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MORPHOLOGICAL AND TAXONOMIC STUDIES ON VESPINE
LARVAE, WITH REFERENCE TO THE PHYLOGENY
OF THE SUBFAMILY VESPINAE
(HYMENOPTERA: VESPIDAE)

Studies on the vespoid larvae. I.

By SEIKI YAMANE

Abstract

YAMANE, SK. 1976. Morphological and taxonomic studies on vespine larvae, with reference to the phylogeny of the subfamily Vespinae (Hymenoptera: Vespidae). *Ins. matsum. n. s.* 8: 1-45, 3 tabs., 65 figs. (7 text-figs., 8 pls.).

External morphology of vespine larvae is presented with emphasis on the features important taxonomically or phylogenetically. Decision of sex is referred to. Generic and infrageneric classifications based upon larval characters are given in a close agreement with those based upon adult characters. Useful generic characters are shown. A key to the mature larvae of the Japanese and Taiwanese species is given. Elements of the larval behaviour are enumerated and the basic behavioural pattern is explained. Morphology and behaviour of the *Polistes* larva are also explained and compared with those of the vespine larva. Different evolutionary trends between the larvae of *Vespa* and *Polistes* are discussed with the aid of the functional morphology and the theory of preadaptation advocated by W. J. Bock. A phylogenetic diagram within the Vespinae is proposed, and their branching pattern and evolution are briefly illustrated.

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1. INTRODUCTION

Up to now most of the taxonomic and phylogenetic studies of the subfamily Vespinae have been made in terms of adult morphology and behaviour (Buysson, 1903, 1904, 1905; Bequaert, 1932; Vecht, 1957; Blüthgen, 1961; Guiglia, 1972). Several authors have dealt with the larvae of the European species (Semichon, 1923; Giordani Soika, 1934; Grandi, 1935), but these works might be no better than descriptions. Reid (1942) has given an extensive treatment of the vespine larvae and concluded that the Eumeninae and Vespinae are more closely related to each other than they are to the Polistinae and Polybiinae. His opinion is of special interest, since it has usually been thought that Eumeninae are the most "primitive", being largely solitary, among the four and are qualified as a distinct family. On the other hand, Vespinae are the most "advanced" in social structure. He has attempted to conform the classification of vespine larvae to the generic system already established by adult characters, resulting in overlooking useful generic characters. After him, while the species are probably distinguished, the genera are difficult to separate on the basis of larval characters.

One of the purposes of this paper is to give a reason for the resemblance between eumenid and vespine larvae and for the marked gap between them and polistine larvae. (In this paper Polybiinae and Ropalidiinae of some authors are included within the Polistinae as tribes, although the other tribe Polistini is mainly discussed.) Another purpose is to find larval characters which have been overlooked by Reid as many as I can and to re-examine the generic and infrageneric classifications currently accepted. In order to make morphological descriptions and phylogenetic discussions easy, external morphology of vespine larvae will be first explained somewhat in detail, although excellent figures and terminology of the *Dolichovespula sylvestris* larva have been presented by Short (1952).

2. MATERIAL EXAMINED

Examinations were made primarily on the mature larva because its structures are easy to observe. Developmental changes were observed for the growth ratio in *Vespa analis insularis* and for mandibular shape in almost all forms available. The material was cleared in hot KOH solution, and then heavily stained with acid fuchsin. Illustrations of whole heads were made from the cleared material in 95% alcohol. Mouth parts, spiracles and cuticular structures of genital rudiments were observed with material mounted on microscopic slides.

The following forms collected in Japan and Taiwan (Formosa) were examined:

- Vespa mandarinia nobilis* Sonan — Taiwan
- V. m. latilineata* Cameron — Hokkaidô
- V. tropica pseudosoror* van der Vecht — Taiwan
- V. analis nigrans* Buysson — Taiwan
- V. an. insularis* Dalla Torre — Honshû
- V. affinis affinis* Linné — Taiwan
- V. basalis* Smith — Taiwan
- V. velutina flavitarsus* Sonan — Taiwan
- V. xanthoptera* Cameron — Honshû
- V. simillima* Smith — Hokkaidô
- V. crabro flavofasciata* Cameron — Hokkaidô

Vespula (Paravespula) vulgaris vulgaris Linné — Honshū
V. (P.) karenkona Sonan — Taiwan
V. (P.) lewisi Cameron — Honshū
*V. (P.) A** — Hokkaidō
V. (Allovespula) rufa schrenckii Radoszkowsky — Hokkaidō
Dolichovespula (Dolichovespula) media media Retzius — Hokkaidō
D. (Boreovespula) saxonica nipponica Sk. Yamane — Hokkaidō

Figures and descriptions of seven forms in the literature, *Vespa bicolor* Fabricius (Ma, 1936), *Vespula (Paravespula) germanica* Fabricius (Giordani Soika, 1934), *V. (P.) flaviceps* Smith (Ma, 1936), *V. (P.) pensylvanica* Saussure (Duncan, 1939), *Vespula (Allovespula) rufa rufa* Linné (Grandi, 1935), *Dolichovespula (Metavespula) sylvestris* Scopoli (Short, 1952), and *D. (Boreovespula) norwegica* Fabricius (Reid, 1942), are also referred to for more extensive comparisons. Many fine figures and descriptions of Eumenidae and Polistinae given by authors are naturally consulted for the purpose of discussing at the subfamilial level.

3. EXTERNAL MORPHOLOGY OF THE VESPINE LARVA

The following description and interpretation are presented with the object of providing a basis for the classification of the vespine larvae and the terminology used in this paper. Therefore, features important taxonomically or phylogenetically will be explained in detail. As to the head Short's terminology for Apocrita larvae is mainly consulted.

The larva is whitish, soft and entirely apodous, with few outstanding structures. The body consists of a yellow, well chitinized head, three thoracic and ten abdominal segments, with no constriction between the thorax and abdomen (Figs. 14, 15).

3.1. Head

3.1.1. *Shape of the head.* The head in frontal view is almost rounded and compressed antero-posteriorly. The head shape is somewhat variable and is expressed by the use of the cranial width : cranial height ratio (CW/CH), cranial width : mouth parts width ratio (CW/MW) (Fig. 1), or relative position of the temporal band. Relative position of the temporal band is defined by the following

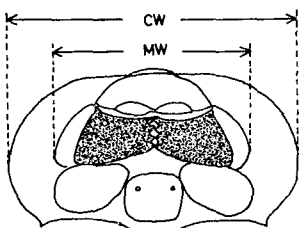


Fig. 1. Ventral view of the larval head. CW: cranial width, MW: mouth parts width.

three distances: the shortest distance between the mid-cranial sulcus and the dorsal end of the temporal band (*a*), the shortest distance between the postocciput and the dorsal end of the temporal band (*b*), and the distance between the antenna and the ventral end of the temporal band (*c*) (Figs. 31–34). The ratio CW/MW is smallest in *Vespa mandarinia* and largest in *Dolichovespula saxonica*, being mediated by other species (Fig. 7). In the species of the genus *Vespula* the head is often somewhat depressed in the male, suggesting the occurrence of sexual dimorphism (Fig. 22 vs. 23). The head shape may also change ontogenetically,

* Cf. Sk. Yamane & K. Kamijo (1976).

Table 1. Growth ratios of cranial width and mouth parts width in *Vespa analis insularis* larvae.

Instar	No. of specimens examined	Cranial width (A)	Mouth parts width (B)	A/B (range)	Growth ratio in A	Growth ratio in B
1	2	0.84	0.75	1.11—1.19		
2	8	1.19	1.07	1.09—1.21	1.412	1.420
3	8	1.76	1.49	1.12—1.26	1.482	1.399
4	5	2.43	1.95	1.24—1.26	1.384	1.310
5	21	3.16	2.20	1.37—1.48	1.298	1.128

with increasing values for the ratio CW/MW (Table 1). This change is caused by the different growth ratios between the two widths.

3.1.2. *Cranium*. The cranium consists of the vertex (*v*), frons (*fr*), temporal or parietal region (*tr*), gena (*g*), clypeus (*clp*), and labrum (*lm*). The term epicranium is applied to the upper part of the cranium.

The mid-cranial sulcus (*mcs*) divides the epicranium into large symmetrical halves. This sulcus, which was called the median suture by Reid (1942) or metopic suture by Parker (1943), is always incomplete and visible only near the top of the head and rarely also just above the clypeus. Degrees of the development of this sulcus are taxonomically important. The frontal arm of dorsal ecdysial cleavage line (*fa*) is obscure, extending towards the laterobasal angle of the clypeus. The epistomal sulcus (*es*), separating the clypeus from the epicranium, is usually more thickened than the pleurostoma (*plst*), which is fused with the mandibular corium (*mc*). In *Dolichovespula* the epistomal sulcus is much reduced (Figs. 24, 25, 32). The labro-clypeal suture (*lcs*) is less conspicuous than the epistomal sulcus. The postoccipital sulcus (*pos*) along the posterior margin of the cranium merges anteriorly into the hypostomal sulcus (*hs*), which runs along the lateral margin of the cranium to the base of the mandible (*md*). Michener (1953) called both the sulci combined the marginal thickening of the head capsule.

The antenna (*ant*) is a small, circular area slightly swollen conically and is surrounded with a thickened ring of cuticle (antennal socket, *ant sk*). It is situated somewhat dorsad of the clypeus, whose width is almost equal to inter-antennal distance. Each antenna is provided with three minute sensillae arranged in a straight line or a triangle (Fig. 26). In the temporal region of each cranial half is present a distinct band or fossa called the temporal band (*tmb*) by Reid, the function of which is unknown. Its condition varies among hymenopterous larvae from a mere line to a deep groove so that various terms have been adopted for each condition such as the ocular line for Ichneumonoidea by Short, parietal band for bees by Michener, ocular fossa for *Polistes* by Parker, etc. A groove on each frontal arm of the dorsal ecdysial cleavage line is the depression in cranial wall at the origin of the frontal muscle (*dfm*).

The clypeus is somewhat swollen and its ventral border is fused with the labrum which is narrower than the clypeus and incised medially on the ventral margin. The inside of the labrum is called the palate (*pl*) by Reid.

3.1.3. *Labrum and palate*. The labrum and palate form a twofold structure fused at the ventral border, and the shape in frontal view involves two distinct types. In *Vespa* and *Vespula* the labrum is deeply notched medially on

the ventral border and is widest at the base (Type A) (Figs. 41–46). In *Dolichovespula* it is gently emarginate on the ventral border and is widest at some distance from the base (Type B) (Figs. 47, 48). The labrum bears sensory bristles, which so greatly vary in number and distribution even within a species that they can not be used to separate species or genera. The palate, on each side, bears a sclerotized patch (*cp*) in which several conical sensillae are found. The shape and degree of sclerotization of the patch are useful in the supraspecific classification, since their variations are largely regular concerning the range. The palate bears microscopic spinous or warty processes (*spr*) as well. Usually these processes are borne mainly in the median region, partly in the lateral region, of the palate, but in *Dolichovespula* nearly all over. Reid's description of *Vespula vulgaris* lacks those located on the lateral sides. In some species of *Vespa* there is a median patch (*mp*) on the palate, which has hitherto received no attention (Figs. 41, 44, 45).

3.1.4. *Tentorium*. The tentorium (Figs. 18, 20, 21) consists of the tentorial bar (*tb*), anterior tentorial arms (*ata*), dorsal tentorial arms (*dta*), and posterior tentorial arms (*pta*). The tentorial bar forms a bridge between the posterior tentorial arms, into which the hypostomal and postoccipital sulci flow. From each extreme of the tentorial bar arises anterior tentorial arm, which attains the anterior tentorial pit (*atp*) on the epistoma and branches off about halfway into the slender dorsal tentorial arm towards the dorsal tentorial pit (*dtp*). The dorsal tentorial pit, situated slightly mesad of the antenna, is very obscure, because the attaching point of the dorsal tentorial arm is very small. The tentorium is very uniform among Vespinae, but careful examinations may find higher categorical value in it.

3.1.5. *Mandible*. The mandible is well chitinized, especially in its concave apical part. The upper and lower margins of the apical part are nearly parallel. There are usually three apical teeth (I, II and III, counted from below), of which Tooth III is subdivided into two small teeth (IIIa and IIIb) (Fig. 53). The abductor apodeme (*aba*) and adductor apodeme (*ada*) are processes to each of which a corresponding muscle attaches (Fig. 55). The former is far shorter than the latter which bears a branch at some distance from the base. This branch is of the same size as the abductor apodeme.

The mandibles of all the species examined in this study are identical in their general characters, while based upon some properties they can be assigned to two distinct types. One of these types (Type A), in which *Vespa* and *Vespula* fall, is the distinctly tridentate mandible, and the other (Type B), to which *Dolichovespula* belongs, is the practically monodentate mandible (Figs. 53–55 vs. Fig. 57). Reid (1942) proposes the same division based upon the European species. Although the mandibles of *Vespa* and *Vespula* exhibit an apparent resemblance and this fact is indeed important phylogenetically, there exist some noteworthy differences between these genera in both mature and immature larvae as stated later. Ontogenetic changes must also be taken in consideration, although morphological changes during the larval development so far have not been studied except for Kirmayer's histological work (Kirmayer, 1909). In the first to at least third instar of Type A larvae Tooth II is longest and sharply pointed or nearly so, but in the mature larvae Tooth I is longest and very huge. In Type B larvae such a change is not seen, but from the third instar on cusps are observed on the inner surface at some distance from the apex (Fig. 57).

3.1.6. *Maxilla and labium.* The maxilla is a soft lobe located below the mandible and composed of the cardo (*cd*), which is the basal part, and stipes (*st*) (Fig. 18). However, this distinction is not so apparent as in Sphecidae. The stipes occupies the greater part of maxilla and is provided with the maxillary palp (*mplp*) and galea (*ga*), each with a variable number (3-6) of small sensillae similar to those upon the antenna. The galea is somewhat smaller than maxillary palp. Reid termed *en bloc* the maxillary palps.

Between the maxillae is found the prelabium (*prlb*) which was called the mentum by Reid, labium by Parker, or prementum by Michener. It bears a pair of palps (labial palp, *lplp*), which are smaller than the maxillary palp, each with 3 to 6 sensillae. Salivary opening (*so*) (Fig. 21) is longer than the distance between the labial palps and surrounded with a lot of piliform processes which form lips. Reid (1942) lays emphasis on a strongly developed ridge upon the prelabium of *Vespula rufa rufa* as a character of specific importance. I believe that he gives a false emphasis following Grandi's exaggerated figure of the lip. The area between the foot of the prelabium and thorax is the postlabium (*plb*), which is often called the postmentum.

The hypopharynx is fused with the maxillae and prelabium to form an underlip complex (Short, 1952). Beneath the labrum the mouth is open, leading into the foregut through the cibarium, pharynx and postpharynx in the mentioned order.

3.1.7. *Sensory bristles and microscopic denticles.* The sensory bristles on the cranium, maxilla and labium are generally sparse and inconspicuous, but those on the maxilla and prelabium are often thicker and longer than those on the cranium (Figs. 35-40). In *Vespa affinis* the sensory bristles are exceptionally long in comparison with other species (Fig. 37).

The microscopic denticles (*dt*) are observed dorsally on the stipes and sometimes around the galea, as well (Figs. 49-52). Vertex and gena also bear them sparsely in *Vespula* and somewhat densely in *Dolichovespula*. *Vespa* lacks them on the cranium.

3.2. Thorax and abdomen

3.2.1. *General feature* (Figs. 14, 15). There are thirteen postcephalic segments, three thoracic and ten abdominal. Intersegmental lines are recognizable in dorsal and ventral sides of the body, but somewhat indistinct laterally. The first and second abdominal segments are to some extent lobed out ventrally, forming the tropholopade of Grandi (1959).

Remarkable protuberances are present dorsally on the first to eighth abdominal segments (one on each segment), and laterally on the second to ninth segments (one on each side of each segment), those on the third to six being much larger than the rest. The last segment has the anal opening.

The cuticle is almost wholly covered with dense microscopic denticles and sparse sensory bristles. These denticles and bristles are sparser or absent on the protuberances.

There are two thoracic spiracles between the pro- and meso- and the meso- and metathoracic segments. Abdominal spiracles exist on the first eight segments, towards the anterior edge of each segment. Thus the spiracles involve a total of ten pairs, with the second and tenth pairs distinctly smaller than the rest. The

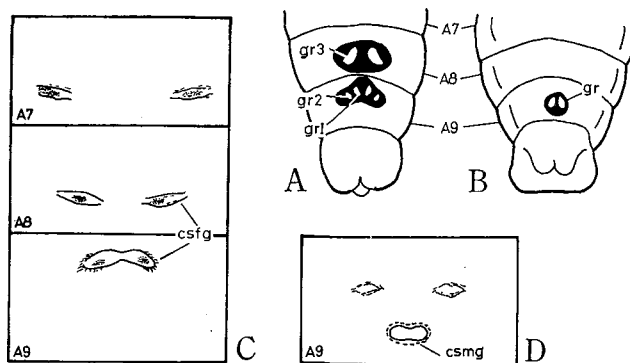


Fig. 2. Genital rudiments of vespine mature larvae. A. female, B. male (after Zander, 1900), and their cuticular structures, C. female, D. male.

tracheal opening shows a cup-shaped atrium (*at*), which bears a lot of microscopic processes (atrial processes, *apr*) on the inside wall and a variable number of collar processes (*clpr*) near the bottom (Figs. 58, 60).

The cuticular structures of the rudiments of the wings, legs and genitalia can be observed in the cuticular mount. Transparent circular areas on the ventral surface of the thorax mark the corresponding positions of wings and legs, being situated towards the posterior edges of the thoracic segments. The male structure of the 9th abdominal sternite (cuticular structure of male genitalia, *csmg*) is a small, transverse oblong, with the edge sclerotized to some extent. Slightly anteriorly to this structure are found a pair of small somewhat transparent areas with the circumference stained with acid fuchsin (Fig. 2D). The cuticular structures of female genitalia (*csfg*) are observed on the 8th and 9th sternites (Fig. 2C). Each of them is a pair of round transparent areas, situated near the posterior margin on the 8th sternite, and near the anterior margin on the 9th, the paired areas on the 9th coming in touch with each other at the middle of the sternite. In addition, there are on the 7th sternite a pair of structures like those on the 8th sternite, but not so sharply defined.

3.2.2. Spiracle. Spiracular structure has been used by some authors in the classification of Aculeate larvae (for example, Ritcher, 1933; Michener, 1953). Reid (1942) examined the spiracles of four species of the Vespinae. After him the spiracular processes alone do not suffice to separate the species; nevertheless, if taken in conjunction with other characters, these processes may be very useful. From the present study dealing with further species it can be said that the shape and size of these processes afford good generic rather than specific characters. The spiracles of the examined species are classified into four types chiefly based upon the atrial and collar processes (Reid's spiracular processes) of mature larvae. Here, the term atrial processes is used to exclude the collar ones. The divisions based upon these features agree with those in current classifications based upon adult features.

Type A. Collar processes are usually thickened and complex, with many branches arising all over. The inside wall of the atrium usually bears a lot of minute or rather conspicuous spines (Figs. 58-60).

Type B. Collar processes are very similar to those in Type A, but they are

relatively elongate and simple, with a few or no branches near the base (Fig. 65).

Type C. Collar processes are long and straight, sometimes bifid apically, but usually without branches (Fig. 64).

Type D. Collar and atrial processes are always inconspicuous and short (Figs. 62, 63).

3.3. Decision of sex

The decision of sex in hymenopterous larvae should be based on the genital rudiments and their cuticular structures on the posterior abdominal sternites. Most of the recent taxonomists dealing with hymenopterous larvae have found little interest in the sexual difference so that their descriptions lack reference to sex.

Dewitz (1875) studied the structure and development of the sting and ovipositor of *Apis mellifica*, *Bombus* sp., "*Vespa*" *vulgaris* and *Cryptus migrator*, and of the male genitalia of *C. migrator*. His figures of *C. migrator* show sexual differences on the posterior abdominal sternites of the prepupa. Later Michaelis (1900) studied the postembryonic development of the genital organs of the honeybee larva, and his study was extended by Zander (1900) to include larvae of the genera "*Vespa*" and *Bombus*. The genital rudiments of the female larva were also noticed for *Vespa lewisi* by Takamatsu (1949). Their works have resulted, regardless of their purposes, in suggesting the possibility of distinguishing the sexes of wasps and bees in the larval period. The female larva possesses the genital rudiments (gr1-gr3) on the 8th (in one pair) and 9th (in two pairs) abdominal segments (Fig. 2A), while the male possesses them only on the 9th segment (Fig. 2B), because the preceding segment does not take part in the formation of the genitalia. Further, the structure and position of the rudiments on the 9th segment are somewhat different sexually. Nelson (1924) figured not only the rudiments of genitalia located on the 8th and 9th segments but also two pairs of unnamed structures on the 7th segment of the female honeybee larva.

Recently, Nielsen and Bohart (1967) turned their attention on Michaelis' and Zander's results to sex hymenopterous larvae and emphasized the usefulness of sexing in experimental designs for wild bee pollination investigations and also in the taxonomy of bee larvae. They studied the 9th abdominal sternite in 12 species belonging to seven families of bees and demonstrated that a structure diagnostic of the male sex (a narrow transverse slit) was found on the 9th sternite of all species, while female structures on the same segment were less defined or invisible. The genital rudiments in hypodermal structures (Nelson, 1924) are not easy to observe externally without dissection. On the other hand the cuticular structures of them can be seen in cuticular mounts or sometimes externally in living or fixed materials without staining (S. & Sk. Yamane, 1975) (Fig. 2C, D). In the course of my examinations Nelson's paired structures have always been observed on the female 7th sternite, while they have not been referred to by other authors. The nature of these structures is unknown to me, but as they are seen in all the vespine species studied by me, *Polistes* spp., *Apis mellifera* (Nelson, 1924), etc., and never seen in the male of any species, they must always be associated with the female sex in Hymenoptera.

3.4. Characteristics of the *Polistes* larva.

In this occasion characteristics of the *Polistes* larva are given for a comparison with the vespine larva. Characteristics of the *Polistes* larva were properly summarized by Reid (1942). By examining the Japanese species and the figures of *P. gallicus* given by Parker (1934), I will explain the morphology of the *Polistes* larva somewhat in detail in order to make the phylogenetic consideration easy.

(1) The head is often coloured dark brown. The epicranium is somewhat thick antero-posteriorly, with the vertex and frons rather gently sloping (Fig. 10).

(2) The mid-cranial sulcus is always incomplete and visible only at upper portion of the cranium (Fig. 9).

(3) The pleurostoma is distinct, while the upper portion of the epistomal sulcus is entirely absent so that the clypeus is not separated from the frons; a white membraneous area is found between the clypeus and labrum as in the vespine larvae, but it is larger and more conspicuous in the *Polistes* larvae (Fig. 9 vs. Fig. 16).

(4) The lower border of the clypeus is not situated below the level of the mandibular bases. The labrum is wider than or as wide as the clypeus; it is nearly rectangular and not emarginate at the ventral border (Fig. 9).

(5) The basic structure of the tentorium does not differ from that of the vespine larva, but differs by the posterior tentorial arms being very short.

(6) The mandible is weakly chitinized, slender, nearly circular in cross section and ends in two or three attenuating and pointed teeth (Figs. 11-13). The mandibular corium and articulations are very obscure as compared with those of the Vespinae. The abductor and adductor apodemes are rather slender and feeble.

(7) The maxillary lobes are prominent and nearly spherical and bear long and conspicuous palps (Figs. 9-11). The prelabium is considerably longer than that of the vespine larva, and also bears long palps (Fig. 9).

(8) The body is widest at the anterior part of the abdomen, tapering towards the posterior end; the pleural lobes are less conspicuous than in the Vespinae (Fig. 8).

4. GENERIC AND INFRAGENERIC CLASSIFICATIONS

Most of the modern workers engaging in vespid taxonomy have basically concurred in recognizing four distinct groups in the subfamily Vespinae, basing their studies on the adult morphology. These groups are the genera *Provespa*, *Vespa*, *Vespula* and *Dolichovespula*, the last often being ranked as a subgenus of the genus *Vespula*. Exclusive of Blüthgen's (1961) more split classification of *Vespula* and *Dolichovespula* with emphasis on ethological properties, this classification has been accepted as neat and reliable as well, and on the whole is reinforced by the larval features treated in this paper. But there exist several problems awaiting solution from the phylogenetic viewpoint. First, one concerns with the possibility of subdividing the genus *Vespa* into natural groups in a phylogenetically significant fashion. A second problem is to determine the phylogenetic position of *Vespula rufa* which seems to be transitional between the subgenus *Paravespula* of the genus *Vespula* and the genus *Dolichovespula* in adult features. One may also ask whether in larval features the genus *Dolichovespula* proves "primitive", because it has

sometimes been considered as "primitive" for its comparatively small colony. These problems together with other related ones will be discussed on the basis of further information concerning larval characters in this section and 6.2. Since the larva of *Provespa* has not been known, I exclude this genus from discussion.

4.1. Genus *Vespa*. Body large. Head in frontal view nearly circular (*V. mandarinia*) or somewhat depressed dorsoventrally (Figs. 16, 17). CW/CH: 1.21–1.50, CW/MW: 1.33–1.61. Relative position of the temporal band: $a \leq b \gg c$ (Figs. 28, 29) except for the *velutina*-group (Fig. 30). Mid-cranial sulcus well developed at the upper half and sometimes visible just above the clypeus (Figs. 33, 34). Labrum of Type A, widest at the base, the ventral border deeply notched medially (Figs. 41–45). Sclerotized patch of the palate rather developed, extending towards lateral side (Figs. 41, 43–45), rarely weak and divided into several fragments (Fig. 42); in some species median patch is present (Figs. 41, 44, 45). Mandible (Figs. 53, 54) relatively short, apically tridentate, without cusps; Tooth I not markedly projecting as compared with that in *Vespula*; Tooth IIIa more projecting or nearly as large as IIIb (figs. 53, 54b) with the only exception of *V. crabro* (Fig. 54a). In all instars Tooth I and III obviously visible; in the first three instars Tooth II most projecting of the three, but less than in *Vespula*. Cephalic microscopic denticles hard to observe. Denticles on the maxilla moderate in density (Fig. 28). Spiracle of Type A with the only exception of *V. basalis* (Type B), collar processes thickened and complex, with a lot of branches arising all over; otherwise atrial wall usually with a lot of minute or rather conspicuous spines (Figs. 58, 59, 61). Spiracles of the first to third instars without visible collar and atrial processes, but those of the fourth instar bearing small rounded or pointed processes (Figs. 58c, 60a).

Infrageneric division of the genus *Vespa* by adult features is not easy because of structural uniformity and of behavioural variability seemingly little associated with phylogeny. Bequaert (1930) subdivided the genus into four groups, and considered that they are highly artificial and not of subgeneric value. Vecht (1957, 1959) proposed to establish the subgenus *Nyctovespa* and the *luctuosa* species-group, but as they are not distributed in Japan and Taiwan it is impossible to judge whether or not his treatments are acceptable also in larval classification. Some Japanese and Taiwanese species such as *V. mandarinia*, *V. tropica*, *V. dybowskii* and *V. basalis* have been thought of as specialized chiefly on account of their behavioural properties (Sakagami & Fukushima, 1957; Matsuura & Sakagami, 1973; S. Yamane, personal communication). For example, *V. mandarinia* is outstanding in its huge size and enormously developed genae, and also in some ethological characters such as frequent extranidal trophallaxis and attacks on nests of other social wasps and honeybees.

My observations, while strongly indicating the structural uniformity of the larvae within the genus, suggest that *V. velutina*, *V. xanthoptera*, *V. simillima* and *V. crabro* may constitute a distinct species-group, the *velutina*-group. They are common in some characters, for example, in the *Vespula*-like head shape, ventrally weakly margined temporal band (Fig. 30), rather developed mid-cranial sulcus (visible above the clypeus) (Fig. 34), much developed sclerotized patch on the palate, occurrence of the median patch of the palate (Figs. 44, 45), and the rounded collar processes of the fourth instar spiracle (Fig. 58c). *V. mandarinia*, *V. analis* and *V. tropica* are also to some extent similar to each other, for example, in

the ventrally well margined temporal band (Figs. 28, 29), lack of mid-cranial sulcus just above the clypeus (Fig. 33), and the pointed collar processes of the fourth instar spiracle (Fig. 60a). However, the specialized head shape of *V. mandarinia*, the resemblance of *V. analis* to the *velutina*-group, and other facts suggest that these three species should not be grouped at once. *V. affinis* is unique in having long sensory bristles on the head and trunk (fig. 37) but in other respects it resembles either of the *velutina*-group and *V. analis*.

4.2. Genus *Vespula*. Body smaller than that of *Vespa*. Head more depressed dorsoventrally than that of *Vespa*, especially in the male (Figs. 22 vs. 23). CW/CH: 1.24–1.51, CW/MW: 1.40–1.58. Relative position of the temporal band: $a \geq b \gg c$ (Fig. 31). Mid-cranial sulcus less developed than in *Vespa*, always invisible above the clypeus (Fig. 31). Shape of the labrum as in *Vespa* (Type A) (Fig. 46). Sclerotized patch on the palate not extending towards the lateral side; spinous processes somewhat dense on each side of the median line; without median patch. Mandible (Figs. 55, 56) relatively elongate and narrow, apically tridentate, without cusps; Tooth I markedly projecting as compared with II; Tooth IIIb almost always more projecting than IIIa. In the second and third instars, Tooth II markedly long and sharply pointed; in the first instar Tooth I and III hard to observe. Microscopic denticles of the gena feeble and sparse. Maxillary denticles moderate or sparse in density (Fig. 50). Spiracle of Type C and D, collar processes short (in *V. rufa* exceptionally long) and simple, without branches (Figs. 62–64). Spiracles of the first to fourth instars without any atrial and collar processes.

Reid (1942) found *Vespula vulgaris* and *V. germanica* appearing much closer to *Vespa crabro* than to *Dolichovespula norwegica* in larval features. The present results also indicate that *Vespula* is more similar to *Vespa* than to *Dolichovespula* in the shape of the head, labrum, mandible, etc. *Vespula* larvae are quite uniform, with only *V. (Allovespula) rufa* larva exceptional in having the long collar processes of the spiracle. In this character *V. rufa* is similar to *Dolichovespula* (Fig. 64 vs. 65). It is well known that, among Old World *Vespula*, *V. rufa* is the only member which does not construct the nest of brittle carton (Type A) which is employed by *Vespa* and *Paravespula*; it constructs the nest of pliable carton (Type B) which is employed by *Dolichovespula*. It is clear that *V. rufa* is transitional between *Paravespula* and *Dolichovespula* as far as the combination of the tridentate mandible, pliable nest material, and simple, long collar processes is concerned. *Dolichovespula (Metavespula) sylvestris* is another example presenting similar conditions on the part of *Dolichovespula*, that is, *D. sylvestris* also possesses tridentate mandibles (Short, 1952) and constructs the nest of pliable material. These facts suggest that *Vespula* and *Dolichovespula*, in spite of their notable dissimilarity, may be related and connected by the transitional forms in both genera. As Simpson (1953) mentioned the higher categories did not arise as such and recognition of a higher category is *ex post facto*. Therefore, recently evolved taxa naturally involve transitional forms less adaptive than the members of a new taxon, which occupies a new adaptive zone, or than those of a stem taxon, which is adaptive in their own way. In fact *V. rufa*, though with a wide distribution, is without exception less dominant than *Paravespula* or *Dolichovespula* at any locality in Japan, and probably so in other places of the Old World.

4.3. *Genus Dolichovespula*. Body nearly equal to that of *Vespula* in size. Head in frontal view rather depressed dorsoventrally in both sexes (Figs. 24, 25). CW/CH: 1.39–1.59, CW/MW: 1.51–1.77. Relative position of the temporal band: $a \gg b \geq c$ (Fig. 32). Mid-cranial sulcus less developed than that of *Vespa*, always invisible above the clypeus. Epistomal sulcus lacking in the upper half (Fig. 32). Labrum of Type B, widest at some distance from the base, with ventral border gently emarginate (Figs. 47, 48). Palate with many spinous processes almost all over and denser than in *Vespa* and *Vespula*; sclerotized patch not extending towards the lateral side; median patch absent. Mandible (Fig. 57) produced to a prominent tooth at lower apical angle (Type B), the upper apical margin serrate, but the serration variable to a great extent and sometimes supposed rudimentary II and III are found (Fig. 57); with cusps, which are variously sized spines, on the inner surface at some distance from the apex, but not visible during the first and second instars and hardly so in the third instar. In the first instar the dentition is very obscure and apical margin often wholly serrate; from the second instar on Tooth I differentiated and projected. Cephalic microscopic denticles distinctly visible near the vertex and on the gena. Maxillary denticles dense (Figs. 51, 52). Spiracle of Type B, collar processes very similar to those of *Vespa*, but relatively elongate, with fewer branches, and mainly on the apical half (Fig. 65); spiracles of the first to fourth instars without any atrial and collar processes.

Recently *Dolichovespula* has been treated as a distinct genus on the basis of morphology and biology (for example, Blüthgen, 1961; Guiglia, 1971; Sk. Yamane, 1975) and Fluno (1973) presents a chemical support to this. As discussed above, in the larval as well as behavioural characters *Vespula* and *Dolichovespula* are connected by the transitional *V. rufa* and *D. sylvestris*. Other species of *Dolichovespula*, however, notably differ from *Vespa* and *Vespula*, while the latter two are very similar to each other. Sequences of some important characters among these genera find the order *Vespa*—*Vespula*—*Dolichovespula*; such characters are shape of the head (Fig. 7), developing degrees of the mid-cranial and epistomal sulci (Figs. 31–34), and microscopic denticles on the cranium. If *Vespa* is most ancestral among them as generally accepted, *Dolichovespula* may be said the most derived of the three. The situation, however, is rather complex, so that the phylogenetic relations of these genera will be discussed at length in Section 6.

Before going further, I present a key to the mature larvae of the Japanese and Taiwanese species of *Vespa*, *Vespula* and *Dolichovespula* studied by me.

Key to the Japanese and Taiwanese species (mature larva)

- | | |
|--|----|
| 1. Mandible tridentate, without cusps (Figs. 53, 55); labrum widest at the base (Type A) (Figs. 41–46). | 2 |
| Mandible monodentate, with cusps on inner surface (Fig. 57); labrum widest at some distance from the base (Type B) (Figs. 47, 48). | 10 |
| 2. Collar processes of spiracle long, usually thick and branched (Figs. 58, 59, 61); mandible wide and stout (Figs. 53, 54). | 3 |
| Collar processes of spiracle remarkably short, if rarely long, slender and simple (Figs. 62–64); mandible somewhat elongate (Fig. 55). | 9 |
| 3. Palate with median patch (Figs. 41, 44, 45); temporal band weakly margined ventrally (Fig. 30), with the only exception of <i>Vespa affinis</i> | 4 |
| Palate without median patch (Figs. 42, 43); temporal band distinctly margined ventrally (Fig. 28). | 6 |

4. Mid-cranial sulcus not visible above the clypeus (Fig. 33); temporal band distinctly margined ventrally (Fig. 29); sensory bristles on the cranium rather long, as long as those on the maxilla and prelabium. *Vespa affinis*
Mid-cranial sulcus visible above the clypeus (Fig. 34); sensory bristles on the cranium short, shorter than those on the maxilla and prelabium (Fig. 35). 5
5. Tooth IIIb of mandible distinctly longer than IIIa (Fig. 54a). *Vespa crabro*
Tooth IIIb of mandible as long as or shorter than IIIa.
. *Vespa velutina*, *V. simillima*, *V. xanthoptera*
6. Head in frontal view nearly circular (Fig. 16); cranial width : mouth parts width ratio 1.33–1.43 (Fig. 7); the largest species. *Vespa mandarinia*
Head in frontal view somewhat depressed dorso-ventrally; cranial width : mouth parts width ratio usually larger than 1.43 (Fig. 7). 7
7. Sclerotized patch on the palate developed to extend towards the base (Fig. 43).
. *Vespa tropica*
Sclerotized patch on the palate divided into small fragments (Fig. 42). 8
8. Spiracle practically without atrial processes; collar processes somewhat slender, with a few branches (Fig. 61). *Vespa basalis*
Spiracle with atrial processes; collar processes thick, with many branches (Fig. 59). *Vespa analis*
9. Collar processes of spiracle long, but simple (Fig. 64). *Vespula (Allovespula) rufa*
Collar processes of spiracle short, even rudimentary (Figs. 62, 63).
. *Vespula (Paravespula) A*, *V. lewisi*, *V. karenkona*
10. Collar processes of spiracle with branches nearly all over; atrial wall with distinct spines (Fig. 65). *Dolichovespula (Dolichovespula) media*
Collar processes of spiracle with branches only on apical half; atrial wall nearly without spines. *Dolichovespula (Boreovespula) saxonica*

5. NOTES ON THE LARVAL BEHAVIOUR

I have attempted to observe the larval behaviour in connection with the present study. The larva of the social wasps is reared in a comb cell throughout the developmental period. Since main activities required of them are those related to eating, only the eating behaviour will be described and discussed here.

5.1. *Vespinae*

In vespine nests the cell top and, therefore, also the larval head, always face downwards, while the mouth opening of the larva faces the lateral wall of the cell. Although behavioural differences in the larval stage among species and genera are undoubtedly important and quite interesting, the main elements and basic pattern seen in the *Vespa* larvae are given below.

5.1.1. *Elements of the behaviour.* The following six elements are distinguished:

(1) *Backward bending* of the anterior half of the body. This action is observed throughout the larval stage. In the first and second instars, the larva bends back the head and thorax at a right angle to the body axis. In the final instar the head is pressed to the cell wall.

(2) *Forward bending* of the anterior half of the body. This is also observed throughout the larval stage. The larva bends the head towards the ventral surface of the thorax and following abdominal segments. In the fourth and fifth instars the labrum and mandibles are completely hidden beneath the tropholopade by this action.

(3) *Dropping of saliva* by the salivary opening. This action is always

associated with the preceding action and is observed throughout the larval stage.

(4) *Opening and closing* of the mandibles. This action is associated with the above three actions and is observed in the second to final instars. The mandibles do not touch or cross medially in the first and second instars, and are never used for biting in any instar.

(5) *Raising* of the mandibles. This action to open and erect the mandibles at an angle of more than 90 degrees is always associated with the head shaking and characteristic exclusively of the final instar.

(6) *Shaking* of the head. This action is easily distinguished from the backward-forward bending complex by that it is always associated with the raising of the mandibles and by that it is practised quickly and repeatedly by the final instar larva alone.

Bock and von Wahlert (1965) distinguished "biological role" from "function" which had been confused. The function of a feature (structure) is its action or how it works, and the form-function complex is termed the faculty of the feature. The biological role of a feature is defined as the action or use of the faculty by an organism in the course of its life history. I will follow their terminology as far as possible. The above listed elements are in other words the functions of corresponding parts of the body, organs or structures. One function of an organ may produce one or more biological roles, or functions of different organs may be intimately associated to produce a biological role. For example, the food-intake (biological role) is practised by the opening-and-closing of the mandibles (function); the scraping for food requirement (biological role) is produced by the raising of mandibles and head shaking (functions).

Unlike the *Vespa* larva the scraping behaviour is much obscure in the *Dolichovespula* larva and even not observed in the *Vespula* larva (also see Ishay & Brown, 1975). This fact worries me to some extent, for the latter two genera are considered to have evolved from the *Vespa*-type ancestor. A possible explanation for this will be given in Section 6.

5.1.2. *Basic behavioural pattern.* The most basic behavioural pattern observed in the mature larva is described as follows. A hungry mature larva is known to require the food by scraping the cell wall with its mandibles (Ishay & Landau (1972) mentioned that this action is observed also in the fourth instar in *Vespa orientalis*). This behaviour has been confirmed in almost all the *Vespa* species observed by me. Scraping larvae, if fed with a pellet, always accept it, whereas non-scraping larvae often reject the food. A scraping action of the larva would be caused as a reaction to the stimulus by the adult. It can be artificially caused by means of touching the comb by the hand or scratching with tweezers.

If one pokes at the head of a scraping larva with tweezers, then it bends back the head towards the cell wall and opens and closes the mandibles violently. In natural condition the stimulus towards the larval head would be practised by the adult mandibles and the biological role of the mandibular movement of the larva at this time is probably the reception of the food. Following this, even if the larva is not fed, it usually bends forward and opens and closes the mandibles in front of the tropholopade; this action is accompanied with the secretion of saliva. The biological role of the mandibular movement in this case is no doubt the food-intake. Thus, one mandibular function takes part in two biological roles, the food-reception and food-intake.

From the above mentioned facts, the head shaking and the raising of the mandibles seem to be functions specific to the final instar larva that has the strongest appetite among larval instars, and form a biological role, the scraping for food requirement. The head shaking, however, may have originated from the backward-forward bending complex which is seen throughout the larval stage and associated with feeding by the nurse. Raising of the mandibles also may have originated from the opening-and-closing of the mandibles which is also correlated with eating. Thus, it can be inferred that the mature larva-specific functions are modifications of the pre-established functions associated with the biological roles of food-reception and intake (eating). In no other social Hymenoptera the scraping behaviour of the larva has ever been reported.

5.2. *Polistini*

Observations have been made on *Polistes snelleni*, *P. rothnei* and *P. biglumis*, all inhabiting Japan, for a comparison with the Vespinae. In the nest of *Polistes* the cell top, therefore the larval head, faces sideways or downwards, and the mouth opening tends to face the cell top.

5.2.1. *Elements of the behaviour.* The following five elements are distinguished:

(1) *Protruding* of the head. This action is observed throughout the larval stage and is sometimes preceded by the backward bending of the body which is done feebly and less frequently than in the vespine larvae.

(2) *Dropping of saliva* by the salivary opening. This action always occurs immediately after the head protrusion or after the food-intake and is seen throughout the larval period.

(3) *Opening and closing* of the mandibles. This action occurs simultaneously with the dropping of the saliva and is observed in the third to final instars. The mandibles do not touch or cross medially in any instar.

(4) *Raising* of the labrum. This action precedes the dropping of the saliva.

(5) *Drawing in* of the labrum, maxillae and prelabium. When the larva takes food in by the opening-and-closing of the mandibles, the labrum, maxillae and prelabium draw in and the maxillary tip touches the anterior margin of the labrum.

5.2.2. *Basic behavioural pattern.* If one pokes at the head of a hungry mature larva with tweezers, it protrudes the head violently and secretes saliva. In *P. biglumis*, however, it does not protrude the head but merely secretes saliva. The sticky saliva fills up the hollow enclosed by the raised labrum, prominent maxillae and prelabium. The maxillary and labial palps are very sensitive and active in this time. If the larva is fed, it usually opens and closes the mandibles; the biological role of this is the food-intake. The *P. rothnei* larva seldom uses the mandibles when it is fed with a small food pellet or liquid.

It should be given attention that the forward bending of the body, shaking of the head and raising of the mandibles, and their biological role, the scraping for food requirement, are not found in the *Polistes* larva. Instead the *Polistes* larva signals its hunger by protruding the head in response to the stimulus by the nurse. Moreover, the mandibles do not serve for food-reception but food-intake alone. Food-reception may be aided by the secreted saliva that sticks the food, immediately followed by intake, when the larva absorbs it with the aid of the mandibles and other appendages. Grandi (1959) refers to the term "trophothylax"

(humped ventral surface of the first urite) and mentions that the "trophothylax" serves as a support for the alimentary bolus, which, sticky as it is, adheres to the "trophothylax" even when the comb openings are turned downward and therefore the larva is downheaded. This is the case of vespine larvae, but the *Polistes* larvae in at least three species I have observed neither bend forward nor take the food at the "trophothylax", but take the food in the protruding posture mentioned in preceding lines. The enlarged abdominal segments may serve merely as a support to prevent the body from dropping out of the cell.

6. PHYLOGENETIC CONSIDERATIONS OF THE SUBFAMILY VESPINAE

6.1. *Different evolutionary trends between the larvae of Vespa and Polistes*

Many of the characters used in the classifications of Aculeate larvae have not been known of their adaptive significances so that these classifications have remained rather phenetic. Reid's excellent work is not an exception in this respect. He described several important findings, but he did not interpret their meanings in the wasp's life. However, some investigators have attempted to interpret the larval characters in terms of adaptation. For example, Michener (1953) in his extensive study on bee larvae argues that the mandibular form has changed in association with the food change from insects or spiders to pollen or honey during evolution from sphecids wasps to bees; he also shows that the antennae and palpi bear the sensillae that enable the larva to apply its silk properly in cocoon construction. Grandi (1959) compares the larvae of Polistini with those of Vespinae and concludes that the head of the Polistini is seemingly modified to form a lid for the comb cell. The fact here concerned is that in the nest not covered by protective envelopes, as in the Polistini, the larva is in direct contact with the external environment.

A notable resemblance of Eumenidae to Vespinae in larval appearance has been pointed out by Reid (1942). Both have the lower margin of the clypeus ventral to the level of the mandibular bases. The mandibles are stout, angular in cross section, strongly sclerotized, and usually tridentate apically. In both the palate bears sclerotized patches in which conical sensillae are found. The maxillae, prelabium and postlabium show no particular characters in size and form. By these properties the Vespinae and Eumenidae look alike in general. On the other hand, larval Polistini are characterized as follows. The lower border of the clypeus is not ventral to the level of the mandibular bases. The mandibles are slender, nearly circular in cross section, and end in two fine pointed teeth, with the ventral larger tooth sometimes bearing a small subsidiary tooth. In the latter case the number of teeth alone is equal to that in the vespine mandibles, but the pattern of tooth arrangement is distinctly different. The palate usually bears no sclerotized patches. The maxillary lobes are prominent and nearly spherical, and the postlabium is considerably enlarged.

Of the above mentioned characters the shapes of the mandibles and maxillo-labial complex are of special interest in the field of functional morphology. The mandibles of the vespine and eumenid larvae are known to serve for eating. For example, the larval stage of Eumenidae may be divided into two periods: In the early period the larva sucks on only the body fluid of the prey and in the later period it feeds upon the residue of the prey, masticating with the stout mandibles

(Iwata, 1953). On the other hand, according to my own observations, the larval Polistini use mandibles for food-intake by means of opening and closing them (see 5.2.) During the first two instars the mandibles are very minute and apparently functionless. This well agrees with the observation that the young larvae of *Polistes* are mainly fed with fluid substance (S. Yamane, 1971). At any rate the *Polistes* larvae, whether young or old, never masticate the food pellet with the mandibles. This is also the case in vespine larvae as described in 5.1. Thus there is a clear-cut difference between the solitary and social wasps in the function and biological role of the larval mandibles. In the social wasps the larva is fed by the nurse and has need of masticating by itself no longer. To be sure, the *Polistes* larva has slender mandibles which appear quite feeble; the same is seen in Polybiinae (Reid, 1942). They have lost one function of mandibles, that is, the crossing, and as a matter of course also one biological role, the masticating of food pellet, with the development of the substitute masticating by the nurse. Thus, the biological role of the mandibles has been diminished to the food-intake alone, this being associated with a notable reduction in the mandibular structure. On the other hand, the larvae of Vespinae and especially of *Vespa*, whose societies are the most "advanced" and in some respects even comparable with the honeybee societies, have nevertheless huge, robust mandibles. The mandibles are not different from those of eumenid larvae except for the first tooth much projecting. It seems to me that this combination of the mandibular form and feeding habit in vespine larvae can be explained as follows: The mandibles of the larva of the vespine ancestor, prior to any possible reduction, might have acquired, in association with an evolving society, another function (raising) and biological role (scraping for food requirement) possibly in need of informing the nurse wasps. In such a case the stout mandibles of eumenids, which produced the vespine ancestor, may present an example of "preadaptation" (Bock, 1959). The assumption here adopted is strongly supported by the fact that the larva of *Vespa tropica*, fed with fluid substance throughout its development, has stout mandibles in the last instar.

The functions and biological roles of well-developed maxillo-labial complex in *Polistes* larvae (probably also in other tribes of Polistinae) have not been given a satisfactory explanation. Grandi's opinion seems somewhat inadequate to me, because the complex together with the cranium is not so large as to close the cell top. In this connection it must be noted that in the comb cell the mouth opening is directed nearly towards the cell opening (while it is nearly opposite the cell wall in vespine larva). The mouth opening directed towards the cell opening combined with the well-developed maxillo-labial complex with prominent palps should make the food-reception easy in the comb cell (see 5.2.). Instead, an enlargement of the maxillo-labial complex will make it difficult for the larva to shake the head repeatedly, and this may be a reason for the absence of scraping movement. On the other hand, the *Vespa* larva possessing the mouth opening opposite the cell wall must bend backward in food-reception and then bend forward in food-intake. It is doubted whether these actions themselves have any adaptive meaning in the social life. However, when the backward-forward bending of the body is combined with mandibular movements, all these actions produce a new biological role, the scraping for food requirement. The development of this biological role might have favoured the mouth opening directed against the cell wall. A comparison of forms, functions, and biological roles of the mandibles in

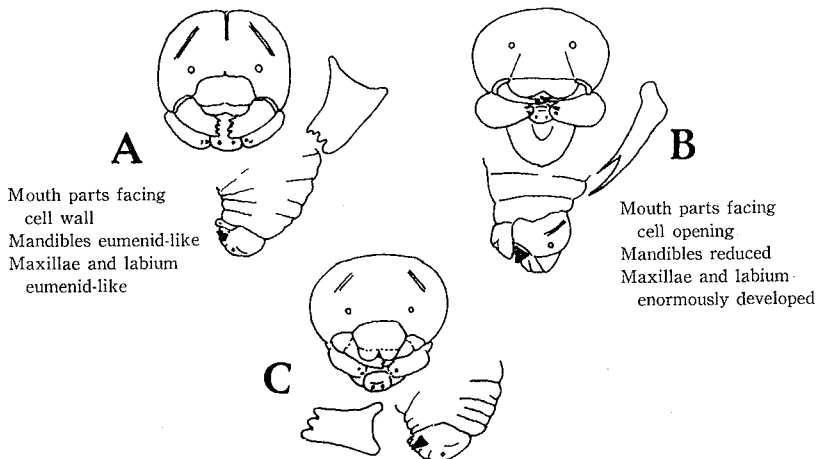


Fig. 3. Morphological features of the larval head in *Vespa* (A), *Polistes* (B), and Eumenidae (C).

Table 2. Forms, functions and biological roles of the mandibles in Eumenidae, *Vespa* and *Polistes*.

Form	Function	Biological role	Taxonomic group
wide and stout	crossing	food-mastication	Eumenidae
		opening and closing	
elongate and feeble	raising	food-reception	<i>Vespa</i>
		scraping for food requirement	
	opening and closing	food-intake	<i>Polistes</i>

Vespa, *Polistes* and Eumenidae is given in Fig. 3 and Table 2.

At any rate *Vespa* and *Polistes* have evolved different tendencies as far as the larval eating habit and the larva-adult communication are concerned. As already mentioned the Vespinae have reserved such "primitive" characters as seen in the existent eumenid larvae. Richards (1971) mentioned: "The Vespinae are in [adult] structure rather more like the solitary Eumenids than are the Polistinae and probably branched off earlier from some common social ancestor." He denies Ducke's (1914) opinion that the social wasps might have evolved polyphyletically from the solitary Eumenidae.

If Richards' view, which is also mine, is correct, then the common ancestor of the Vespinae and Polistinae must have reserved eumenid-like appearances in both the larva and the adult. After that they have come along different ways, so that it is quite doubtful that the Vespinae have passed through such stages of social structure as shown by the existent taxa of the Polistinae, which ostensibly fill up the gap between the solitary Eumenidae and the most "advanced" Vespinae. Yoshikawa's simple-minded hierarchy of social structure based upon the existent taxa is not acceptable from the phylogenetic viewpoint, much less is his opinion (Yoshikawa, 1973) that the Vespinae have evolved multilinearly in North America, Asia, and Europe from solitary eumenids and by passing through polistine-like societies.

6.2. *Phylogeny of the subfamily Vespinae*

As stated in the preceding section the Vespinae and Polistinae probably branched off from the ancestral stock of social wasps in an early stage in societal evolution and have evolved along the different adaptive trends. At present, however, we can neither infer the time when the branching occurred nor precisely picture the ancestral form, because no reliable fossil record for Vespinae has been known (Bequaert, 1930) and the Vespinae form a very compact group without supposed links connecting to the ancestral stock. Consequently, we can not help accepting the phylogenetic tree proposed by Evans (1956) (Fig. 4).

It may be helpful to the following discussion to give here a brief note on the distribution of the vespine genera under consideration. The Vespinae are distributed in the Holarctic and Oriental regions. The genus *Vespa* is restricted largely to Asia and dominant in the subtropical and warm-temperate zones. On the other hand, the genera *Vespula* and *Dolichovespula* are Holarctic; *Vespula* is successful in the temperate zone and *Dolichovespula* is mainly found in the cold-temperate and subarctic zones. It has generally been considered that the Vespinae originated in Indomalaysia, where *Vespa* is abundant in species number, and spread over the Holarctic region; this assumption is based on the fact that *Vespa* is most "ancestral" of the three in adult characters.

The branching pattern within the Vespinae has not so far been thoroughly studied in spite of its importance in evolutionary understanding of the subfamily. I will try to propose a branching pattern for six groups which seem to be monophyletic and to briefly interpret their evolution in connection with larval features. The genus *Provespa*, for which we have only a few information, and two parasitic groups, i.e., the subgenera *Vespula* and *Pseudovespula*, are excluded from the following discussion. Though the phylogenetic diagram here proposed (Fig. 5) is in the form of cladist's argumentation plan, it is adopted merely to show my interpretation concise. The features used in Fig. 5 are listed in Table 3, followed by their ancestral and derived states. These features are only a part of those which

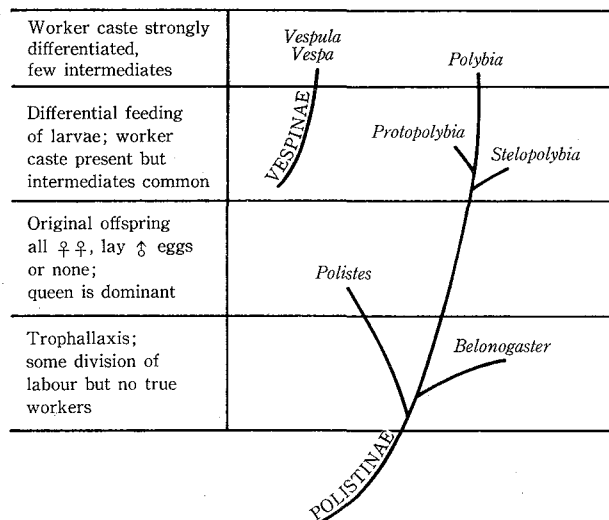


Fig. 4. Phylogenetic diagram of the family Vespidae (redrawn from Evans, 1956).

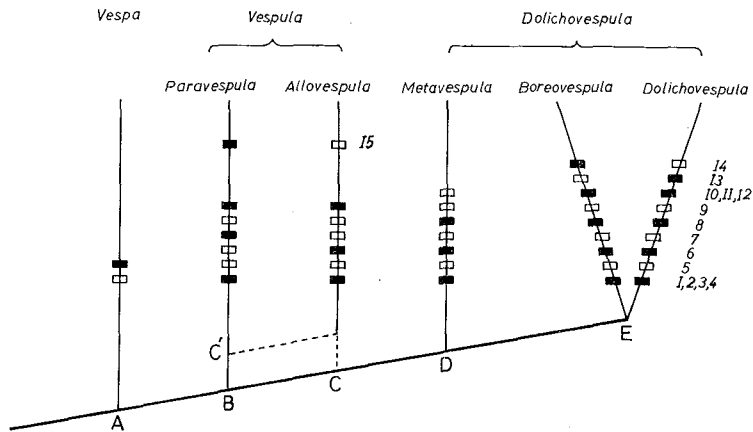


Fig. 5. Phylogenetic diagram of the subfamily Vespinae. Numbers 1–14 indicate the used features which are listed in Table 3. Squares represent ancestral (white) and derived (black) characters. A–E, see text.

Table 3. Features used in phylogenetic tree (Fig. 5).

Feature	Character	
	Ancestral	Derived
1. Third segment of labial palpi [A]	with one or two strong setae	without setae
2. Hamuli of hind wing [A]	beginning before the tip of subcostella	beginning at the tip of subcostella
3. Humeral calli [A]	separated from the sides of pronotum by a suture or carina	not separated from the sides of pronotum
4. Pedicel of embryo nest [B]	thick, not twisted	twisted
5. Stigma of fore wing [A]	well developed	small, inconspicuous
6. Nest material [B]	brittle; brown or buff	pliable; grey
7. 7th gastral tergite of male [A]	not depressed	posterior half heavily depressed
8. Oculo-malar space [A]	short	long
9. Vertical carina of the sides of pronotum [A]	upper portion distinct	lacking in upper portion
10. Mandible [L]	apically tridentate	apically monodentate
11. Labrum [L]	Type A	Type B
12. Male antenna [A]	without tyloides	with tyloides
13. Envelope of embryo nest [B]	ball-shaped	flask-shaped
14. Dorsal terminal process of male genitalia [A]	distinctly projecting	indistinct
15. Stem of aedeagus of male genitalia [A]	thick	thin

A: adult, B: behavioural, and L: larval features.

are used in the vespine taxonomy, and are selected to make the understanding easy.

Though the genus *Vespa* is treated as a monophyletic group, this treatment is somewhat questionable and needs further analyses. Character sets supporting the branching A are 1–4. Some characters, however, conflict with this view. For

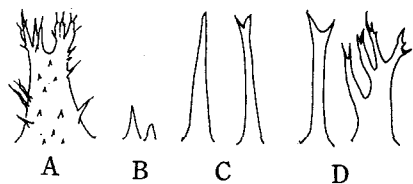


Fig. 6. Collar processes of the mature larval spiracle, showing a morphocline (B-C-D). A. *Vespa*, B. *Paravespula*, C. *Allovespula*, D. *Dolichovespula*.

processes are much reduced, the diameter of the primary tracheal opening is smaller than in *Vespa* and *Dolichovespula*. Concerning the degree of development of the collar processes a morphocline can be seen in the sequence *Paravespula*—*Allovespula*—*Dolichovespula*; the state in *Vespa* is, as mentioned above, similar to that in *Dolichovespula*. (Fig. 6). The tylodes occur in *Vespa* and the subgenera *Boreovespula* and *Dolichovespula* of *Dolichovespula*, this also presenting a contradiction, which can not be explained.

The branching sequence B—C' is presented on the basis of character sets 8, 9 and 15, while 6 and 7 support an alternative sequence, B—C. Apart from this contradiction it is shown by Fig. 5 that *Paravespula* branched off prior to the differentiation of the subgenera *Boreovespula* and *Dolichovespula*. *Paravespula* larvae do not scrape the cell wall to inform their hunger to the nurse, whereas larvae of the subgenera *Boreovespula* and *Dolichovespula* behave like *Vespa* larvae though more feebly and less frequently than the latter. As mentioned in the preceding section (6.1.) the acquisition of the scraping behaviour by the larva is thought to belong to the early societal evolution in the Vespinae. Therefore, the absence of this behaviour in *Paravespula* must be a secondary loss. All *Paravespula* species construct a subterranean nest in contrast with the aerial nesting habit of *Vespa* and *Dolichovespula*. In temperate and cold climates the underground nesting is quite favourable for the thermoregulation within a colony. However, the supposed change of the nesting site in the ancestral stock of *Paravespula* must necessarily have caused other changes. The subterranean nesting habit may demand a smaller body size in order to rear offspring as many as possible in a limited space. On the other hand, the reduced body size is probably disadvantageous in hunting large insects and may be associated with the preference for dipterous insects. Further, more workers may be needed to enlarge the nest cavity. On the other hand, the subterranean nest can be constructed with a small quantity of material in comparison with the weather-beaten aerial nest. The Type A nest (cf. 4.2.) is made largely of rotten part of trees (Spradbery, 1973) and so brittle by nature; if the material is saved as seen in *Paravespula*, the nest firmness will remarkably decrease. In fact, we can hardly excavate the *Paravespula* nest without damaging it. The scraping action by the larva may damage the cell wall, and it may not be compatible with the thrift in nest material.

The *Vespa*-like head of the *Paravespula* larva disagrees with my opinion that a mouth opening facing the cell opening is favourable and indeed general among the social wasps which do not scrape. However, some slight modifications

example, *Vespa* and *Dolichovespula* share the branched collar processes of the larval spiracle which are without doubt regarded as derived in the Vespidae. Such a contradiction is often due to mosaic evolution (Mayr, 1974). Branched collar processes might have been regained by *Dolichovespula*. Hymenopterous larvae with a large primary tracheal opening tend to possess developed collar processes to prevent soil particles from clogging tracheae (Evans, 1964). In *Paravespula* larvae, whose collar

probably associated with the loss of scraping behaviour are seen in *Paravespula*, for example, the comparatively elongate and feeble mandibles. Nevertheless, a similarity between *Paravespula* and *Vespa* in the larval head structure is still notable.

A few pieces of information have been accumulated on the biology of *Allovespula* species except for the Palearctic *V. rufa*. A recent work on *V. atropilosa* by MacDonald et al. (1974) added valuable data, but the biological information about most of the American species still remains fragmentary. As mentioned above *V. rufa* is transitional between *Paravespula* and *Dolichovespula* in some adult and larval characters, and also in behavioural ones. The nest paper of *Allovespula* is more similar in design and strength to that of *Dolichovespula* rather than of *Paravespula*. The supports for the comb are vertical ribbons in *V. atropilosa* and the European *V. rufa rufa* like those of *Dolichovespula*, whereas they are pillars in the Japanese *V. rufa schrenckii* as in *Paravespula* (MacDonald et al., 1974; Sk. Yamane, unpub.). In the Japanese race the comb shape is also quite similar to that of *Paravespula*. The grey-coloured, pliable nest material (Type B) of *Allovespula* is evidently a derived character within the Vespinae. The sharing of this character with *Dolichovespula* strongly supports the branching B-C, for this character would have been a prerequisite for the evolution of *Dolichovespula*. Though the adaptive nature of the pliable nest material for *Allovespula*, which nests underground, is not known, once this type of nest was acquired the aerial nesting site would have easily been exploited.

The branching D is supported by the character sets 10, 11 and 12, and E by 13 and 14. The wasps of the genus *Dolichovespula* construct the nest made of the grey-coloured, pliable material (Type B). This choice is adaptive to the aerial nesting habit and differs from the strategy which *Vespa* has developed (strengthening of the Type A nest). The present-day geographical distribution of *Dolichovespula* suggests that the genus evolved during the glacial epoch. The combination of its distribution in cold climates and its twig-nesting habit is inconsistent with my view that the subterranean nesting is an adaptation in temperate and cold climates. Though this contradiction is at present not thoroughly explicable, the following assumption should be probable. The ancestral forms of *Dolichovespula* spread out their distribution far north where available underground cavities were much limited, resulting in the frequent occurrence of intra- and interspecific competitions for nesting site. Such competitions are commonly observed among the existent subterranean species. Under this condition it was advantageous for them to be able to utilize both the aerial and subterranean nesting sites. As *Vespa* was lacking there the aerial nesting site was wholly open for them. The evolving *Dolichovespula* was nearly completely evicted from underground cavities when its distribution area later overlapped that of *Paravespula* in the southern periphery. Though thermoregulation operates within *Dolichovespula* nests (Gibo et al., 1974), they need a lot of envelopes to shut out the external atmosphere; besides, the colonial span is considerably shortened, consequently they can produce only a small amount of offspring. The short colonial span makes it possible to utilize the flower nectar as the food of adults during the whole active season (Sk. Yamane & Kamijo, 1976). The long oculo-malar space of the adult wasp might have been favoured by increasing visits to flowers.

The sporadic occurrences of the flask-shaped embryo nest among *Vespa* and

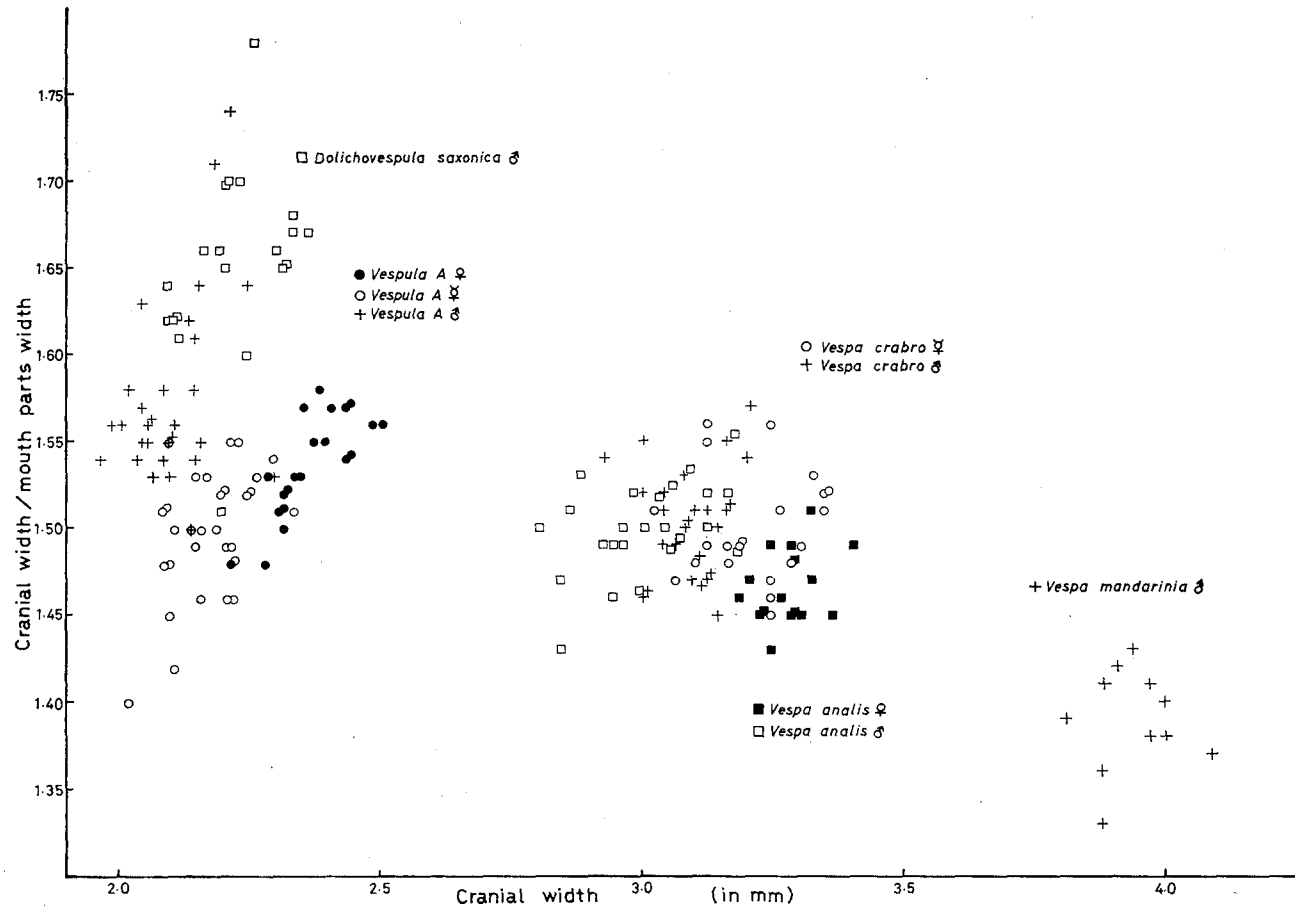


Fig. 7. Cranial width/mouth parts width ratio against cranial width in mature larvae of some available species.

the subgenus *Dolichovespula* give another puzzling problem. That all the species with the flask-shaped embryo nest, i.e., *Vespa analis*, *V. affinis* (S. Yamane, personal communication), *Dolichovespula media*, and *D. maculata* (Bohart, 1957), build nests exclusively in open places suggests an adaptation for protecting the immature from arthropod predators during the solitary stage. Some derived larval characters of *Dolichovespula* are not explained in terms of functional morphology, though they seem necessarily to be significant in the bionomics of the wasps.

LIST OF ABBREVIATIONS IN FIGURES

aba	abductor apodeme	hs	hypostomal sulcus (hypostoma)
ada	adductor apodeme	lcs	labro-clypeal suture
ant	antenna	lm	labrum
ant sk	antennal socket	lplp	labial palp
apr	atrial processes	mc	mandibular corium
at	atrium	mcs	mid-cranial sulcus (median suture, epicranial suture)
ata	anterior tentorial arm	md	mandible
atp	anterior tentorial pit	mp	median patch on palate
cd	cardo (proximal part of maxilla)	mplp	maxillary palp
clp	clypeus	mx	maxilla
clpr	collar processes	pl	palate
cp	sclerotized patch on palate	plb	postlabium (submentum, postmentum)
csfg	cuticular structures of female genitalia	plst	pleurostomal sulcus (pleurostomal ridge)
csmg	cuticular structure of male genitalia	pos	postoccipital sulcus
dfm	depression in cranial wall at the origin of frontal muscle	prlb	prelabium (mentum, prementum)
dt	microscopic denticles on maxilla	pta	posterior tentorial arm
dta	dorsal tentorial arm	so	salivary opening
dtp	dorsal tentorial pit	spr	microscopic spinous processes on palate
es	epistomal sulcus (epistoma)	st	stipes (distal part of maxilla)
fa	frontal arm of dorsal ecdysial cleavage line	tb	tentorial bar (tentorial bridge)
fr	frons	tmb	temporal band (parietal band, ocular fossa)
g	gena (genal region)	tr	temporal region (parietal region)
ga	galea (one of maxillary palps)	v	vertex
gr	genital rudiments		

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PLATES

Plate I

- Figs. 8-11. Mature larva of *Polistes biglumis*. 8. lateral view of the body; 9. frontal view of the head; 10. lateral view of the head; 11. ventral view of the head.
Fig. 12. Mandible of *Polistes (Megapolistes) rothnei iwatai*, mature larva.
Fig. 13. Mandible of *Polistes* sp., mature larva.

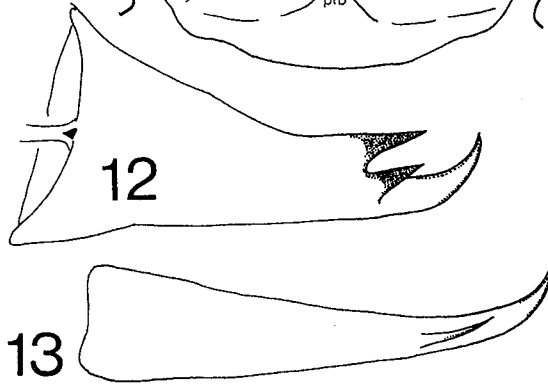
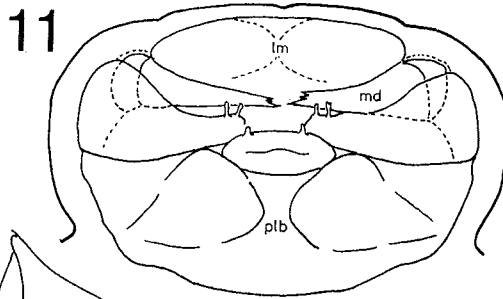
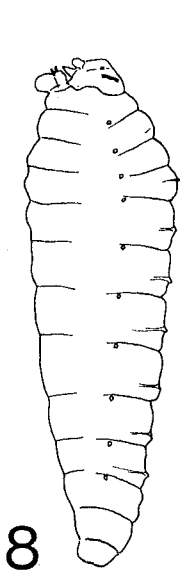
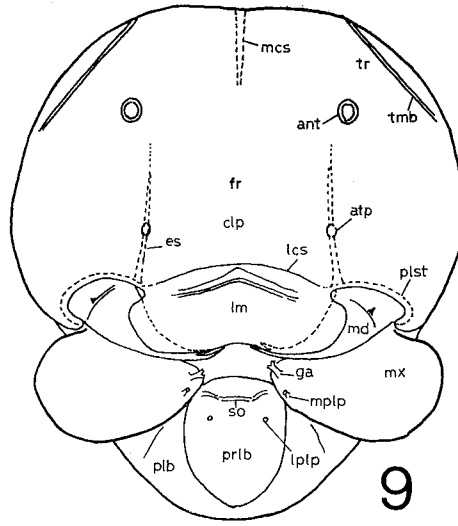
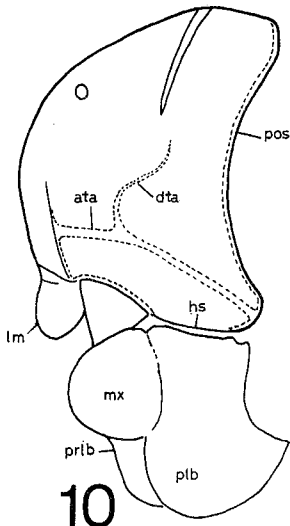
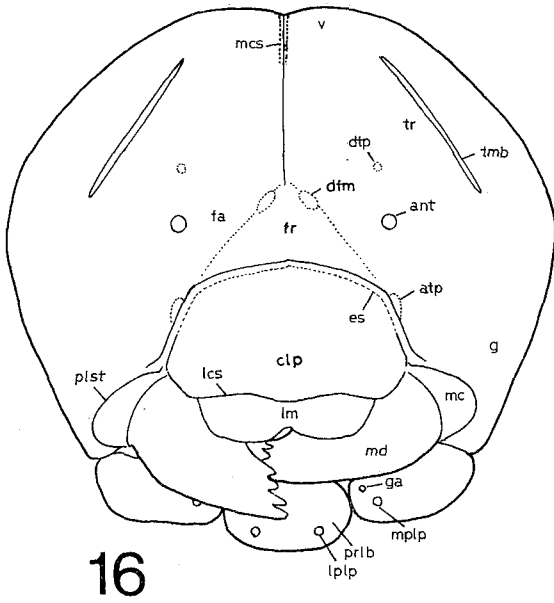
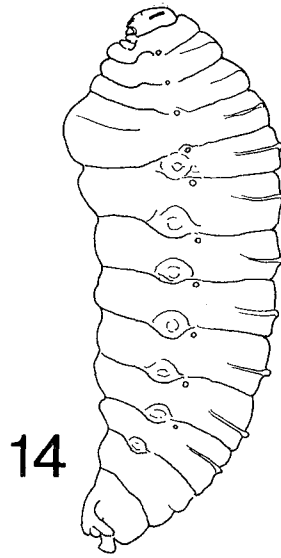


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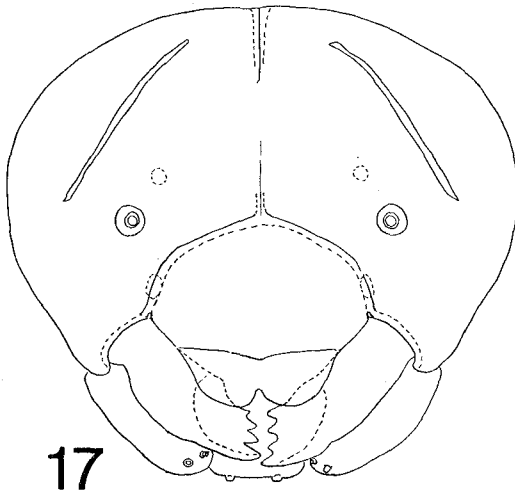
Figs. 14-16. Mature larva of *Vespa mandarinia nobilis*. 14. lateral view of the body; 15. dorsal view of the body; 16. frontal view of the head.
Fig. 17. Frontal view of the head of *Vespa velutina flavitarsus*, mature larva.



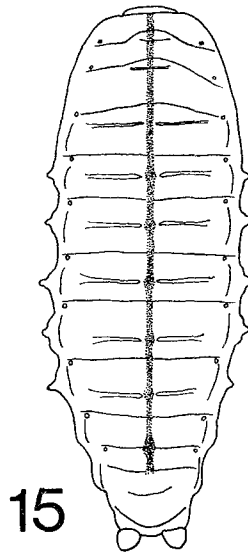
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17



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Plate III

Larval head of *Vespa mandarinia nobilis*.

Figs. 18 & 19. Mature larva. 18. lateral view; 19. ventral view.

Figs. 20 & 21. 3rd instar larva. 20. lateral view; 21. ventral view.

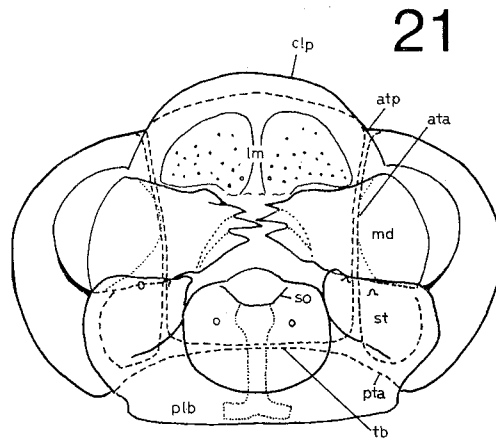
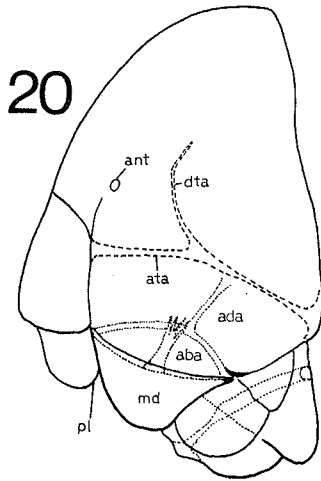
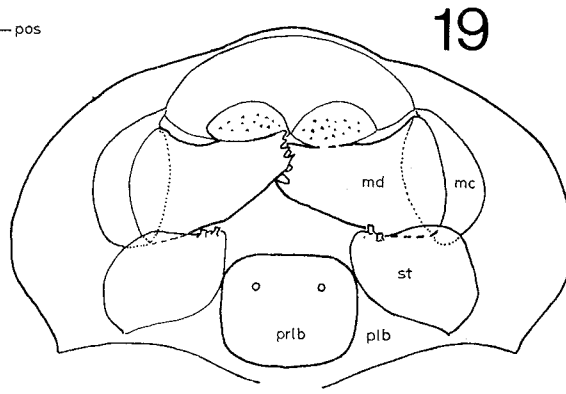
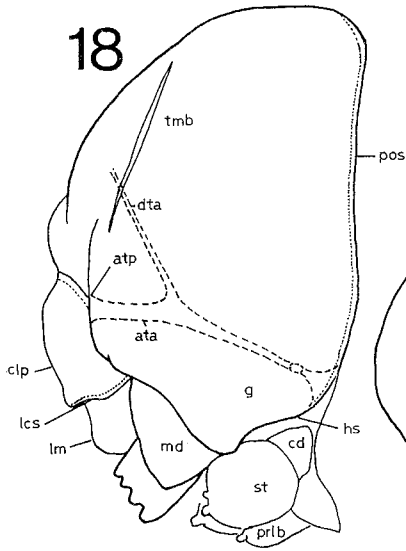


Plate IV

Frontal view of the head of vespine mature larvae.

Fig. 22. *Vespula vulgaris*, female.

Fig. 23. *Vespula vulgaris*, male.

Fig. 24. *Dolichovespula saxonica nipponica*.

Fig. 25. *Dolichovespula media media* (in this figure the labrum appears to be improperly deeply emarginate; see Fig. 47).

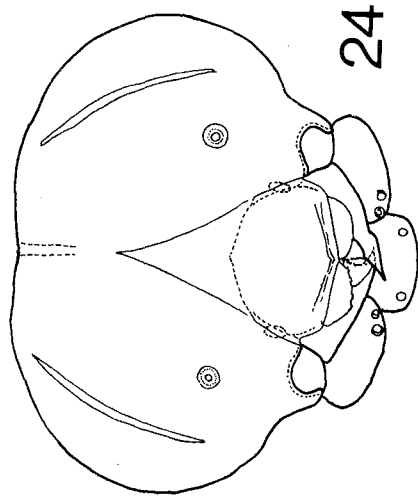
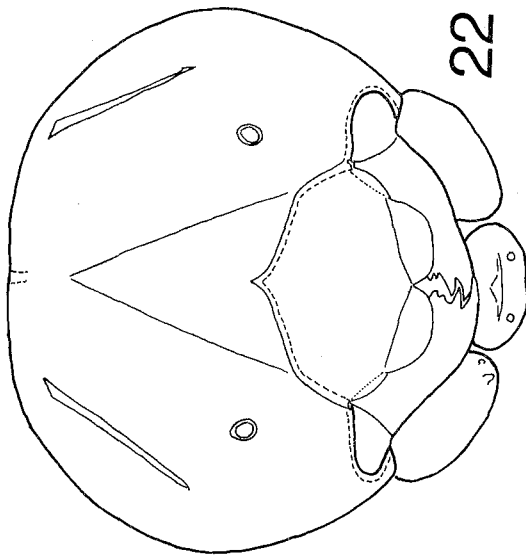
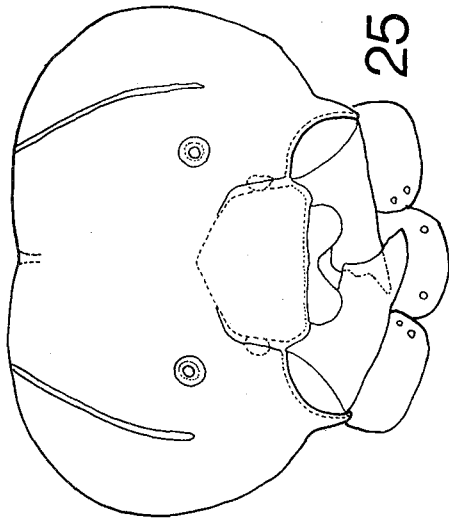
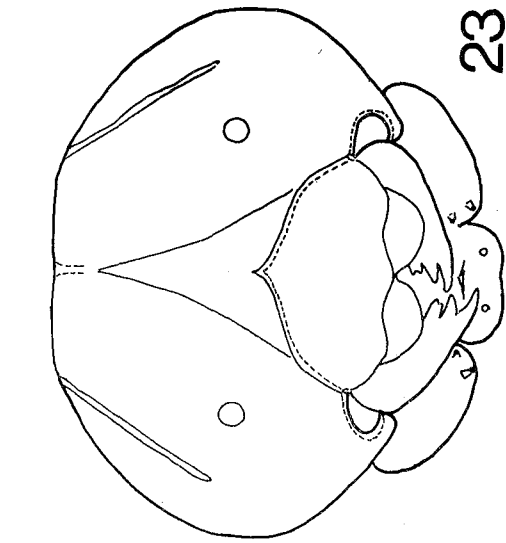


Plate V

- Fig. 26. Antenna of the vespine mature larva.
- Fig. 27. Palps on the prelabium (a) and maxilla (b) of the vespine mature larva.
- Figs. 28-30. Temporal band of vespine mature larvae. 28. *Vespa analis insularis*; 29. *Vespa affinis affinis*; 30. *Vespa velutina*-group.
- Figs. 31-34. Left half of the cranium of vespine mature larvae. 31. *Vespula*; 32. *Dolichovespula*; 33. *Vespa* other than *V. velutina*-group; 34. *Vespa velutina*-group. a-c, see text.
- Figs. 35-40. Sensory bristles on the cranium (a) and maxilla and prelabium (b) of vespine mature larvae. 35. *Vespa* other than *V. basalis* and *V. affinis*; 36. *Vespa basalis*; 37. *Vespa affinis affinis*; 38. *Dolichovespula media media*; 39. *Vespula vulgaris*; 40. *Vespula A.*

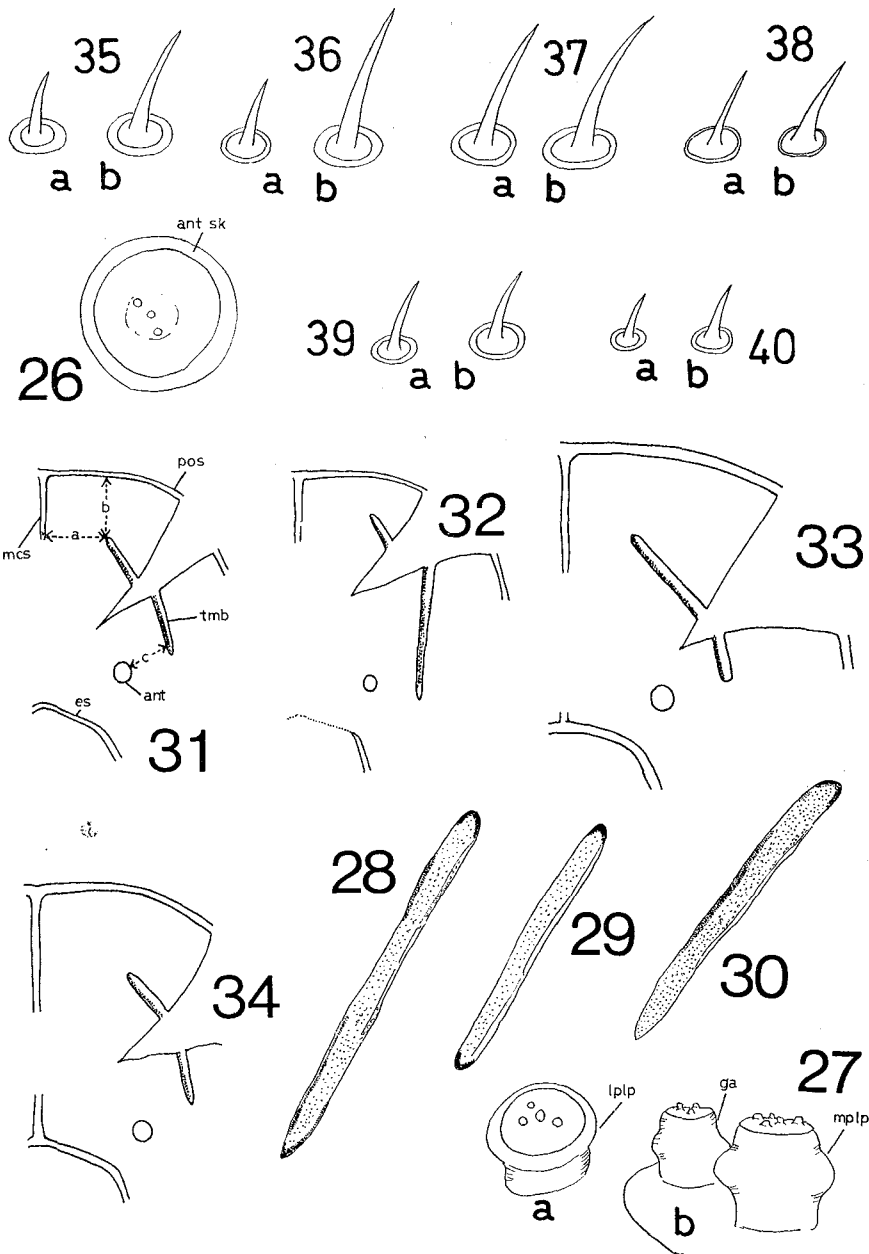


Plate VI

Figs. 41-48. Labrum (right) and palate (left) of vespine mature larvae. 41. *Vespa affinis affinis*; 42. *Vespa analis insularis*; 43. *Vespa tropica pseudosoror*; 44. *Vespa crabro flavofasciata*; 45. *Vespa simillima*; 46. *Vespula A*; 47. *Dolichovespula media media*; 48. *Dolichovespula saxonica nipponica*.

Figs. 49-52. Stipes of vespine mature larvae. 49. *Vespa analis insularis*; 50. *Vespula vulgaris*; 51. *Dolichovespula saxonica nipponica*; 52. *Dolichovespula media media*.

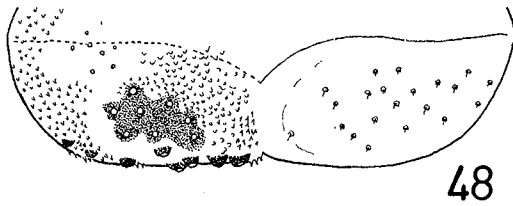
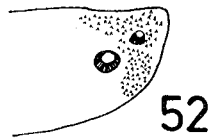
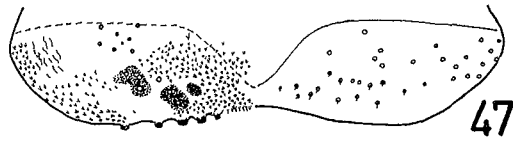
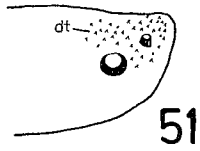
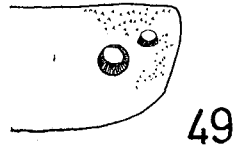
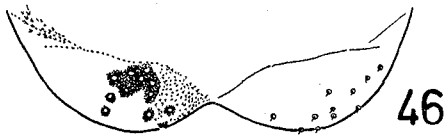
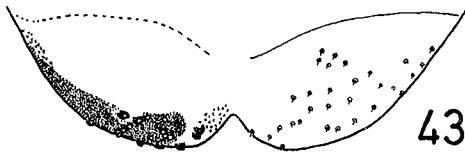
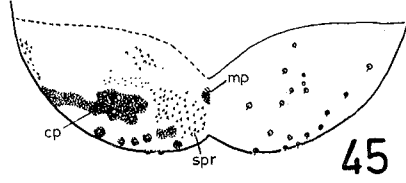
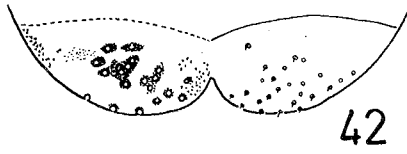
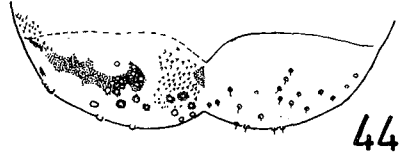
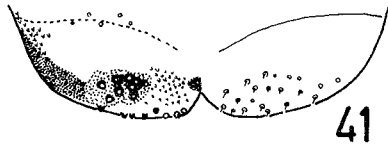


Plate VII

Mandibles of vespine mature larvae. Numerals indicate larval instars.

Fig. 53. *Vespa mandarinia latilineata*.

Fig. 54. a. *Vespa crabro flavofasciata*; b. *Vespa analis insularis*.

Fig. 55. *Vespula vulgaris*.

Fig. 56. *Vespula rufa schrenckii*.

Fig. 57. *Dolichovespula media media*.

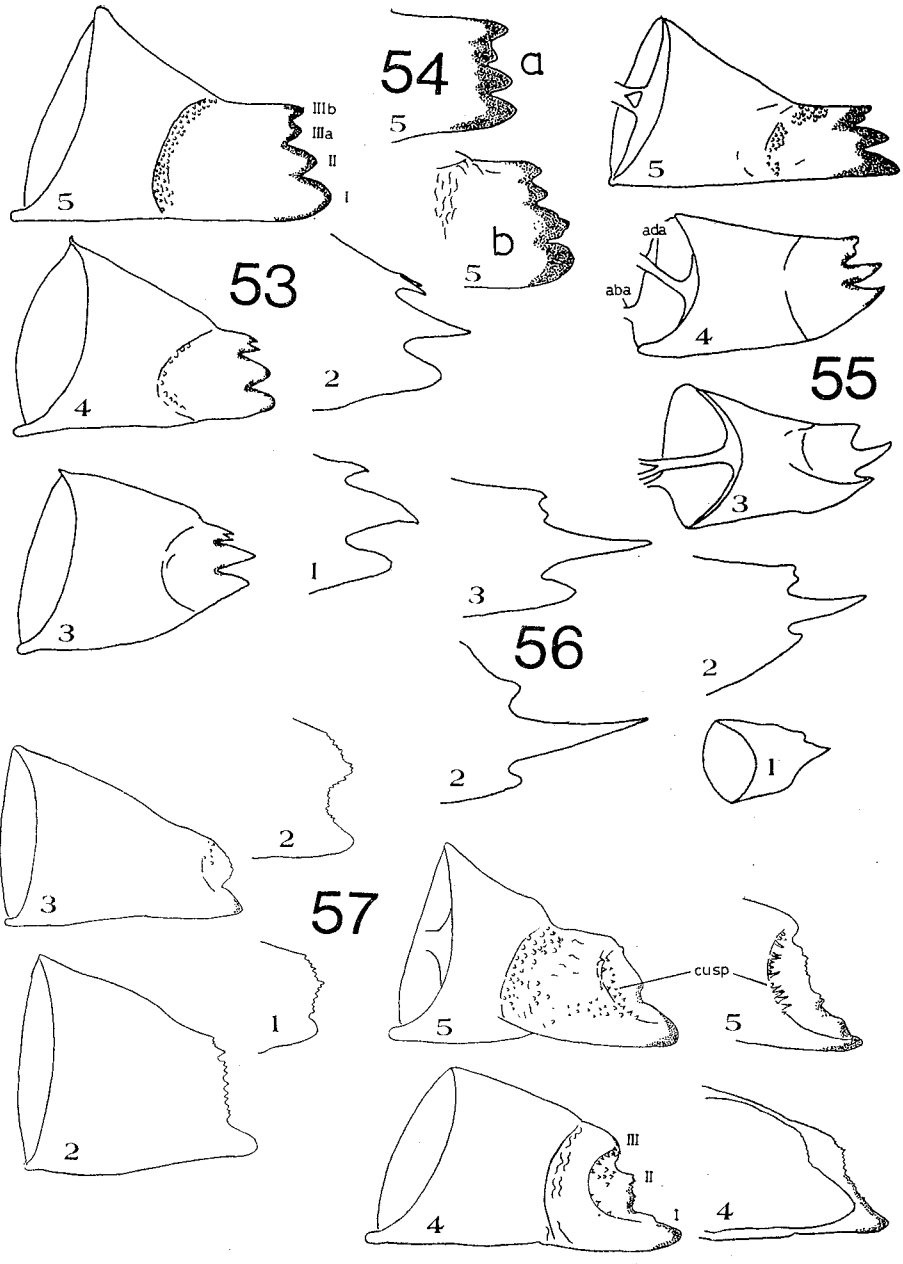


Plate VIII

Spiracles of vespine larvae.

- Fig. 58. *Vespa crabro flavofasciata*. a. surface view (mature larva); b. collar process (mature larva); c. surface view (4th instar larva).
Fig. 59. *Vespa analis insularis*, surface view (mature larva).
Fig. 60. *Vespa tropica pseudosoror* (4th instar larva). a. surface view; b. longitudinal sectional view.
Fig. 61. *Vespa basalis* (mature larva). a. surface view; b. collar process.
Fig. 62. *Vespula A*, surface view (mature larva).
Fig. 63. *Vespula karenkona*, surface view (mature larva).
Fig. 64. *Vespula rufa schrenckii* (mature larva). a. surface view; b. collar process.
Fig. 65. *Dolichovespula saxonica nipponica* (mature larva). a. surface view; b. collar process.

