Occurrence and Location of Exocrine Glands in Some Social Vespidae (Hymenoptera)[1]

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ABSTRACT

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Queens of 12 species of yellowjackets (*Vespula* Thomson/*Dolichovespula* Rohwer), as well as *Vespa crabro* L., *Polistes fuscatus* (F.), and *Mischocyttarus flavitarsis* (Saussure), were dissected in a search for exocrine glands. Fourteen glands or gland systems were found, including 4 previously unreported glands associated with the mouth parts and an additional abdominal gland. Another unreported abdominal gland was found in males of *Mischocyttarus flavitarsis*. Most appear to be widely occurring in the social Vespidae. Some changes in gland development were documented in relation to season and colony development, suggesting possible functions. There were differences in the occurrence of certain glands among species groups and genera. The extensive exocrine gland systems found in vespid queens are probably associated with colony founding by queens as well as intensive use of chemical communication.

Social vespids appear to rely heavily on pheromones for communication in the social organization of their colonies, and exocrine glands are important in their production. A number of pheromones important in the colony life of vespine wasps has been documented. *Vespula vulgaris* (L.) has an alarm pheromone (Maschwitz 1966) and a footprint pheromone (Butler et al. 1969). Thermoregulatory pheromones are produced by larval *Vespula germanica* (F.) to stimulate adults to warm them (Ishay 1972). A queen pheromone, distributed by workers licking the queen's head and thorax (queen court), was reported in *Vespa orientalis* F. (Ikan et al. 1969). It also appears likely a queen pheromone exists in yellowjackets (*Vespula* Thomson/*Dolichovespula* Rohwer) (Landolt et al. 1977). Undoubtedly, many other pheromones are produced by such wasps. Their investigation is necessary for a proper understanding of yellowjacket social behavior.

Information on yellowjacket exocrine glands is scattered and incomplete. A few papers deal with specific glands: Hammad (1965) and Hermann and Dirks (1974) on sternal glands and van der Vecht (1968) on sternal brushes, and Hermann et al. (1971) on mandibular glands. Heselhaus (1922) discussed principally glands of bees but also covered a number of glands of vespines and included a few illustrations showing their location. Spradbery (1973) included a discussion of yellowjacket glands based on his dissections of *Paravespula* spp (*Vespula vulgaris* species group). These studies involved a limited number of species and did not include a number of glands present in yellowjacket wasps.

This study was undertaken to provide a more complete account of the exocrine glands of yellowjackets and some related wasps. It is hoped this information will aid investigators of social wasp behavior, particularly in the study of pheromones and their sources.

Materials and Methods

Most specimens examined were collected in eastern Washington and northern Idaho in spring and summer, 1976 and 1977. Eastern U.S. species were obtained primarily from Maryland in spring 1977. Specimens were preserved for dissection by injection of Kahle's solution under an anterior abdominal tergum until the gaster swelled. Most were injected within several minutes of being killed in a cyanide killing vial. They were then stored in 70% ethanol to avoid excessive brittleness of internal structures.

The emphasis of the study was on yellowjacket queens, principally *Vespula pensylvanica* (Saussure), *Vespula atropilosa* (Sladen), *Dolichovespula arenaria* (F.), and *Dolichovespula maculata* (L.), because these species were most abundant locally. These included early spring queens just out of diapause with little ovarian or glandular development, late spring queens that should have had young colonies, and summer foundress queens collected with their colonies. In addition, other species of yellowjackets, and *Vespa crabro* L., *Polistes fuscatus* (F.), and *Mischocyttarus flavitarsis* (Saussure), were examined for comparison (Table 1).

Wasps were dissected with watchmaker's forceps under a Bausch and Lomb binocular dissecting microscope. Measurement of glands was made at 30× and 60× with the aid of an ocular micrometer. Gland cells were also examined with a compound microscope at 400×. Cells with associated ducts leading to the exterior were assumed to be secretory and are regarded as glandular in function.

Results

Glands found in queens of the various species (Table 1) are given in Table 2. Some glands listed were not found consistently within a species. Possibly they are not developed and functional in all stages of the life cycle. Some species were represented by few specimens, so it is likely that glands could have been missed. Therefore, the omission of a gland for a species in the table does not necessarily mean that it does not occur,

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Table 1.—Number of wasps dissected of each species.

Wasp	Queens	Wasp	Queens
V. pensylvanica	9	*V. acadica*	2
V. maculifrons	3	*D. arenaria*	7
V. germanica	1	*D. arctica*	2
V. vulgaris	3	*D. maculata*	6
V. squamosa	2	*Vespa crabro*	1
V. atropilosa	3	*Polistes fuscatus*	3
V. consobrina	1	*Mischocyttarus flavitarsis*	2
V. vidua	2		

only that it was not observed in dissected specimens. Unless indicated otherwise, general remarks refer to glands of yellowjacket queens.

Most of the glands observed consisted of clusters of either globular cells or acini (thoracic gland). The globules were 0.025 to 0.07 mm wide, each associated with a small duct usually leading directly to the exterior through a membrane or sclerite. When undeveloped (e.g., in diapausing queens) the cells were smaller, compacted, and flattened, making them difficult to recognize. The thoracic glands differed in having a united network of ducts. The Dufour's and poison gland cells, which empty into reservoirs, lack the characteristic globular shape.

Observed differences in glands among the species examined were minor, consisting of size differences and the complete absence of certain glands in some species.

Glands of the Abdomen

Dufour's Gland.—Dufour's gland, also known as the alkaline gland, is associated with the female reproductive system and opens into the sting chamber near the base of the sting (Fig. 3). It is found throughout the aculeate Hymenoptera and usually consists of an elongate thin-walled sac encompassing a lumen. Its oily secretion was thought to be either a lubricant for the sting or material for the attachment or coating of eggs (Wigglesworth 1972, p. 607). It is known to be the site of production of alarm or trail pheromones in ants (Wilson 1971) and cell lining material in Halicitidae (Batra 1968) and Colletidae (Lello 1971, 1976). Little is known of its function in Vespidae. Spradbery (1973, p. 277) stated it may produce a sting lubricant.

Excepting size differences, the appearance of the gland was the same for all species examined. In most species, the gland in queens just out of diapause was 0.1 to 0.2 mm wide, 1.5 to 2.5 mm long, and often tapering near the distal end. Apparently inactive at this time, it was opaque white, often with no apparent lumen. The gland became active in early spring (or 2 to 3 days after eclosion in workers) and had increased in diameter to 0.2 to 0.3 mm but without any apparent change in length. A lumen existed, the walls were partially transparent, and the gland was often fully distended, filled with a yellow oily substance. In late spring and foundress queens, the gland was only partially full and appeared collapsed, flattened, and folded, with only a slight yellow color.

In the obligate social parasite *Dolichovespula arctica* Rohwer (Jeanne 1977a, Greene et al. 1978) and the facultative social parasite *Vespula squamosa* (Drury) (MacDonald and Matthews 1975), the Dufour's gland was extremely large. In two summer *D. arctica* queens, the gland was greatly folded around itself and the intestine. The end was broken off and lost in both specimens, making measurements conservative. Remnants of the glands were 5.5 and 7 mm long, respectively, and 0.5 mm wide. In a fall queen the gland was 14 mm long and 0.3 mm wide. The Dufour's glands of two *D. arctica* spring queens dissected by Jeanne (1977a) were 12.8 and 27.2 mm long. *D. arctica*'s apparent pheromonal control over the host queen, as described by Greene et al. (1978), may be a function of the parasite's Dufour's gland as Jeanne (1977a) suggested. Those of autumn and spring queens of *Vespula squamosa* were ca. 0.2 mm wide and 6 mm long. It is possible the hyperdeveloped

Table 2.—Occurrence of exocrine glands in queens of each species studied.

Wasp	Poison	Dufour's	6th sternal	7th sternal	8th tergal	thoracic	hypopharyngeal	sublingual	labial palp	maxillary-labial	maxillary-hypopharyngeal	ectal mandibular	mesal mandibular	endostipal
V. pensylvanica	+	+		+	+	+	+	+	+	+	+	+	+	+
V. maculifrons	+	+		+	+	+	+	+	+	+	+	+	+	
V. vulgaris	+	+		+	+	+	+	+	+	+	+	+	+	
V. germanica	+	+		+	+	+	+	+	+	+	+	+	+	
V. squamosa	+	+	+	+		+	+		+	+	+	+	+	
V. atropilosa	+	+	+	+	+	+	+	+	+	+	+	+	+	
V. acadica	+	+	+	+	+	+	+	+	+	+	+	+	+	
V. consobrina	+	+	+	+	+	+	+	+	+	+	+	+	+	
V. vidua	+	+	+	+	+	+	+	+	+	+	+	+	+	
D. arenaria	+	+		+		+	+	+	+	+	+	+	+	
D. arctica	+	+		+	+	+	+	+	+	+	+	+	+	
D. maculata	+	+		+	+	+	+	+	+	+	+	+	+	
Vespa crabro	+	+	+	+	+	+	+	+	+	+	+	+	+	
Polistes fuscatus	+	+	+	+		+	+	+	+	+	+	+	+	+
Mischocyttarus flavitarisis	+	+	+	+		+	+	+	+	+	+	+	+	

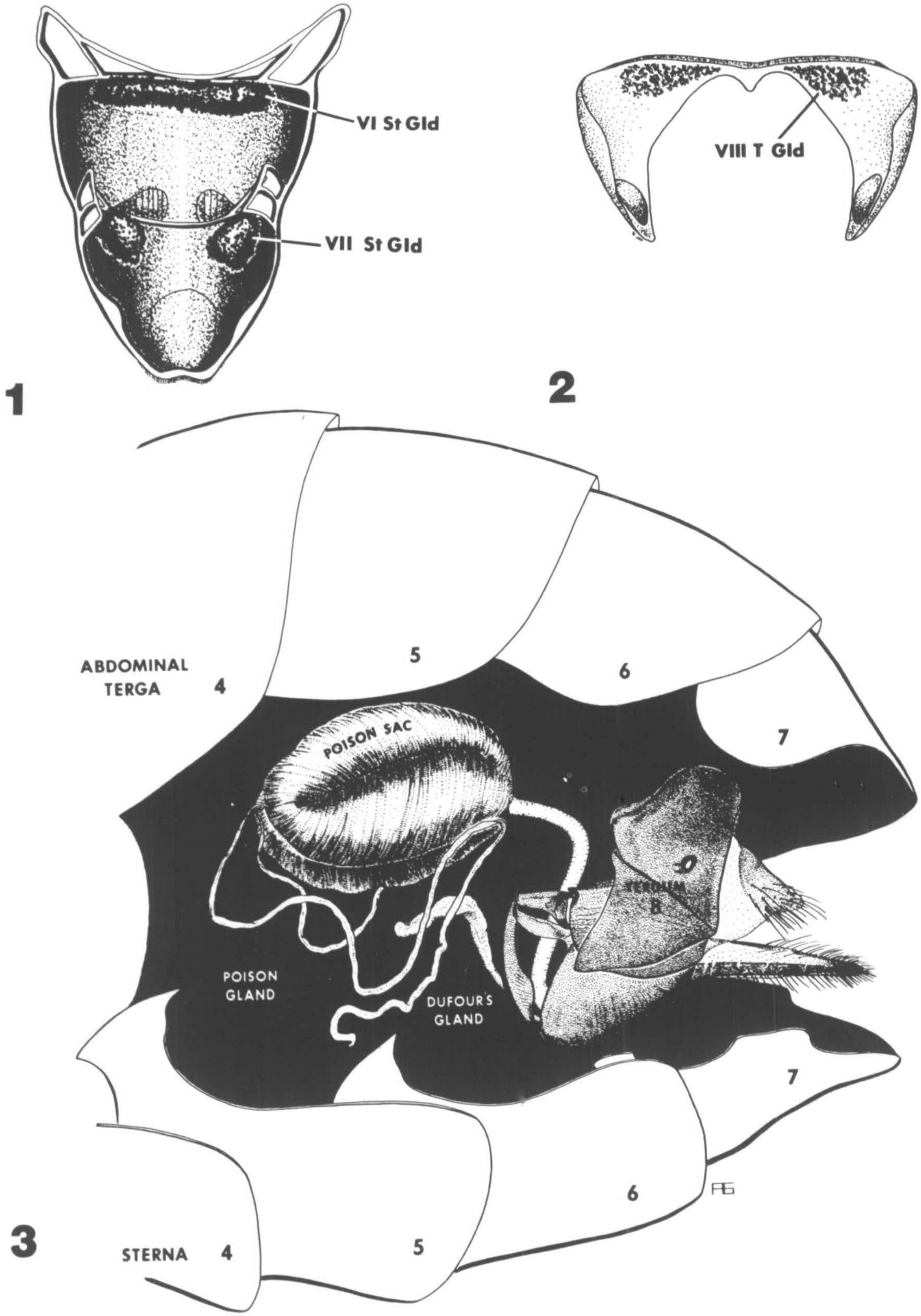

FIG. 1.—Inner view of sixth and seventh abdominal sterna of yellowjacket queen, showing sixth sternal gland (VI St Gld) and seventh sternal gland (VII St Gld). 2. Inner view of eighth abdominal tergum, showing eighth tergal glands (VIII T Gld). 3. Posterior of *Vespula* abdomen, opened laterally, showing sting, poison gland, poison sac, and Dufour's gland.

condition of this gland in both of these species is related to their parasitic way of life.

Poison Glands.—The poison glands and associated reservoir or poison sac are well known for their role in venom production. They are widespread in aculeate Hymenoptera and probably occur in all female social wasps. They consist of a pair of long tubules joined as a common duct just before its connection to the surface of the reservoir (Fig. 3). They are similar in most respects to those of the honey bee as illustrated by Snodgrass (1956, p. 299). Products of these glands were reviewed by Habermann (1972).

Sternal Glands.—The sternal glands are located at the anterior ends of the inner surfaces of the sixth, seventh, and eighth (male only) abdominal sterna. They are comprised of a large number of closey packed globular cells, each associated with a duct leading to the exterior through a pore in the integument.

The sixth sternal gland occurs as a wide band of glandular cells across the anterior end of the inner surface of the sixth sternum (Fig. 1). Heselhaus (1922) found it in *Vespa crabro* queens. Richards (1971) suggested such a subcuticular gland in *Polybia, Protopolybia, Apoica,* and *Brachygastra,* based on the external sternal brushes. Hermann and Dirks (1974) discussed a sixth sternal gland of *Polistes annularis* (L.). The gland was found in queens of *Vespula squamosa, V. acadica* (Sladen), *V. atropilosa, V. consobrina* (Saussure), *V. vidua* (Saussure), *Vespa crabro, Vespa orientalis, Polistes fuscatus,* and *Mischocyttarus flavitarsis.* It was not found in any species of the *Vespula vulgaris* group dissected (*V. vulgaris, V. germanica, V. maculifrons* (Buysson), and *V. pensylvanica)* and the species of *Dolichovespula.* In *Vespula* queens, the gland extended ca. 2.5 mm across the sternum and was ca. 0.5 mm wide. It apparently developed earlier than the seventh sternal gland, as evidenced by spring queens with undeveloped seventh but developed sixth sternal glands.

The seventh sternal glands are also known as van der Vecht's glands. However, Heselhaus (1922) previously reported these glands and his paper contains illustrations of the gland and brush he found in queens of *Vespa crabro.* Van der Vecht (1968) described the sternal brush in more detail and in a wide range of genera of Vespidae. These glands usually occurred as paired clusters of gland cells (Fig. 1), although some individuals of most species had a continuous band of glandular tissue across the sternum. They are closely associated with a brush, an area of short dense hairs, on the outer surface of the sternum. The glands and brush were found on the seventh segment of all female wasps examined (Table 2). A similar appearing seventh sternal gland was found in a male *Mischocyttarus flavitarsis.* The band of gland cells was 2.7 mm across the sternum, varying from 1.0 mm wide laterally to 0.5 mm wide medially. It also was associated with a sternal brush.

Jeanne (1970, 1972) reported the role of the seventh sternal brush in repelling predators in the polybiine *Mischocyttarus drewseni* Saussure. The wasps smear a substance highly repellent to ants on the pedicel of the nest with the sternal brush. Similar behavior has been observed in species of *Polistes* (Hermann and Dirks 1974) apparently to repel predators and involving both the sixth and seventh sternal glands and brush. The applied material makes the nest paper around the nest pedicel darker and shiny.

Although some material is applied around the nest pedicel by some species of yellowjackets (Greene et al. 1976, Jeanne 1977b), sternal smearing behavior has not been observed. However, a great deal of grooming behavior is associated with this area of the sternum. The function of the glands in this case is not known. Spradbery (1973) suggested that the brush is a dispersal area for a volatile pheromone, possibly a queen substance, or for a colony odor produced by workers. Greene et al. (1978) suggested it as a possible source of *Dolichovespula arctica's* pacifying attractant.

Seventh sternal glands became fully developed, with well differentiated cells, in late spring in queens and within a day or two after eclosion in workers. Although Hermann and Dirks (1974) referred to polygonal cells of the sternal gland, cells of active adult glands are globose. Since extensive development of the gland occurs after eclosion of the adult, the gland cells of the late pupae (pharate adults) sectioned by Hermann and Dirks were most likely undeveloped and inactive. As reported by Spradbery (1973), each gland cell is associated with a duct that opens through a pore in the integument.

An eighth sternal gland was found in the male *Mischocyttarus flavitarsis.* As with the seventh sternal gland, it was associated with a sternal brush on the outside of the sternum. The ducted, globular gland cells were 0.025 to 0.035 mm diam and formed a dense mat 1.7 mm across the sternum and 1.2 mm wide.

Tergal Glands.—A pair of clusters of globular gland cells was found on the anterior edge of the inner surface of the eighth tergum of queens (Fig.2). The cells were small (0.02 to 0.03 mm diam) and were connected to the tergum by individual ducts, similar to those of the sternal gland cells. These glands were found in a diverse assortment of species (Table 2) suggesting that they often have been overlooked and are more widespread. The number of gland cells per cluster ranged from 15 in a *D. maculata* queen to 60 in a *V. vulgaris* queen. All others had 30 to 40 cells per cluster.

Glands of the Thorax

The thoracic gland, also known as the labial or salivary gland, is by far the largest gland in social vespids. It is comprised of two parts, a pair of prothoracic lobes closely appressed to the sides of the pronotum and a mesothoracic section between the second and third sternal apophyses and above the ventral nerve cord (Fig. 9). The gland tissue is comprised of multicellular acini which are 0.05 to 0.07 mm diam. According to Spradbery (1973) each acinus consists of a number of secretory cells enclosing a lumen. However, Heselhaus (1922) working with *Vespa* and *Vespula,* and Deleurance (1955) working with *Polistes,* depicted the acini as without a lumen and with a number of ductules within each acinus, uniting at the base. Each acinus is connected to a racemose system of collecting ducts which join to form a single duct, opening at the salivarium of the hypopharynx.

In spring queens the size of the median section is fairly constant, about 3.0 mm long and 1.5 mm wide in

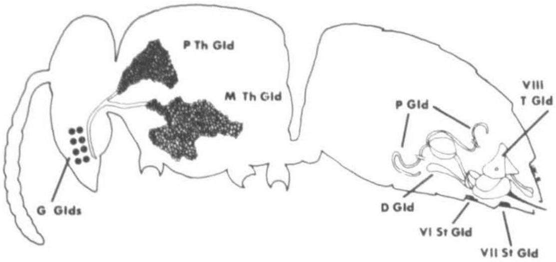

FIG. 9.—Side view of yellowjacket queen, showing positions of sixth sternal gland (VI St Gld), seventh sternal gland (VII St Gld), eighth tergal gland (VIII T Gld), Dufour's gland (D Gld), poison gland (P Gld), prothoracic and mesothoracic sections of the thoracic gland (P Th Gld and M Th Gld), and the eight gnathal glands (G gld).

most species of yellowjackets. However, in *V. atropilosa* and *D. maculata* the gland was larger, 3.3 to 3.7 mm and 3.7 to 4.0 mm long, respectively. This is probably related to the size of the wasps, since *V. atropilosa* and especially *D. maculata* are somewhat larger than most other yellowjackets. The prothoracic lobes were ca. 2×2×1.5 mm in late spring and summer queens.

In queens of *Polistes fuscatus* and *Mischocyttarus flavitarsis,* both parts of the gland were similar in size to that of the smaller species of yellowjackets. Male *P. fuscatus* and a *D. arctica* male had well developed prothoracic lobes and only an anterior remnant of the median section. The situation was reversed in males of *D. arenaria,* with a large median section and no prothoracic lobes. This indicates that the two parts of the gland may have separate functions.

The thoracic gland has been reported to be the site of production of a size or glue to hold the fibers together in nest paper (Spradbery 1973) and a rubbery material of the petiole of *Dolichovespula* nests (Jeanne 1977b). It appears, though, that the gland either functions differently or its role is dependent on caste and timing in the colony cycle. The gland is quite developed both in overwintering queens and in older foundress queens which make little paper carton. This is especially true of yellowjacket queens, which almost completely stop making paper carton after the emergence of the first 6 to 8 workers. The gland must also have a different function in male wasps since they are not involved in nest construction.

Glands of the Head

Eight pairs of glands were found in the head in close association with the mouth parts. In addition, the duct of the thoracic gland opens at the salivarium, a pocket lying between the labium and the distal end of the hypopharynx. This is probably because a wasp's mouth parts are used not only for ingestion, but for all aspects of carton making, soil excavation, trophallaxis, grooming, killing prey, nest cleaning activities, and mauling (Akre et al. 1976). The secretions of some of these glands may be pheromones distributed by trophallaxis between adults, fed to larvae, or added to nest materials.

Vespids are hypognathous. (See Duncan (1939) for a detailed description of the mouth parts of *Vespula pensylvanica.*) Food is pased up through the preoral cavity to the mouth, deeply recessed in the head capsule. This preoral cavity is bounded anteriorly by the labrum-epipharynx, posteriorly by the labium and distal half of the hypopharynx, and laterally by the maxillae. The products of 6 glands are secreted directly from or into this area.

The maxillae and labium are joined by areas of membrane to form the labio-maxillary complex, which can be extended and retracted (Duncan 1939). This structure is exposed at the ventral-posterior area of the head below the postgenal bridge. It appears that the products of one pair of glands are secreted through membranous areas to the exterior in this region.

Ectal Mandibular Glands.—The ectal mandibular gland consists of a sac or reservoir with 50–70 gland cells (Spradbery 1973, mandibular gland I). The reservoir is situated near the ventral-ectal corner of the proximal end of the mandible (Fig. 6). A short sclerous duct from the gland leads directly to the edge of the mandible near the ventral condyle and mandibular groove, although Hermann et al. (1971) reported the duct goes across the end of the mandible to the mesal face and is not aligned with the mandibular groove. The gland was found in all species dissected and appeared to develop late in spring. Although the reservoir was present in overwintering queens, the gland cells were poorly developed and probably inactive. In *Vespula* queens the reservoir was ca. 0.03 to 0.1 mm^3 while in *Dolichovespula* queens they were smaller, only ca. 0.01 to 0.04 mm^3. Spradbery (1973) suggested it is lubricatory or involved in feeding. This gland performs a variety of functions in other social insects (Wilson 1971).

The ectal mandibular gland was greatly enlarged in males of *Poliste fuscatus* with each gland up to 1.36 mm^3, suggesting a function in the mating behavior of these wasps. Males at overwintering sites presumably attract females to the sites and mate with them (Eberhard 1969). Perhaps they "call" the females to the sites with attractant pheromones produced by these glands.

Mesal Mandibular Glands.—The inner or mesal mandibular gland, which Spradbery (1973) refers to as mandibular gland II, is along the mesal edge of the base of the mandible (Fig. 6). The gland cells lie along the membrane connecting the mandible and maxilla and appear to secrete through the membrane to the mesal edge of the mandibular base. Spradbery (1973) suggested this gland may be homologous to the honey bee postgenal gland. Heselhaus (1922) referred to a postgenal gland in *Vespula vulgaris* which may be the mesal mandibular gland. When the mandible is pulled away from the head, this mandibular gland and the membrane often remain behind in the subgenal area. The gland was found to be larger in *Dolichovespula* queens (0.035 to 0.08 mm^3) than in *Vespula* queens (0.02 to 0.045 mm^3).

Sublingual Glands.—Sublingual glands were found in queens of most species examined (Table 2). The pair of glands are at the base of the ligula between the paraglossae of the labium (Fig. 4). Heselhaus (1922) found them in *Vespula vulgaris* queens. In reference to those of honey bees, Ribbands (1964) cited Snodgrass (1925, p. 155) as reporting them as fat cells, which were previously mistaken as glandular cells. However, Snodgrass was referring to fat cells of the pharyngeal plate (posterior-most part of the hypopharynx), not to cells of the

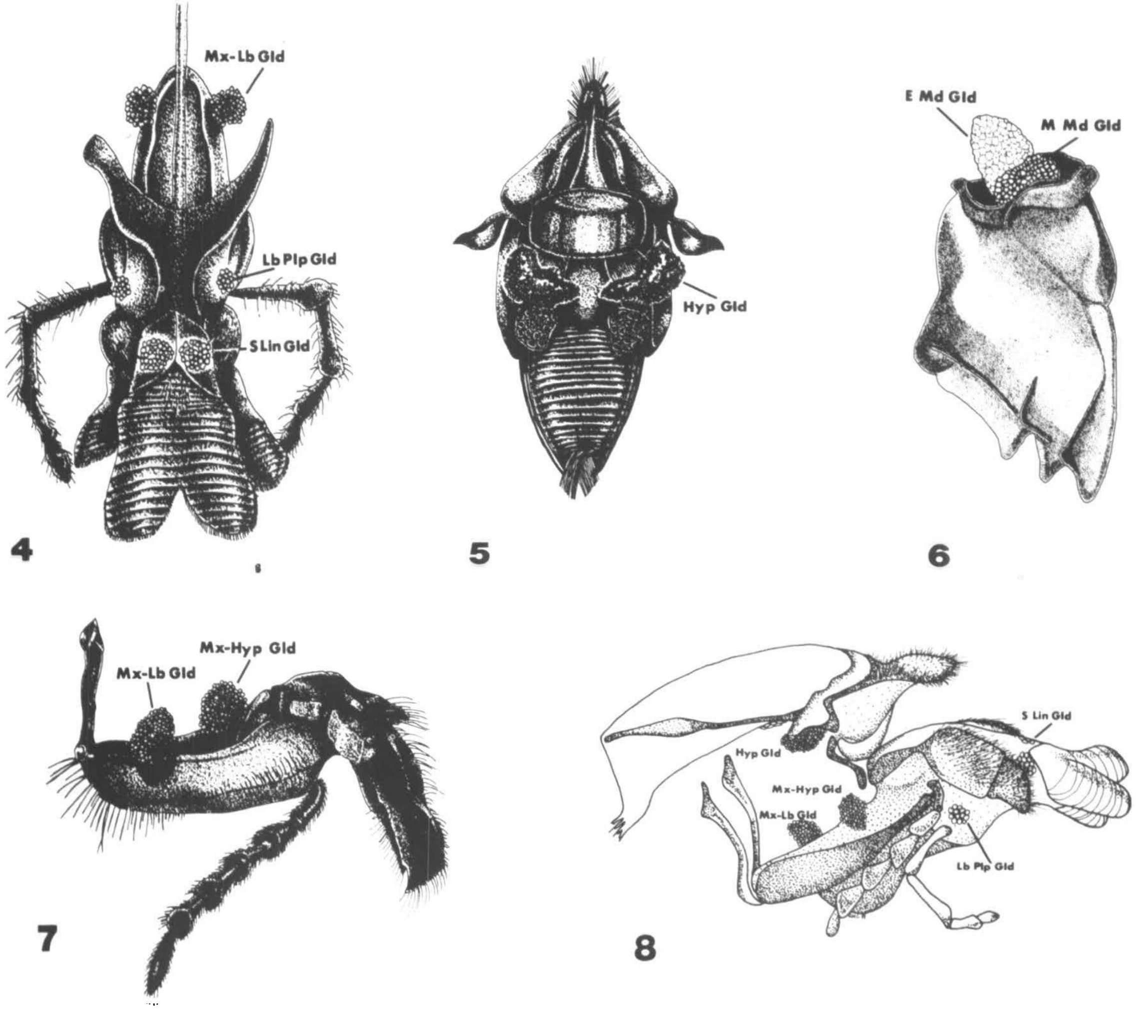

FIG. 4.—Anterior view of labium, showing position of sublingual glands (S Lin Gld), labial palp glands (Lb Plp Gld), and maxillary-labial glands (Mx-Lb Gld). 5. Posterior view of labrum-epipharynx, showing hypopharyngeal glands (Hyp Gld). 6. Mesal face of yellowjacket mandible, with ectal mandibular gland (E Md Gld) and mesal mandibular gland (M Md Gld). 7. Mesal view of maxilla, showing positions of maxillary-labial gland (Mx-Lb Gld), and maxillary-hypopharyngeal gland (Mx-Hyp Gld). 8. Lateral view of labium, maxillae, and labrum-epipharynx, showing positions of sublingual glands (S Lin Gld), labial palp glands (Lb Plp Gld), maxillary-labial glands (Mx-Lb Gld), maxillary-hypopharyngeal glands (Mx-Hyp Gld), and hypopharyngeal glands (Hyp Gld).

ligula. These cells are ducted, as reported by Heselhaus (1922), making it unlikely they are fat cells.

Each gland was a cluster of 10 to 30 cells. Each cell was ca. 0.05 mm diam. In a *Vespula pensylvanica* queen examined the ducts extended distally about 0.3 mm to the anterior surface of the glossa.

Labial Palp Glands.—The labial palp glands are located near the bases of the labial palps (Fig. 4). The cluster of 5 to 15 globular cells was found in all species investigated (Table 2).

The gland cells were about 0.03 mm diam. Each was attached by its duct to the membranous area between the salivarium and prementum. The gland secretions probably pass through this membrane onto the anterior surface of the labium.

Hypopharyngeal Glands.—Known as the hypopharyngeal (Spradbery 1973) or pharyngeal glands (Heselhaus 1922), these paired glands are on the proximal side of the gnathal pouch of the suboral plate of the hypopharynx (Fig. 5).

The ducts of the hypopharyngeal glands pass to the suboral plate (the posterior part of the gnathal pouch) and open immediately outside of the mouth opening and the gnathal pouch. The globular cells were 0.03 to 0.05 mm diam and each was associated with a duct. These glands were found in all species studied (Table 2).

In *Vespula* queens, they appear to become developed early in spring and remain well developed throughout the remainder of the queen's life. In *V. pensylvanica* queens, developed glands were 0.03 to 0.08 mm^3. Although similar sized glands were present in *V. atropilosa* and *V. vulgaris*, queens of *Dolichovespula arenaria* and *D. maculata* had considerably smaller hypopharyngeal glands. Developed hypopharyngeal glands of 4 *D. ma-*

culata queens were 0.012 to 0.024 mm^3, while those of 7 *D. arenaria* queens ranged from no gland at all (2 queens) to 0.022 mm^3.

Nothing is known of the function of these glands. Spradbery (1973) suggested they produce a food for larvae as do the hypopharyngeal glands of honey bees. However, their development before colony founding suggests a nonsocial function, at least initially. Also on the pharyngeal plate but proximal to the hypopharyngeal glands is a pair of cell clusters that might be glandular. Spradbery (1973) considers them sensory in function.

Maxillary-Labial Glands.—The posterior of the labial prementum is connected to the maxillae by membranous areas, forming the labio-maxillary complex (Duncan 1939). The maxillary-labial gland is a roughly spherical to elongate mass of globular gland cells attached to the inner surface of the membrane paralleling the stipes (Fig. 7), and emptying, by ducts, through the membrane in the posterior region of the head below the postgenal bridge.

The gland was found in most queens (Table 2) and in a *D. arctica* male. The gland cells were 0.03 to 0.05 mm diam, forming an elongate gland 0.1 to 0.2 mm wide and 0.3 to 0.7 mm long. It was larger in species of *Dolichovespula* (0.5 to 0.7 mm long) than in species of *Vespula* (0.3 to 0.5 mm long). The gland was found in all spring and summer queens. In summer foundress queens, the cells, normally white, had become yellowed.

Maxillary-Hypopharyngeal Glands.—The maxillary-hypopharyngeal glands were found on the inner surface of the membrane connecting the maxillae to the hypopharnx. Like the maxillary-labial glands, they occurred as a mass of gland cells cells lying along the maxillary stipes (Fig. 7). Each cell was connected by a duct to the membrane, through which the products most likely are secreted. The globular gland cells were ca. 0.03 mm diam.

The gland was found in queens of all species (Table 2). It was not found in all individuals and varied extensively in development from a few scattered cells to an elongate mass 0.2 mm diam and 0.5 mm long.

Endostipal Glands.—The endostipal gland is a small clump of globular ducted cells at the proximal end of the stipes of each maxilla. It was found in some spring queens of *Vespula pensylvanica* and *Polistes fuscatus*. The gland was comprised of 5 to 10 cells.

In *V. pensylvanica* workers examined, the following glands were developed: Dufour's, poison, seventh sternal, eighth tergal, thoracic, mesal mandibular, ectal mandibular, hypopharyngeal, maxillary labial, labial palp, and sublingual. *Dolichovespula arctica* males dissected had thoracic, maxillary-labial, hypopharyngeal, mesal mandibular, and ectal mandibular glands.

Summary and Discussion

Fourteen exocrine glands were found in queens of yellowjackets (Table 2). Five glands occur in the female abdomen: The Dufour's and poison glands associated with the sting, the glands of the sixth and seventh abdominal sterna, and a pair of glands on the eighth tergum. In addition, an eighth sternal gland was found in male *Mischocyttarus flavitarsis*. The large thoracic gland is the only gland of the thorax but empties, by a large duct, through the mouth parts. Eight pairs of glands occur in the head, all associated with the mouth parts. Two pairs are found at the bases of the mandibles, one pair at the bases of the labial palps, one pair at the base of the labial glossae, one pair between the maxillae and labial prementum, one pair between the maxillae and hypopharynx, one pair on the pharyngeal plate of the hypopharynx at the gnathal pouch, and one pair at the proximal ends of the maxillary stipes.

Five glands are apparently unreported in the literature. These are the maxillary-labial, maxillary-hypopharyngeal, labial palp, and endostipal glands of queens, and the eighth sternal gland of male *Mischocyttarus flavitarsis*.

Twelve of the glands in queens appear to occur widely in the social Vespidae (Table 2). However, this may be limited to those species whose colonies are founded by lone queens. The combination of "worker" activities early in the season and "queen" activities later in the season may be one reason for the extraordinary number of glands in queens of these species.

Wasps of the *Vespula vulgaris* species group and the genus *Dolichovespula* had no sixth sternal gland. The gland's otherwise widespread occurrence suggests it was lost secondarily in those groups.

Very little is known about the function of vespid exocrine glands except the role of the poison gland in venom production. Sternal gland secretions are applied to the nest pedicel to repel insect predators in *Polistes* (Hermann and Dirks 1974) and *Mischocyttarus drewseni* (Jeanne 1972). No function is known for this gland in yellowjackets although it may be involved in *Dolichovespula arctica's* parasitism of *D. arenaria* (Greene et al. 1978). The large ectal mandibular gland of *Polistes fuscatus* males may produce an attractant sex pheromone. The small size of this gland in males of *Mischocyttarus flavitarsis* ($^1/_{10}$ that of *P. fuscatus* males) and the extensive development of sternal glands suggest a similar function of sex attractant production for the sternal glands of *M. flavitarsis* males. With the present knowledge of wasp behavior, many functions can be postulated without, however, any idea as to which of the many glands may be involved.

Nine of the 14 glands are associated with the mouth parts. Some probably secrete substances added to prey, or added to food to be ingested or fed to larvae. Undoubtedly, substances are added to pulp used in comb and envelope construction as a size or glue. Bourdon et al. (1975) reported the presence of norepinephrine in envelope of *Vespula vulgaris* nests. The material added to pedicels of embryo nests of *Dolichovespula arenaria* (Greene et al. 1976, Jeanne 1977b) is probably produced by one of the gnathal glands. The extensive occurrence of trophallaxis among all colony members makes it likely that secretions of any of the gnathal glands may have pheromone functions. It is also probable that the secretions of some glands may change with the colony cycle or with caste or sex. For example, the ectal mandibular gland of males of *Polistes fuscatus* may produce a sex pheromone while the gland in workers and queens certainly has a different function. Answers to questions concerning gland functions will probably require studies involving the use of extracts of individual glands in behavioral studies.

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