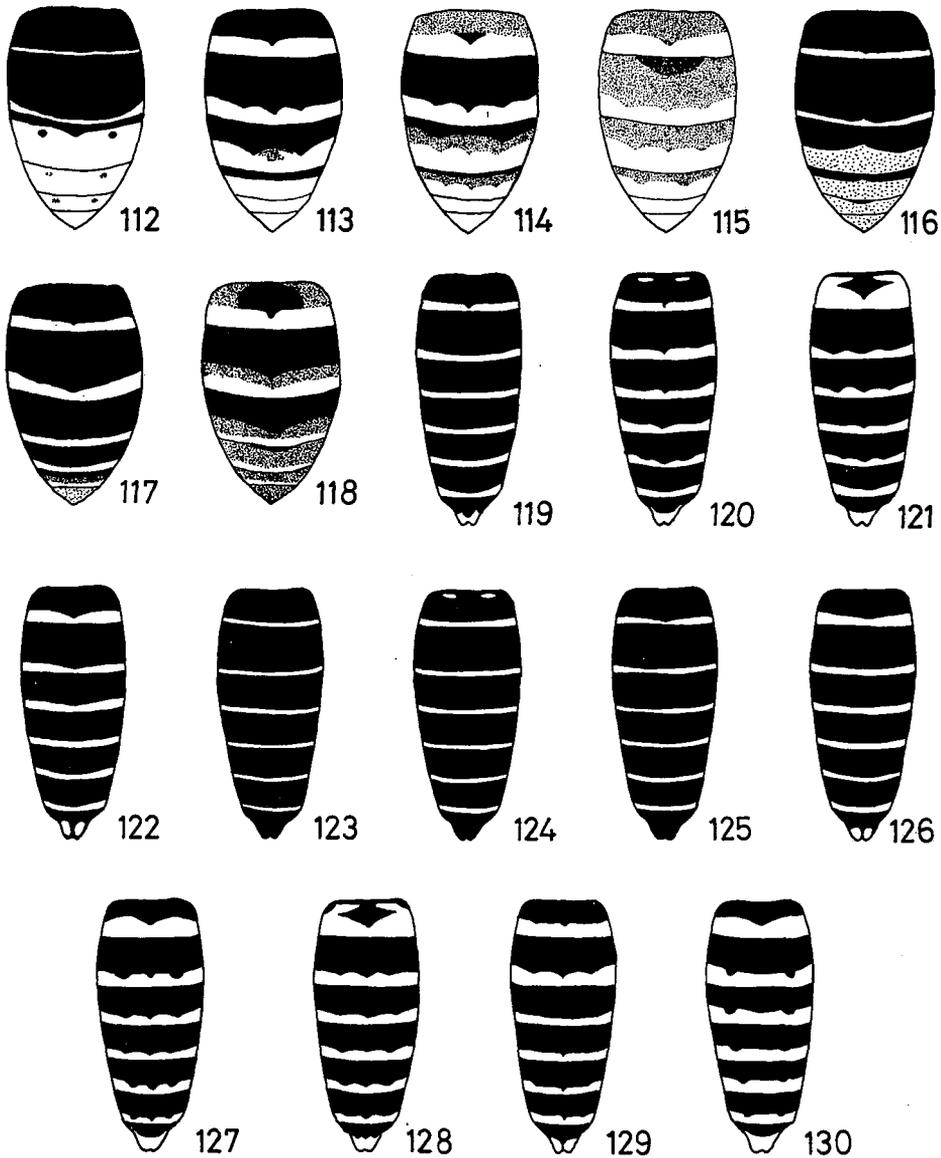
We have examined some worker specimens of a Korean *Vespula* species which agree well with the original description of *V. koreensis* and Buysson's (1904) redescription in color pattern and size. They possess a distinctly striate propodeum which was not mentioned by Radoszkowski or Buysson. Recently we also examined, through the courtesy of Dr. A.S. Menke, some *Vespula* specimens from southern China which have distinct propodeal striae, particularly in the queen. The apparently associated worker and male specimens, though in color pattern notably different from the queens, share important structural characters with the queens (the propodeal striation is less pronounced and rarely almost indiscernible in the worker). The queen specimens had been earlier determined as *Vespula orbata* by Dr. J. Bequaert and subsequently identified under the manuscript name *V. koreensis salebrosa* by Dr. I. H. H. Yarrow. These queens match well with Buysson's description of *Vespa orbata*. Quite recently we have been informed by Dr. R. Ishikawa that the type specimen of *V. orbata* deposited in the National Museum of Paris (N.H.) has a distinctly striate propodeum. This is what we expected.

Most fortunately, Dr. N.V. Kurzenko kindly sent us some queen, worker and male specimens from the Ussuri Valley. These specimens, which he had determined as *Vespula birulai*, possess striate propodea. *V. birulai* was originally described by Gussakovskij (1933) as a species of the genus "*Pseudovespa*" from Ussuri. This form shows a distinct queen-worker dimorphism in color pattern. The worker specimens agree well with the original description of *Vespa koreensis* and with the Korean specimens we have examined.

All the specimens examined agree in the structures of the body and male genitalia. It is our conclusion that these specimens, having the striate propodeum, belong to *Vespula koreensis* and that *Vespa orbata* and *Pseudovespa birulai* are actually synonyms, though the name *orbata* should be retained as a subspecies name. Another redescription of *V. koreensis* was published by Giordani Soika (1976) who

illustrated the propodeal striation based upon worker specimens from North Korea. Thus there appears to be a rather general agreement among recent workers as to the true status of *V. koreensis*. We recognize at least two geographical forms, *V. k. koreensis* (northern China, Korea and southern Siberia) and *V. k. orbata* (southern China, Burma and northern India).





Figs. 87-130. Gastral color pattern. 87-118: ♀, ♂. 87-91: *V. flaviceps flaviceps*, ♀; 92-95: ditto, ♂; 96, 97: *V. f. karenkona*, ♀; 98: ditto, ♂; 99: *V. f. lewisii*, ♀, ♂; 100: ditto, ♂; 101: *V. shidai*, ♀; 102: ditto, ♂; 103: *V. vulgaris*, ♀, ♂; 104: ditto, ♀; 105: ditto, ♂; 106: *V. structor*, ♂; 107: *V. germanica*, ♀, ♂; 108: ditto, ♂; 109: *V. koreensis koreensis*, ♀; 110, 111: ditto, ♂; 112: *V. k. orbata*, ♀; 113-115: ditto, ♂; 116: *V. minuta minuta*, ♂; 117, 118: *V. m. arisana*, ♂. 119-130: ♂. 119-121: *V. flaviceps flaviceps*; 122: *V. f. lewisii*; 123, 124: *V. f. karenkona*; 125, 126: *V. shidai*; 127, 128: *V. vulgaris*; 129: *V. koreensis koreensis*; 130: *V. k. orbata*.

Another problem concerns the true status of *Vespa orbata* var. *aurulenta* Buysson which was described based upon queen specimens from northern China and southern Siberia. At first the original description and the collection data of the type-series seemed to suggest the identity of *aurulenta* with *V. koreensis* (= *V. birulai*). According to Dr. Ishikawa, however, the type of *aurulenta* has a smooth propodeum. This fact strongly suggests that Buysson was not aware of the outstanding character (propodeal striation) at all when he wrote the memorable monograph. At present the taxonomic position of *aurulenta* is not clear to us.

Diagnosis. A large species. Queen and worker: Third mandibular tooth slightly concave along mesal margin (Figs. 26A, B). Occipital carina strong, reaching the base of mandible. Frontal suture absent below the anterior ocellus. Relative length of scape long ($F_1/S=0.70-0.78$, usually less than 0.75). Distance between the lateral ocelli half the diameter of lateral ocellus. Apical margin of clypeus weakly concave or nearly straight. Thorax distinctly punctate. Propodeum with distinct striae (in the worker the striation rarely indistinct). Prebasal depression of tergite I distinct.

Body length ($H+Th+T_1+T_2$): 14.5–16.0 mm in the queen, 9.5–12.0 mm in the worker.

Male: Occipital carina visible in upper 2/3. Antenna without distinct tyloides; terminal segment not slender, nearly parallel-sided and curved in profile. Thoracic punctation distinct. Propodeum with distinct striae. Last gastral tergite with the apical lobe not flat and deeply incised medially. Genitalia very unique, as in Figs. 13 and 14: gonostipes without dorsal terminal processes; aedeagal terminus shaped like a deep cup opened dorsally and with parallel sidewalls. We could not find any important difference in male genitalia between the two subspecies.

Body length ($H+Th+T_1+T_2$): ca. 9 mm.

Vespa koreensis koreensis Radoszkowski
(Figs. 40, 67, 68, 84, 85, 109–111, 129, 134)

Vespa koreensis Radoszkowski, 1887, Hor. Soc. Ent. Ros. 21: 432 (♂♂); Buysson, 1904, Ann. Soc. Ent. Fr. 73: 608–609 (♂♂); Giordani-Soika, 1976, Ann. Hist. -Nat. Mus. Natn. Hung. 68: 289–290, fig. 2 (♂).

Pseudovespa birulai Gussakovskij, 1933, Ark. Zool. 24 A: 52–53, syn. nov.

Specimens examined. USSR. 2♀ ♀ 4♀ ♀ 2♂♂, southern Primor'e (sent by Dr. Kurzenko); 1♀*, Okeanskaya, Siberia, viii 1923 (Cockerell). Korea. 1♀, loc. not stated, 27 vii 1935 (K. Kin); 4♀ ♀, Seoul, 11 viii 1974 (I. Kudo); 1♀, Sognisa, 21 viii 1974 (I. Kudo). China. 2♀ ♀*, Tsin Lung Shan, 65 miles NE of Peking Chileli (A dec Sowerby).

Diagnosis. Queen: Head extensively yellow. Frons above the corona, and vertex black except for eye loops yellow and posterior part brown. Yellow genal band complete. Corona containing a small black spot in the lower part, connected with the yellow of ocular sinus by a narrow line. Clypeus entirely yellow. Antenna reddish brown, much darker above. Thorax black with yellow or brown markings. Pronotum widely brownish with hind margin yellow; hind margin of pronotal tubercle brown, inside of which there is a vertical black line. A triangular spot under wing base yellow (in one specimen also mesepimeron with a

brown spot). Yellow bands on the anterior margin of scutellum and postscutellum interrupted medially. Propodeum black without yellow markings. Coxa partly, anterior face of fore femur, and mid- and hind femora below blackish. The other parts of legs yellowish brown to reddish brown. Gaster extensively yellowish brown. Vertical face and basal half of the horizontal part of tergite I, and basal half of tergite II black. Yellow band on tergite II containing a pair of peninsular extensions of the basal black area. The subsequent tergites basally narrowly black but only yellowish parts visible. Yellowish areas of tergites III-V containing a pair of brownish free spots which are not conspicuous. Sternites lighter in color than tergites. Basal two-thirds of sternite II black. Subsequent sternites basally black, but usually only apical yellow areas visible. Sternites II-V each with a pair of brownish peninsular extensions of the basal black areas. Last sternite entirely yellow.

Queens of this form are in color pattern very similar to the queens of *Vespa simillima* and *Dolichovespula media media* which are sympatric in at least southern Primor'e. These species are likely to represent an example of Müllerian mimicry.

Worker: Head black, extensively marked with yellow. Yellow: gena, clypeus nearly entirely, ocular sinus, corona and mandible. Eye loops present, but not joining with the yellow of temple (eye loops much reduced in some specimens). Corona rather large, separated from the yellow of ocular sinus by a narrow, vertical black line and from the clypeus by a narrow transverse black line; corona with a small black spot at some distance above the clypeus (the spot often connected with the transverse black line bordering the clypeus). Clypeus with small, obscure brownish patches placed in a triangle and rarely with a black line near the base. Antenna with scape and pedicel mostly black or blackish brown; flagellum black above and ferruginous below. Thorax and propodeum black, with yellow markings. Yellow: hind margin of pronotum widely, a triangular marking under wing base, scutellum and postscutellum anteriorly (narrowed medially), and a spot on each side of propodeum. Coxa, trochanter and femur, tibia and tarsus yellow. Outer face of femur of fore leg more extensively colored yellow than on the mid- and hind legs. Gaster black, with a yellow apical band on each segment. Apical band on tergite I as wide as or narrower than half the length of the segment, nearly parallel-sided, with a slight median incision anteriorly; the base of the horizontal part of tergite I rarely with a pair of small yellow spots. Yellow bands on tergites II-V having 3 (a median and 2 lateral) black projections from basal black area (the projections variable in size). Tergite VI nearly entirely yellow. Sternites II-V apically with a narrow yellow band which is somewhat widened in each side.

In the specimens from Tsin Lung Shan, northern China, body markings are very whitish. Corona connected with the white of ocular sinus. Clypeus with a brown spot near the base. Gastral whitish bands very regular. At present it is not known to us whether these states are general in and peculiar to the population of northern China. In a specimen from Siberia gastral tergite I has a black median maculation in the yellow as seen in the workers of *V. vulgaris* and *V. germanica* (Fig. 111).

Male: Very similar to the worker in coloration, except in the following points: Antenna nearly entirely black (only scape with a yellow spot) and gastral yellow bands narrower and more regular.

Distribution. USSR: Southern part of Amur; Korea; northern China.

Vespula koreensis orbata Buysson, stat. nov.
(Figs. 40, 69-71, 86, 112-115, 130, 134)

Vespa orbata Buysson, 1902, Bull. Soc. Ent. Fr. 1902: 140 (♀); Buysson, 1904, Ann. Soc. Ent. Fr. 73: 578-579 (♀).

Specimens examined. China*. Five queens, 31 workers and 1 male from Szechuen (Suifu, Kuanshien, Yachow, Mt. Omei, Ningyuenfu, Chengtu, Hongya, Fooling; 300-1500 m alt.), 2 workers from Fukien (Foochow), and 1 worker from Cheking (Hangchow).

Diagnosis. Queen: Head extensively yellow. Frons above corona and ocellar area irregularly colored black or brown. Eye loops present. Gena yellowish brown throughout; but temple often partly dark, especially near the posterior margin. Yellow of sinus of eye usually isolated from corona by a brownish bar. Clypeus nearly entirely yellow. Antenna yellowish brown; scape black or dark brown at least partly. Thorax nearly entirely black; yellowish or brownish color restricted to the following parts: posterior margin of pronotum (only in the middle), mesepimeron and posterior margin of scutellum. Propodeum entirely black. Coxae, trochanters and femora of all legs blackish brown to black; tibiae, especially on upper face, sometimes dark brown; other parts yellow or yellowish brown. Gastral tergites I and II black, each with a narrow brownish apical band; the apical band on tergite II wider than that on tergite I, slightly widened laterally. Visible parts of the subsequent tergites largely yellow to yellowish brown; tergites III-V each with a pair of small brownish or blackish spots. Gastral sternites similar to tergites in coloration. Last sternite wholly yellow.

Worker: Distinctly differing from queen in color pattern which is very variable. Head extensively yellow. Frons above corona, ocellar area and vertex brown to black; shape and dimension of the dark areas considerably varied. Yellow area of ocular sinus usually separated from corona by a brown vertical line. Clypeus yellow, very rarely with a brown bar near the base. Interantennal area lighter in color below; scape blackish brown to brown (sometimes lighter below). Thorax and propodeum black with yellow markings; the following parts yellow: posterior margin of pronotum widely, a triangular spot on dorsal mesepisternum, a wide band along the base of scutellum which is medially narrowed, anterior margin of postscutellum, and a pair of large spots on propodeum. Coxae, trochanters of all legs and basal half of mid- and hind tibiae dark brown; other parts yellow. Gaster black, or brown instead of black, with yellow bands. Basal part of horizontal face of tergite I often colored light brown; this color stretching over the whole vertical face. Yellow bands on tergites wide and somewhat irregular. Between the basal black area and the yellow apical band on each tergite there often being a brownish area. Gastral sternites similar to tergites in coloration, but yellow bands less developed; last sternite entirely light or dark brown.

Male: Only one specimen could be examined. Similar to the worker in color pattern, but different from the latter by lacking the brownish color; also similar to the male of the nominate form, differing by the more developed yellow markings. Head extensively yellow. Frons above corona, ocellar area, vertex and posterior margin of gena black. Corona connected with the yellow of sinus of eye. Eye

loops reduced. Antenna brown, darker above; scape above with a black patch. Yellow thoracic markings much as in the worker. Propodeum without yellow spots. Gaster black with yellow bands which are wider than in the nominate form. Vertical face of tergite I wholly black. Last tergite black with the narrow apical band yellow. Gastral sternites similar to tergites in coloration.

Distribution. China: Cheking, Fukien, Szechuen; Burma: Tenasserim; North India: Darjeeling, Sikkim.

Vespula minuta Dover, comb. nov.

(Figs. 5, 134)

(=*Vespa minuta* Dover, *Vespa arisana* Sonan)

This species was described by Dover from Tenasserim (Burma), and thereafter has received little attention. In 1929 Sonan described another "new" species allied to "*Vespa minuta*" from the mountainous region of Taiwan. Having made a careful comparison between the two forms we reached the conclusion that they are conspecific and belong to different subspecies. Although the male is unknown, this species, in at least structural characters of the worker, is very similar to *Vespula koreensis*.

Diagnosis. Third mandibular tooth slightly concave along mesal margin. Frontal suture obsolete or absent. Apex of clypeus nearly straight and lateral angles not projecting (in subsp. *arisana*), or apex somewhat concave and lateral angles projecting (in the nominate subsp.). Occipital carina distinct and reaching the base of mandible. Relative length of scape long ($F_1/S=0.73-0.76$). Distance between the lateral ocelli half the diameter of lateral ocellus or less. Cubital vein IIa shorter than IIb. Punctuation on thorax less distinct than in the preceding species. Propodeum very weakly striate; medio-basal area with a short vertical carina. Prebasal depression of gastral tergite I distinct. Queen and male unknown.

Body length ($H+Th+T_1+T_2$): about 10 mm.

Vespula minuta minuta Dover

(Figs. 41, 72, 116, 134)

Vespa minuta Dover, 1925, J. Proc. Asiatic Soc. Bengal 20 (1925): 304-305.

Specimens examined. Nepal. 1♀, Godavari, Phulchoki, Bagmati, 19 viii 1975 (S. Takagi); 1♀, Ghora Tabela—Syabru, Bagmati, 30 ix 1975 (S. Takagi). India. 1♀, Lal Tibba, Mussooree (2100-2200 m alt.), U.P., 14 xi 1978 (Jap. Ind. Co. Tr.). Dr. M.E. Archer kindly compared one of our specimens with the type material in the British Museum (N.H.) and confirmed our identification.

Diagnosis. Worker: Yellowish and brownish color predominating. Head yellowish brown. Vertex darker except at margins of eyes yellow. Corona not clearly defined from the yellow of ocular sinus. Gena and clypeus entirely yellow. Mesoscutum brown in anterior 2/3 and black in posterior part (brown area often diamond-shaped). Mesepisternum and/or mesepimeron dorsally with a brown spot. Scutellum yellowish brown, widely notched with black in the middle. Postscutellum largely black, with a narrow yellow line at the anterior margin which is somewhat interrupted medially. Propodeum black with or without a pair of yellow spots. Fore leg yellowish brown except for coxa,

trochanter and femur above blackish brown. Mid- and hind legs blackish brown except for apical part of femur above and tarsus yellowish. Gastral tergites I and II blackish brown, each with a narrow yellow band apically. Three subsequent tergites basally black; apical band yellowish brown and much wider than in the preceding tergites. Last tergite entirely yellowish brown. Sternite II blackish brown with a narrow apical band of yellow. Subsequent sternites extensively colored yellowish brown.

Distribution. This form coexists with *Vespula structor* in Nepal and with *Vespula flaviceps flaviceps* in N.W. India.

Nepal: Bagmati; India: Mussooree; Burma: Tenasserim.

Vespula minuta arisana Sonan, stat. et comb. nov.

(Figs. 42, 73, 117, 118, 134)

Vespa arisana Sonan, 1929, Trans. Nat. Hist. Soc. Formosa 19: 147-148.

Specimens examined. *Taiwan.* 3♀ ♀, Kwantauchi (750 m), Nantou, 3-4 vii 1973 (S. Yamane); 4♀ ♀, Lushan (1000 m), Nantou, 29 x 1976 (Sk. Yamane). Dr. M.E. Archer kindly compared one of our specimens with the specimens determined as *Vespa arisana* by Dr. J. Sonan and confirmed our result. He suspects that this form is a distinct species (personal communication).

Diagnosis. Head extensively yellow; frons above the corona and vertex largely black except at margins of eyes; posterior parts of vertex and temple brown. Corona defined from the yellow of ocular sinus by a brown indistinct line. Antenna blackish brown above and brown to yellowish brown below. Thorax black with yellow markings. Pronotum with a yellow band of various widths at the posterior margin; lower part brown to blackish brown. Mesoscutum rarely with brownish markings in the anterior half. Yellow triangular spot on dorsal mesepisternum large. Mesepimeron and dorsal metapleuron often each with a small yellow or brown spot. Scutellum yellow in anterior 4/5; the yellow deeply notched with black in the middle; posterior margin brownish. Postscutellum anteriorly with a yellow band not interrupted medially. Propodeum with a pair of large yellow spots. All legs light brown, partly marked with yellow. Gaster blackish brown. Gastral tergite I apically with a somewhat wide yellow band, laterally colored brown; vertical face brown. Tergite II apically with a similar band; subsequent tergites each with a narrow yellow band; inner part of each yellow band often tinged with brown (widely especially on tergites III-V; Fig. 118). Last tergite brown. Sternites colored similarly to tergites.

Distribution. Central mountainous parts of Taiwan.

SUBDIVISION OF THE GENUS VESPULA

The genus *Vespula* has been subdivided into two species groups or subgenera, the *V. vulgaris* group (subgen. *Paravespula*) and the *V. rufa* group (subgen. *Vespula*) (cf. Bequaert, 1932; Guiglia, 1972). On the other hand, Blüthgen (1938) restricted the genus *Vespula* to *austriaca* alone and transferred other species to the distinct genus *Paravespula* because of the parasitic habits and related morphological specializations of *austriaca*. He recognized two subgenera in *Paravespula*: the nominate subgenus to include *vulgaris* and *germanica* and

Allovespula for *rufa*. This view was criticized by Guiglia (1971) who attached importance to the recency of a common ancestor in her grouping of taxa. These subdivisions, however, were based upon European and N. American species. Asiatic species have been poorly studied probably because of the difficulty in obtaining full series of the forms. However, since eastern Asia is most likely the original center of the genus, a closer study of Asiatic forms is necessary to clarify phylogenetic relations within the genus. The present study together with recent works on Nearctic species by MacDonald and Matthews (1975) and Jacobson et al. (1978) have revealed the inappropriateness of the classical concepts of the groups. Our results are as follows:

- Group 1: *V. flaviceps* and *V. shidai*. This is very close to Group 2, but distinguished from the latter by the occurrence of a distinct pad on each side of the ventral inner margin of gonostipes of male genitalia (this character is peculiar to this group and *V. germanica*). Further, the occipital carina is evanescent in lower 1/3 of the gena even in the queen as in Group 5-7. Confined to eastern Asia.
- Group 2: *V. vulgaris*, *V. structor*, *V. maculifrons* and *V. flavopilosa*. This group is distinguished from Group 3 in the following details: occipital carina less developed especially in the worker, third mandibular tooth straight or nearly so along the mesal margin, aedeagal terminus basally with lateral spine-like processes, and nest material brown or buff and brittle as in Group 1. (*V. structor* is included in this group on the basis of worker characters only.) Holarctic in distribution.
- Group 3: *V. germanica* and *V. pennsylvanica*. Occipital carina is complete except in the male. Third mandibular tooth is concave along the mesal margin. Aedeagal terminus does not have pointed lateral processes. Nest material is gray and pliable as in Group 5 and 6 (Sk. Yamane (1976) failed to evaluate this character in the reconstruction of the vespine phylogeny), but the envelope is composed of shell-like structures somewhat similar to those of Group 1 and 2. Holarctic in distribution.
- Group 4: *V. koreensis* and *V. minuta*. This is a very unique group because the relative length of the antennal scape is long and cubital vein IIa is shorter than IIb, presenting some affinities to *Vespa*. The type of punctation on the thorax has some resemblance to that of Group 5 and 6. *V. koreensis* is quite unique in having the propodeum provided with numerous distinct striae and the unusual male genitalia. (*V. minuta* is included here on the basis of worker characters only.) Confined to eastern Asia.
- Group 5: *V. squamosa* and *V. sulphurea*. Probably closely related to Group 6, but the two groups are very distinct in their male genitalia. In the relative length of scape, however, it approaches Group 4. Nearctic in distribution, but *V. squamosa* extends to Central America.
- Group 6: *V. rufa*, *V. "rufa" schrenckii*, *V. intermedia*, *V. atropilosa*, *V. acadica*, *V. consobrina*, *V. vidua*. This group is composed of structurally very uniform species. According to M.E. Archer (personal communication) two other unnamed species inhabit Asia. Characters are well illustrated in literature (e.g., Bequaert, 1932). Holarctic in distribution.
- Group 7: *V. austriaca*. This is closely related to Group 6. The parasitic

nature and its consequent structural peculiarities may characterize this group. Holarctic in distribution.

These groups are, however, rather phenetic, because at present no reliable cladogram (phylogenetic tree) can be drawn on the basis of the characters available. The relations of our division with Blüthgen's and Bequaert's groupings are as follows:

	Blüthgen (1938)	Bequaert (1932)
Group 1-4	Subgen. <i>Paravespula</i> of gen. <i>Paravespula</i>	} <i>V. vulgaris</i> group <i>V. rufa</i> group
Group 5-6	Subgen. <i>Allovespula</i> of gen. <i>Paravespula</i>	
Group 7	Gen. <i>Vespula</i> .	

In this paper we have tentatively followed Guiglia's (1972) view in which the *V. vulgaris* and *V. rufa* groups are treated as subgenera *Paravespula* and *Vespula*, respectively. However, the presence of Group 4 in the subgenus *Paravespula* on one hand and that of Group 5 in the subgenus *Vespula* on the other hand throw doubt on such a simple division. They have characters both peculiar to them and transitional between the two subgenera.

WORLD DISTRIBUTIONAL PATTERN OF THE GENUS VESPULA

The distribution of the Nearctic *Vespula* and *Dolichovespula* has been well studied (Miller, 1961; Wagner, 1978; Jacobson et al., 1978), while in eastern Asia the study of this topic is quite rudimentary, especially regarding *Paravespula*. We, however, can make some comparisons between the faunae of the two regions (N. America and eastern Asia). It is likely that the genus *Vespula* originated in Eurasia, because it seems to have been differentiated from a *Vespa*-type ancestor and the genus *Vespa* is essentially of the Old World, unless the latter has become extinct in the New World, which is an unlikely assumption. Though an imbalance has persisted in the direction of flow of land-mammal dispersal across the Bering Land Bridge throughout Cenozoic times, especially in later Quaternary (Old to New World dispersals have always predominated; Simpson, 1947; Repenning, 1967), at present, it is not known which is the original center of each species group of *Vespula*.

First, we consider the *Vespula* species which in distribution actually enter the Arctic or approach very near to it as exemplified for some *Cryobius* species by Ball (1963). The species include *V. vulgaris*, *V. rufa*, *V. "rufa" schrenckii*, *V. intermedia*, *V. acadica* and *V. austriaca* (Fig. 131). They are either Holarctic (*V. vulgaris* and *V. austriaca*; *V. intermedia* may be also Holarctic)¹⁾ or have one of the closest relatives (vicariant) on the opposite side of the Bering Strait (*V. "rufa" schrenckii* vs. *V. acadica*). (A comparison of the eastern Asiatic *V. "rufa" schrenckii* vs. the Nearctic *V. acadica* shows that the former differs from the latter only in the color of gastral bands and other markings: white instead of yellow. Both the forms often have red spots on the second gastral tergite, but the first tergite is never extensively marked with red.) This is also true of *Dolichovespula* species

1) Though the sporadic occurrence in Asia and southern USSR of a form similar to *V. intermedia* has been noted by some authors (Buysson, 1904; Birula, 1930b), Birula (1930b) and Bequaert (1932) believe it to be a variant of *schrenckii* or *rufa*. Recently we have examined specimens which indicate that *V. intermedia* actually occurs in Asia, and that at least two distinct species of this group inhabit northeastern Asia. The relationships of the European *V. rufa* to *intermedia* and *schrenckii* are still unclear to us. These problems will be discussed in a separate paper.

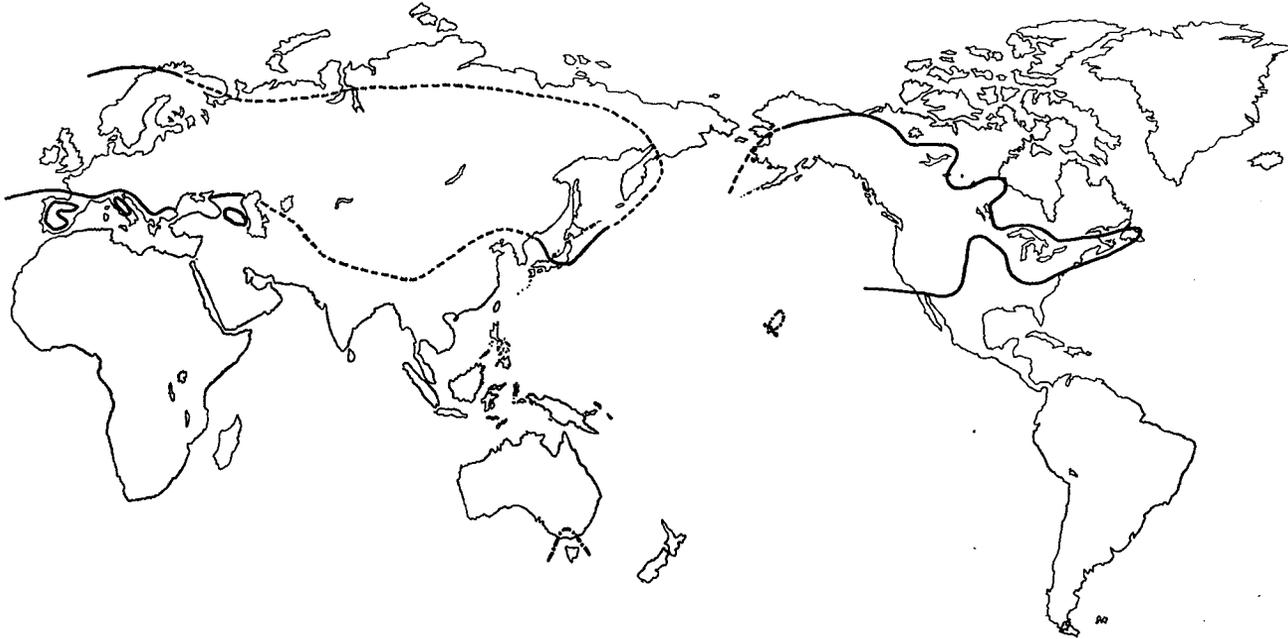


Fig. 131. Distribution of *V. vulgaris*. —: known natural range; ----: supposed range; -·-·-: artificial range.

which occur in the Arctic (Holarctic *D. saxonica*; *D. "norwegica"* subsp. vs. *D. albida*; *D. pacifica* vs. *D. norvegicoides*; *D. adulterina* vs. *D. arctica*).^{1),2)} These species or forms must have spread over the Beringia, where the main vegetation had been tundra (Hopkins, 1976) during the last glacial age, and following the disappearance of the land bridge have been isolated from each other. The ancestors of Group 2 and 6 might have passed the Beringia several times during the last two glacial times (Illinoian and Wisconsin), having produced some new species on each continent. But, the relations of the Asiatic forms of Group 6 (*V. rufa* and its close relatives) to Nearctic ones remain unsolved, because the Asiatic forms have not been precisely revised (according to Archer at least three species occur in Asia, personal communication). Since most of Group 6 species clearly do not extend to the Arctic in their present distributions, there is a possibility that at least some of them had passed the land bridge during warmer periods such as the Neogene or early Pleistocene. Similar events can be expected to have occurred in some of the Group 2 species.

V. germanica has a more southern distribution and is found in Europe below about 62°N, the northern limit roughly agreeing with 16°C July isotherm (Gusenleitner, 1975) (Fig. 132). This isotherm in turn roughly coincides with the border between the deciduous and coniferous forests. The northern limit of this species in eastern Asia has not been well delimited. The Nearctic relative *V. pennsylvanica* seems to have less resistance to low temperature (Fig. 132). Further, the two species are somewhat differentiated from each other even in structural characters. They, however, share many important structural and behavioral characters as listed for Group 3 species. The areas recently invaded by *V. germanica* and the endemic range where its occurrence is very dense such as in the Mediterranean region are largely under arid climates during at least the summer³⁾. *V. pennsylvanica* also inhabits the most arid areas during summer in N. America (Washington, California, Utah, Colorado, Arizona, Mexico, etc.)⁴⁾. These facts indicate that they are somewhat more differentiated from each other than are the cases for the pairs of Arctic inhabiting forms, but are still the closest relatives to each other, having the most recent common ancestor. If their physiological and behavioral traits had been roughly the same as now⁵⁾, they would not have been able to travel across the land bridge throughout at least Illinoian and Wisconsin times, the severest periods, suggesting an earlier migration during warmer periods.

Group 1 species (*V. flaviceps* and *V. shidai*) are confined to eastern Asia and

- 1) We are inclined to the opinion that the eastern Asiatic form of *D. "norwegica"* may be conspecific with *D. albida*, because some specimens from southern Siberia have whitish gastral bands and rufous markings, a character combination indistinguishable from that of *D. albida*. Though the taxonomic relation of *D. albida* to the European *D. norwegica* is at present not clear, the close faunal relation between eastern Asia and North America rather than between Europe and North America is obvious (see also Sk. Yamane, 1975).
- 2) Among the Arctic inhabitants, the Nearctic *D. arenaria* may be an exception to the vicariant rule here presented, because it actually enters the Arctic while eastern Asia apparently lacks it or its close relative.
- 3) The biology of this species in New Zealand was reviewed by Thomas (1960).
- 4) There is an excellent biological review of this species in Washington (MacDonald, et al., 1974).
- 5) Coope (1978) lays stress on the constancy of insect species versus inconstancy of Quaternary environments, chiefly based upon Coleoptera.



Fig. 132. Distributions of *V. germanica* (—: known natural range; ---: supposed range; - · - · -: artificial range), *V. pennsylvanica* (- · · - ·) (introduced to Hawaii several years ago), and *V. maculifrons* (· · · · ·).

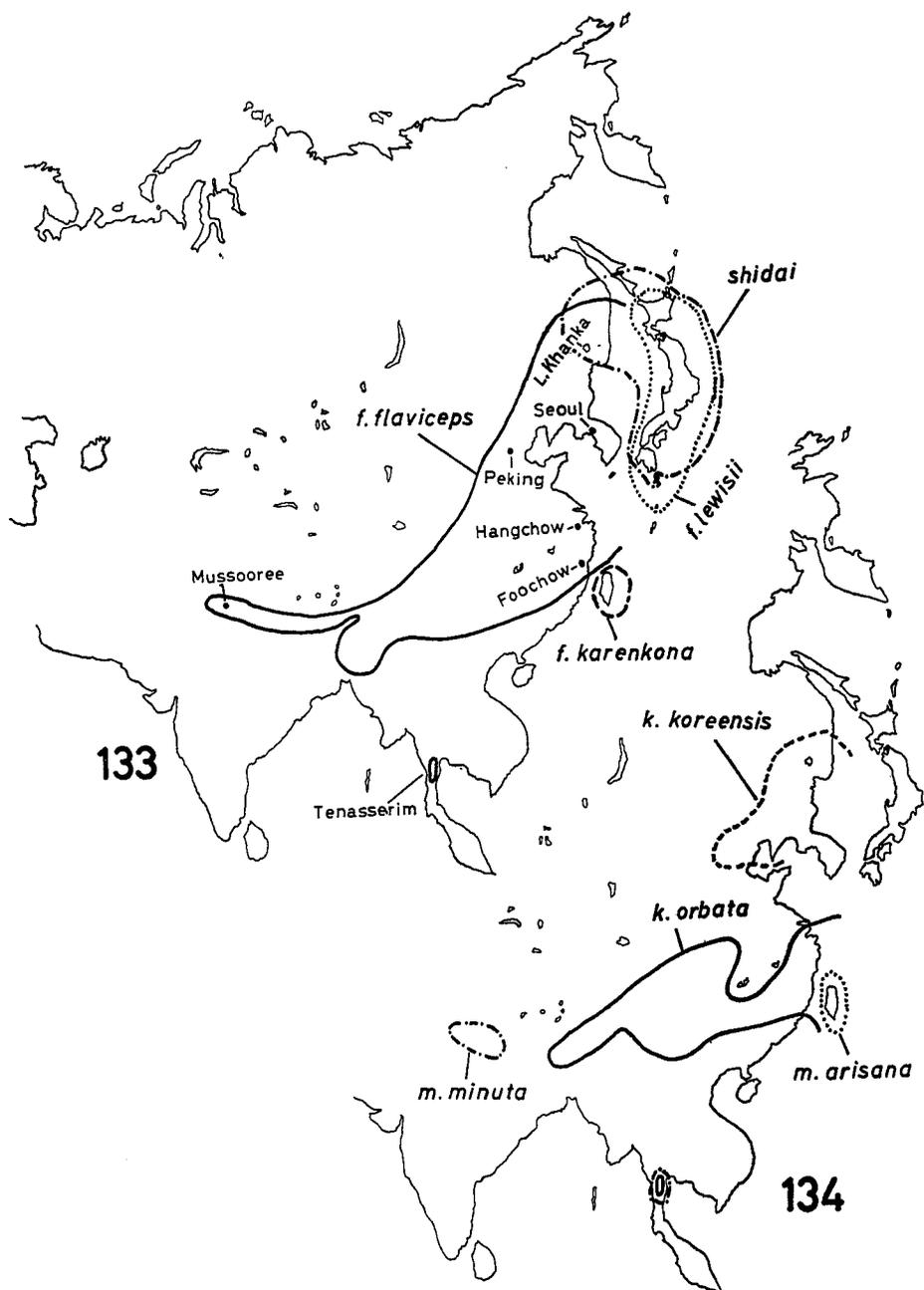


Fig. 133. Distributions of *V. flaviceps* and *V. shidai*. (The ranges in continental areas are largely tentative based upon a small number of records.)

Fig. 134. Distributions of *V. koreensis* and *V. minuta*. (The ranges are largely tentative based upon a small number of records.)

range from N. India through China to at least southern Primor'e, and are also found in Taiwan and Japan (Fig. 133). The present day ranges of the Group 1 species indicate that it is impossible for them to have inhabited the Beringia during the last two glacial times. In interpreting the lack of this group in N. America we may simply assume that the development of this group started after the Illinoian ice age when the dispersal of Group 3 species had already finished (probably via an earlier land bridge under warmer climates). It is, however, somewhat surprising that this group has not spread over Eurasia through the post-glacial time. Group 4 (*V. koreensis* and *V. minuta*) has a range similar to that of Group 1, but it is lacking in Japan and one of the species is also missing in Taiwan (Fig. 134). As mentioned before, Group 4 is rather differentiated from the rest of the genus, but shares some characters with Group 5 (*V. squamosa* and *V. sulphurea*). Though at present there is no positive evidence of a close relation between the two groups, more attention should be paid to them.

In this connection, the lack of the genus *Vespa* in the New World needs interpretation. The northern limits of some *Vespa* species (e.g. *V. simillima* and *V. crabro*) reach very near to that of *Vespula germanica* which has its closest relative in N. America¹⁾. It is clear that the ancestors of the species of *Vespa* could not migrate via the Bering Land Bridge during the last two glacial times, to judge by the present distribution. But, it is still unclear why they could not travel there when the ancestor of *V. germanica* did migrate, for the branching of *Vespa* from the rest of Vespinae other than *Provespa* seems to be earlier than the division between the genera *Vespula* and *Dolichovespula* (cf. Sk. Yamane, 1976). The latter two groups each contain one or more Asiatic species with a rather southern distribution which have one of its close relatives in N. America, suggesting that they migrated through the land bridge covered at least partially with forests and therefore under warmer climates than in the last two glacial times. Some evidence is available that supports the delayed arrival of *Vespa* in north-eastern Asia from the supposed original center (eastern Himalayas and southern China; Vecht, 1957): The number of species drastically decreases towards the northern limit of distribution. For example, compare the numbers of species occurring along the archipelagos from Taiwan to Sakhalin, 7 (Taiwan), 5 (Kyûshû), 6 (Honshû), 4 (Hokkaidô), 2 (Sakhalin) for *Vespa* with 2 (Taiwan), 2 (Kyûshû), 9 (Honshû), 9 (Hokkaidô), 9 (Sakhalin) for *Vespula* plus *Dolichovespula*. The relative diversity of the latter two groups in northern latitudes might have enhanced the chance of migration when a land bridge came into existence at any time.

Needless to say the present study is merely one step to a thorough understanding of distribution and phylogeny of this group in eastern Asia. We hope intensive studies will be made on the continental fauna, especially by the vespidologists of USSR, China and India, since European and American students can work with museum specimens alone.

1) Bequaert (1931) mentions that *Vespa crabro crabro* occurs in all of Scandinavia, but according to recent studies (Løken, 1964; Guiglia, 1972) in Norway this form is confined to the southern part. The most recent list of Scandinavian social Aculeates does not include records of this form at all (Løken, 1978).

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Appendix

DESCRIPTION OF A NEW SPECIES OF THE GENUS VESPULA FROM NORTH-EASTERN ASIA (HYMENOPTERA: VESPIDAE)

By RYÔSUKE ISHIKAWA*, SEIKI YAMANE and ROBERT E. WAGNER

In 1858 Saussure described a vespid from Japan under the name *Vespa japonica*. As this name was a homonym of *Vespa japonica* Radoszkowski, 1857, Cameron proposed a new name, *Vespa lewisii*, for it in 1903. Later this species was transferred to the genus *Vespula*. About twenty years ago, one of us (R.I.) noticed the occurrence in Japan of two very closely allied but distinct species which had been confused under the name *Vespula lewisii* Cameron (or *Vespa japonica* Saussure) by Japanese authors. The occurrence of the two species was, however, first suggested by Mr. T. Shida in the course of his biological survey on *Vespula* species. The differences noticed between them in the female characters were slight and found only in the shapes of the whitish marking on the ocular sinus and the black bar on the clypeus, though they were known to be rather stable. Later some male characters including genitalia proved useful for discriminating between the species.

At that time no Japanese entomologist examined the type-material of *Vespa japonica* Saussure deposited in the National Museum of Paris (N.H.) Neither the original description nor the redescription by Buysson (1904) referred to the discriminating characters. Under these circumstances some Japanese authors preferred to apply the name *lewisii* (often spelled *lewisi*) to the form with a broader whitish area on the ocular sinus perhaps because of the common occurrence of it in the lowland. The other, more melanic species has been treated as *Vespula* sp. or *Vespula A*.

In 1979 R.I. examined the vespid collection in the National Museum of Paris (N. H.). The oldest specimens he examined of the species concerned were three workers all belonging to *Vespula A*. However, judging from the collection data ("Japon, Coll. O. Sichel, 1867") they can not represent the type-material, which, therefore, may be lost. Giving first consideration to the recent action of Japanese entomologists in the biological study on these species, we prefer to follow them in applying the name *lewisii* to the less melanic form, which is treated in the preceding pages as a subspecies of *Vespula flaviceps*. The other form should be described below as a new species.

Vespula shidai sp. nov.

Queen and worker: Third mandibular tooth straight or nearly so along mesal margin. Occipital carina distinct in upper 3/4 only in the queen and more reduced in the worker. Relative length of scape short: length of flagellar segment I/length of scape ratio 0.72-0.80, usually more than 0.76. Distance between the lateral

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ocelli more than half the width of lateral ocellus. Thoracic punctation weak. Cubital vein IIa as long as or longer than IIb. Propodeum smooth, without striae or carina. Gastral tergites smooth even in the queen. Prebasal depression of gastral tergite I weak. Sternites III-V in the apical half and VI wholly strongly punctate in the queen; the punctation less pronounced in the worker.

Body length (H+Th+T₁+T₂): 12.0-13.0 mm in the queen and 7.5-10.5 mm in the worker.

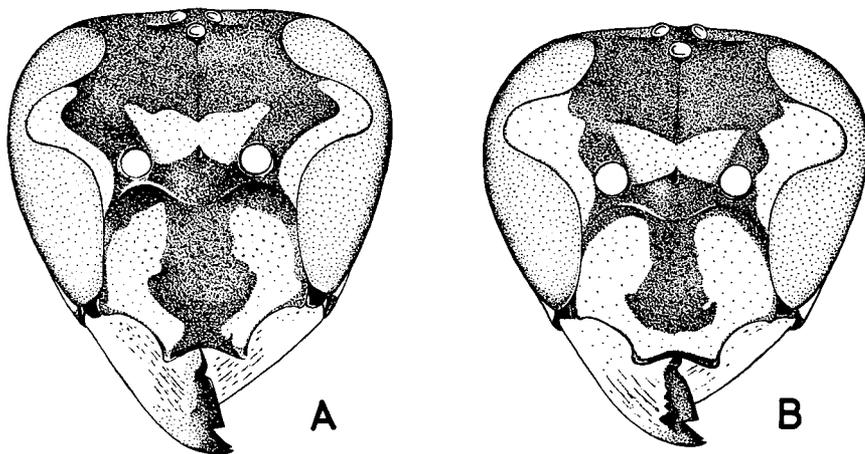


Fig. 135. Fascial color pattern of *Vespula shidai* sp. nov. (A) and *V. flaviceps lewisii* (B) (queen and worker).

Body black with white or ivory white markings. The following parts whitish: mandible except for teeth, clypeus (with a broad black bar), corona on the frons, gena (sometimes interrupted by brown medially), ocular sinus narrowly, a band on the anterior margin of pronotum (medially evanescent), a triangular spot under wing base, anterior margins of scutellum and postscutellum, small spots around the base of hind wing, anterior face of mid- and hind coxae, femora of all legs partly, tibiae and tarsi of all legs largely (two or three apical segments of mid- and hind tarsi often dark brown), narrow regular bands on gastral tergites I-VI, wider but irregular bands on sternites II-VI.

Male: Similar to the queen and worker. Disk of the last gastral tergite depressed; the apical margin of the last sternite nearly straight. Sternites smooth. Genitalia basically of the *Vespula vulgaris*-type. Gonostipes with a pad on each side of ventral inner margin (the pad is lacking in *V. vulgaris*). Aedeagus with a slender shaft, a subcircular spoon-like terminus, and a pair of lateral processes at the base of the terminus.

Body length (H+Th+T₁+T₂): 7.0-10.5 mm.

The black clypeal bar narrower than in the females. Mandible basally with a black spot. Mid- and hind coxae usually black on anterior face. Whitish band on postscutellum often much reduced. Whitish bands on gastral sternites narrower and more regular in shape than in the females.

Differs from *V. flaviceps lewisii* in the following points: whitish marking on ocular sinus deeply concave along the mesal margin (at most weakly concave in

lewisii). Black clypeal bar broader and usually reaching the ventral margin of clypeus (usually detached from the ventral margin in *lewisii*). Male mandible basally with a black triangular spot (without it in *lewisii*). Two or three apical segments of mid- and hind tarsi often dark brown; less dark in the worker (pale brown in *lewisii*). Male genitalia relatively elongate; lateral processes of aedeagal terminus longer, with nearly parallel outer sides (outer sides not parallel in *lewisii*).

The name *shidai* is dedicated to Mr. T. Shida who first discovered this species.

Distribution: Japan, the Kuriles and eastern Siberia.

Holotype: Male, 9. ix, 1975, Sapporo, Hokkaidô, Japan (from Nest SP7509). Deposited in the collection of the Entomological Institute, Hokkaidô University.

Other specimens examined: Many queens, workers and males collected in Japan (Hokkaidô, Honshû, Shikoku, and Kyûshû), the Kurile Islands, and Ussuri (for part of them see p. 18).