

CHEMICAL COMMUNICATION IN INSECT COMMUNITIES: A GUIDE TO INSECT PHEROMONES WITH SPECIAL EMPHASIS ON SOCIAL INSECTS

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I. INTRODUCTION

The study of insect pheromones has grown from nothing in three decades to be now far too large to be reviewed comprehensively. It is a subject that impinges upon many aspects of entomology, e.g. pest control, mating, population dynamics and ecology. It is, therefore, important for many scientists to be acquainted with advances in our knowledge of pheromones. We have attempted to provide a general survey of the subject, both for the specialist and for those newly introduced to it. Reviews covering lepidopteran sex pheromones and coleopteran aggregation pheromones are readily available, so this survey emphasizes the more complex but less widely known chemical communication of social insects. The recognized types of chemical communication are examined in turn, with examples from the recent literature. For a comprehensive review of the chemical substances recognized as pheromones, arranged by insect orders,

the reader is directed to the volume edited partly by one of us (Morgan & Mandava, 1988).

II. BEHAVIOUR AND COMMUNICATION

The first essential in the study of pheromones is to recognize a change in behaviour pattern or an organizational change which is probably a response to a communication signal, and then to devise a bioassay that reproduces or tests that change. This can be the most difficult part of the investigation. If a simple bioassay can be devised, and if it is reproducible, then with its help it is possible to move rapidly to study the pheromone.

(1) *Behaviour*

Behaviour can be simply defined as what animals do, or the ways in which an organism adjusts to, and interacts with, its environment (Matthews & Matthews, 1978). Any sensory signal which produces a behavioural change in an animal is an example of communication. The message may emanate from another animal as well as come from a plant. For the signal to evoke a behaviour response the receiver has also to be in the requisite state of readiness.

(2) *Communication*

Animals communicate between each other by means of (1) visual; (2) acoustic; (3) tactile and (4) chemical signals.

Visual communication, as Carthy (1966) pointed out, shares with acoustics the advantage that when used in courtship it permits accurate location of the sender. The disadvantage is that receiver and sender must be close enough to see or hear each other, but the habits of many insects are such that their environment does not permit long visual ranges. Moreover, the distance over which communication can occur is governed by the capacity of the insect eye to distinguish patterns and movements. The ranges will therefore be much shorter than those over which birds, for example, can communicate visually. Vision is clearly of limited value to nocturnal species (Lloyd, 1983). In daylight-feeding Acridoidea, for example, sight dominates over sound (Otte, 1977).

Acoustic communication is important for those animals where small size means that they are frequently hidden by vegetation and hence cannot signal visually. Acoustic communication has distinct advantages, for the caller does not have to leave cover to expose himself to possible dangers (Carthy, 1966). Auditory signals are less hindered by obstacles and can provide extended and detailed communication over distances far greater than those over which the compound eye can function, but such signals are less directional than sight (Lewis, 1984). In the Ensifera, sound is generally of greater importance than smell (Otte, 1977). Communication of alarm by acoustic means may be very common in ants. Stridulatory apparatus on the post-petiole and gaster was found in 83 % of Myrmicinae and 48 % of Ponerinae examined by Markl (1973). The leaf-cutting ants *Atta cephalotes* and *Acromyrmex octospinosus* stridulate when fighting or when trapped by part of the body (Markl, 1967). The ponerine ants *Megaponera foetens* respond to stridulation from sister workers when they encounter its termite prey, *Trinervitermes* (Markl, 1973).

Tactile signals have distinctive qualities for very short-range communication. Examples are the violent kicking among crowded aphids used to achieve immediate spatial orientation (Dixon, 1963) and the zig-zag accelerated running of termites used to raise the general level of colony excitation (Stuart, 1961*a*).

Chemical communication between individuals is widespread among insects, and highly developed among social insects. The chemical compounds may be diffused into the air or water, moved by currents, deposited on food or flowers, or passed by trophallaxis.

Insects in general employ all these senses, and the evolution of greater acuity in one mode seems to change the relative importance of the others. The evolution of insect communication was reviewed by Hölldobler (1984) at the 150th Anniversary of the Royal Entomological Society of London.

An early example of the study of chemical communication within a species is given by Fabre (1914), who placed a single female of the emperor or hawk moth, *Saturnia pavonia*, in a wire cage by an open window one evening from 8.00 to 10.00 p.m. A total of 150 marked males released up to several km away were attracted to the female during the following 8 days. Fabre also placed a female oak spinner, *Lasiocampa quercus*, in a window between 3.00 p.m. and sunset, and attracted up to 60 males a day, even though the female within the screen cage was usually completely motionless. Mell (1928) released from a train a few marked males of the Chinese silkworm moth, *Actias selene*, 4.1 and 11 km from females held in a cage. Respectively 40 and 26 % of the males found their way back to the female. It was claimed that males of the gypsy moth, *Lymantria dispar*, were able to find a female moth from a distance of 3.8 km (Collins & Potts, 1932).

Although it seems obvious today that the sense of smell is involved, Fabre and others at the time could not deduce this. The scientific interest in olfactory communication did not blossom until the late 1950s with the first isolation and chemical identification of an insect pheromone, 'bombykol', from the silkworm moth, *Bombyx mori*, in Germany (Butenandt, 1959).

III. CHEMICAL COMMUNICATION

Any chemical which conveys information between organisms is termed a semiochemical (Law & Regnier, 1971), from the Greek *semeion* = signal. Semiochemicals are divided into two subcategories (Nordlund & Lewis, 1976): (i) allelochemicals (Whittaker & Feeny, 1971) and (ii) pheromones.

Another way to categorize chemicals that modify animal behaviour is in terms of the type of behaviour they induce, according to the scheme of Dethier, Brown & Smith (1960). This scheme has six categories.

(1) *Locomotory stimulant*. A chemical which causes, by a kinetic mechanism, insects to disperse from a region more rapidly than if the area did not contain the chemical. The effect may be to increase the speed of locomotion, to cause the insects to carry out avoiding reactions, or to decrease the rate of turning.

(2) *Arrestant*. A chemical which causes insects to aggregate into contact with it, the mechanism of aggregation being kinetic. An arrestant may slow the linear progression of the insects by reducing actual speed of locomotion or by increasing turning rate.

(3) *Attractant*. A chemical which causes insects to make orientated movements towards its source.

(4) *Repellent*. A chemical which causes insects to make orientated movements away from its source.

(5) *Feeding, mating, or ovipositional stimulant*. A chemical which elicits either feeding, mating or oviposition, respectively, in insects.

(6) *Deterrent*. A chemical which inhibits feeding or oviposition when presented in a place where insects would, in its absence, feed or oviposit.

(1) *Allelochemics*

Allelochemics (Greek *allelon* = of one another) are chemicals which convey information between organisms of different species (i.e. interspecific). Allelochemics are categorized according to the advantage of the behavioural response caused by the releasing compounds. If the receiving individual has the advantage, as with a predator locating its prey using prey odour, the allelochemics are called *kairomones* (Brown, Eisner & Whittaker 1970). For example, volatile compounds originating from larvae of *Drosophila* are attractive for its parasite *Leptopilina heterotoma* and *L. fimbriata* (Vet & van der Hoeven, 1984). If the advantage is turned to the odour-releasing individual, as with secretions deterring competing species from a limited resource or defensive secretions which directly repel predators, the allelochemics are called *allomones* (Brown *et al.*, 1970), e.g. the formic acid sprayed by formicine ants against their predators. Another type of allelochemic is called a *synomone* (Nordlund & Lewis, 1976) which benefits both the releaser and recipient, for example, floral scents that attract pollinating insects (e.g. honey bees); a separate designator, *apneumones* (Nordlund & Lewis, 1976) is applied to signals from non-living emitters.

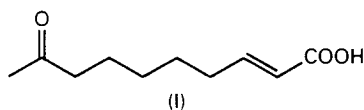
(2) *Pheromones*

The term pheromone is derived from the Greek *pherein*, to transfer (carry); *horman* to excite. Pheromones are defined as substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction (Karlson & Butenandt, 1959; Karlson & Lüscher, 1959).

In 1963, Wilson and Bossert proposed dividing pheromones into two categories according to their mode of influence: (1) primer pheromones which induce relatively long-lasting physiological changes in receiving individuals; (2) releaser pheromones which stimulate the receiving individual to perform immediate behavioural responses. The assumption is often made that all pheromones are dispersed through, and received from the air. That is frequently, but not invariably so. It is equally possible for pheromones to be received by direct contact between individuals, or by contact with a surface. Pheromones can also be dispersed through water.

IV. PRIMER PHEROMONES

Primer pheromones are, for example, secreted by queens (inhibitors of ovary and queen cell construction) as well as workers (caste inhibitors) in social insects such as bees, ants, wasps and termites. Some subsocial insects secrete growth accelerating agents, as in migratory locusts. One primer pheromone is (*E*)-9-oxo-2-decenoic acid [9ODA, (I)] which has been identified as part of the mandibular gland secretion of honeybee queens of *Apis mellifera* (Butler, Callow & Johnston, 1961). It is the most



effective dominance and inhibition signal of the queen. The workers that became egg-layers after removal of the queen also produce 9ODA in their mandibular glands, therefore inhibiting ovarian development in sister workers (Ruttner, Koeniger & Veith 1976; Crewe & Velthuis, 1980). Primer pheromones from queen larvae, and queen pupae, as well as from adult queens are obtained by workers which distribute it to other bees in transferred food and by antennal contact (Free & Ferguson, 1982; Free, Ferguson & Simpkins 1984).

While pheromones must certainly be involved in queen control in ants (Wilson, 1971), none have yet been identified and there is little direct evidence for their existence, because of the difficulties of assaying for them. With the development of a reliable bioassay, Fletcher & Blum (1983) and Vargo & Fletcher (1986) found that queen pheromones are involved in control over the production of male and female sexuals in *Solenopsis invicta*. Queens or freshly killed corpses of egg-laying queens inhibit the development of both male and female sexuals (Vargo & Fletcher, 1986). Also fertile queens of *Monomorium pharaonis* are known to inhibit the development of male and female sexuals from queen-laid eggs (Peterson-Braun, 1977), but virgin queens are unable to inhibit the rearing of new sexuals (Berndt & Nitschmann, 1979). In *Oecophylla longinoda* and *O. smaragdina*, the queens inhibit workers from laying male-producing eggs (Hölldobler & Wilson, 1983). Queens of *Plagiolepis pygmaea* inhibit the sexualization of female larvae (Passera, 1980).

Primer pheromones also play an important role in caste determination. Adult majors (soldiers) of *Pheidole* inhibit to a limited extent the induction of development of major workers from larvae by secreting a contact soldier pheromone (Wheeler & Nijhout, 1984).

Primer pheromones not only act as inhibiting agents but can also have the opposite effect. Adult males of the migratory locust, *Schistocerca gregaria*, secrete a volatile substance (surface pheromone) that accelerates the growth of both male and female young to synchronize maturation within the species (Norris, 1954; 1964).

V. RELEASER PHEROMONES

Releaser pheromones mediate a wide variety of behaviour. At present they are categorized collectively in a simple and broad classification according to the function or the behaviour that they elicit in the receiving insect into; (1) sex pheromones; (2) aggregation pheromones; (3) dispersal or spacing pheromones; (4) alarm pheromones; (5) recruitment or trail pheromones (Birch & Haynes, 1982); (6) territorial or home range pheromones (Cammaerts, Morgan & Tyler, 1977; Hölldobler & Wilson, 1977); (7) surface pheromones (Wilson, 1971); (8) funeral pheromones (Wilson, Durlach & Reth, 1958; Wilson, 1963; Matthews & Matthews, 1978); and (9) invitation pheromones (Ahmadi & McClelland, 1985).

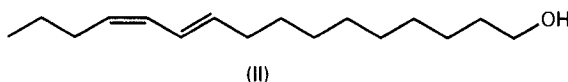
(1) Sex pheromones

Sex pheromones are usually released by the female insect to advertise her presence, i.e. to lure the male for successful mating; if the chemical releases long range mate locating it is called a *sex attractant*, while the chemical which facilitates courtship or prepares the opposite sex for copulation is called an *aphrodisiac* (Birch, 1974; Birch & Haynes, 1982) and is usually released by males.

(a) Sex pheromones of non-social insects

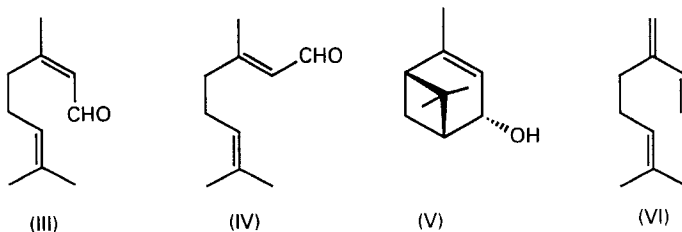
Many non-social solitary insects depend on sex or aggregation pheromones as the major means of bringing individuals together for reproduction and survival. Sex pheromones are produced only at certain times of day and night according to species and are released as they are formed. Typically there is a synchronization between time of release from females and response from male insects of the same species. Closely related species with similar pheromone substances sometimes emit their pheromone at different times of day or night. Pheromone production may also be age-related.

Extensive studies have been made on sex pheromones of many species of the orders Lepidoptera and Coleoptera since research started with the identification of bombykol, (*E,Z*)-10,12-hexadecadiene-1-ol (II), the major component of the female sex pheromone of the silkworm moth, *Bombyx mori* (Butenandt, 1959).



(b) Sex pheromones of social insects

In queens of the honeybee *Apis mellifera*, (*E*)-9-oxo-2-decenoic acid (I) in the mandibular gland secretion (Butler, Callow & Johnston, 1961) acts not only as a primer pheromone but also as a sex pheromone outside the nest, stimulating drones to fly towards the virgin queen (Galy, 1962; Butler & Fairy, 1964). Robacker & Hendry (1977) showed that neral (III) and geranial (IV) from crude extracts of virgin females are components of the sex pheromones of the wasp *Itopectis conquisitor*, eliciting male sexual activity.



In ants, a variety of glands are responsible for sex pheromone secretion, in particular the poison, Dufour and pygidial glands in females, and mandibular glands in males. The females of the myrmicine ant *Harpagoxenus sublaevis* release a sex pheromone from the poison gland (Buschinger, 1972) in a sexual-calling behaviour when they erect their gasters (Buschinger, 1968, 1983). In *Pogonomyrmex* females, poison gland secretions stimulate sexual behaviour in males (Hölldobler, 1978) and sympatric species are reproductively isolated in part by their distinct daily nuptial flight rhythms (Hölldobler, 1977). Females of the myrmicine species *Xenomyrmex floridanus* produce a sex pheromone in the poison gland (Hölldobler, 1971 a). The Dufour gland in *Monomorium pharaonis* queens secretes a sex pheromone (Hölldobler & Wüst, 1973). Both sexes of the carpenter ant, *Camponotus herculeanus*, take off during the nuptial flight and are

synchronized by a secretion released from the mandibular glands of males (Hölldobler & Maschwitz, 1965; Hölldobler, 1978). In the ponerine ants, the wingless virgin females of *Rhytidoponera metallica* attract males by the release of a pheromone from the pygidial gland (Hölldobler & Haskins, 1977; Hölldobler, 1978). Hölldobler (1978) demonstrated that ergatoid *R. metallica* emerge from the nest and group quietly near the entrance with the head and thorax lowered to the ground, the gaster raised and arched, and the intersegmental membrane between the last two segments dorsally extended. Males flying out from other nests are attracted by these 'calling' females.

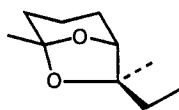
(2) Invitation pheromones

Chemical compounds may be released from a parasite when it has fed on its host, and these increase the number of individuals of the same parasite arriving on the host. For example, female mosquitoes find their host primarily by attraction to kairomones released from the host, then they themselves release chemical compounds (invitation pheromones) to attract other female mosquitoes of the same species for a meal (Ahmadi & McClelland, 1985). Invitation pheromones attract members of the species to a site for feeding or oviposition, but do not lead to build-up of large numbers of individuals at the site, in contrast to aggregation pheromones which do.

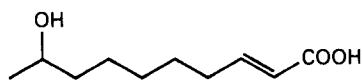
(3) Aggregation pheromones

Aggregation pheromones are chemical compounds which release a behavioural response in members of the same species (conspecifics) leading to congregation, i.e. to increase their density in the vicinity of the source of the pheromone. A wide variety of arthropods assemble for various purposes such as feeding, mating or hibernation. Most aggregations are temporary except in social insect colonies. In many cases, gregarious behaviour functions to bring the sexes together for mating. The bark-beetle *Dendroctonus ponderosae* (Scolytidae), is a well documented example of temporary aggregation to a food site with increased probability of mating. Female *D. ponderosae* release *trans*-verbenol (V) after finding a suitable host tree (Vité & Pitman, 1968; Pitman & Vité, 1969). *Trans*-verbenol attracts males and the attractiveness is synergized by a host-tree monoterpene [myrcene, (VI)] (Conn *et al.*, 1983; Borden *et al.*, 1983). The arriving males secrete (+)-*exo*-brevicommin (VII) (Pitman *et al.*, 1969; Borden *et al.*, 1983; Conn *et al.*, 1983) which attracts mainly female beetles. The combined action of myrcene, *trans*-verbenol and *exo*-brevicommin results in a mass attraction of both sexes.

Of all the types of pheromonally induced insect aggregation, perhaps the most dramatic is exhibited by the fertilized social insect queen, continuously surrounded by a retinue of crowding, licking, food-offering attendants. If a colony of honeybees, *Apis mellifera*, is deprived of its hive and combs it behaves like a reproductive swarm, and will cluster on any convenient support. When the queen is taken from the swarm soon



(VII)



(VIII)

after it has settled, the bees usually become disturbed within 10–15 min and return to the old hive (Simpson, 1963). The queen mandibular gland secretion, (*E*)-9-hydroxy-2-decenoic acid (VIII) is responsible for re-forming and stabilizing the dispersing clusters (Butler, Callow & Chapman, 1964).

(4) *Dispersal or spacing pheromones*

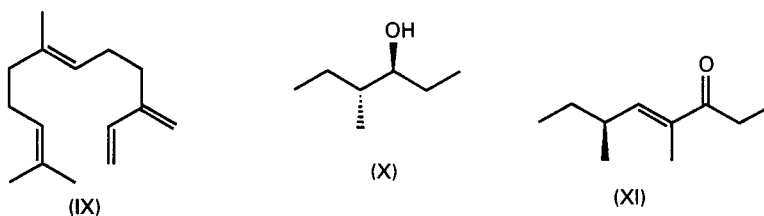
Dispersal or spacing pheromones stimulate behaviour leading to increasing space between individuals (dispersion), with a consequent reduction in intraspecific competition. The compounds may be considered to act as deterrents or repellents.

The presence of an oviposition-detering mechanism among insects was suggested by field work done by Chiang *et al.* (1960) with the European corn borer, *Ostrinia nubilalis*, which showed that heavily infested corn plants deter second-brood moths from oviposition. Dittrick, Jones & Chiang (1983), demonstrated that a methanol extract of frass of fifth-instar larvae of *Ostrinia nubilalis* was a deterrent for oviposition by adults and the effect lasted for at least 72 h under laboratory conditions. Renwick & Radke (1980, 1981) demonstrated that gravid *Trichoplusia ni* were deterred from oviposition up to three days by first-instar larvae feeding on cabbage and by aqueous extracts of larval frass. The mandibular gland secretion of larvae of the flour moth, *Anagasta kuhniella*, induces dispersion between individual larvae. Increased life span and lowering of fecundity of females crowded as larvae (Corbet, 1971) leads to regulation of larval density in this stored product pest. Prokopy (1972) noted that female apple-maggot flies, *Rhagoletis pomonella*, mark the fruit following oviposition with a pheromone by dragging the ovipositor across the surface, the effect being to deter subsequent oviposition and mediate accommodation of larval density relative to food availability. The hymenopterous parasite, *Trichogramma evanescens*, deposits dispersion pheromones on lepidopteran eggs in which it has oviposited, resulting in a uniformity of egg deposition among the available oviposition sites (Salt, 1937). Recently an oviposition deterrent for *Spodoptera littoralis* has been shown to be present in the larval frass (Hilker & Klein, 1989).

(5) *Alarm pheromones*

All' arme was an Italian call to arms during danger, an apt description of some insect behaviour. Alarm and defensive behaviour often go side by side. Chemical releasers of alarm behaviour are volatile compounds producing stereotyped reactions among insects which accelerate movement (or rapid flight in flying insects) and attack (Brown, 1960). Alarm pheromones are known to occur in hymenopterous, isopterous and heteropterous insects. An increased rate of locomotion, characterized by zig-zag or circular movements, often results when colonial insects are exposed to alarm pheromones (Maschwitz, 1964). Löfqvist (1976) studied alarm pheromones of the ant *Formica rufa* and pointed out that the alarm behaviour includes many steps: (1) rousing and waving of antennae in the air; (2) opening the mandibles; (3) slow movements towards the odour source with opened mandibles and raised antennae; (4) fast movements if ants are exposed to a strong stimulus and they are looking for an enemy (fast-running phase); (5) attack behaviour when ants meet an intruder; and (6) cleaning of the antennae and the abdominal tip.

The green peach aphid, *Myzus persicae*, secretes (*E*)- β -farnesene (IX) as an alarm



pheromone from its cornicles (Edwards *et al.*, 1973). Ant-associated (*Myrmecophilus*) aphid species when attacked by predators, secrete sticky droplets, composed largely of triglycerides, which can hinder an attacking predator and result in the release of the aphid prey; the droplets also contain (*E*)- β -farnesene, an alarm pheromone causing aphids to fall, jump or walk away (Nault, Montgomery & Bowers 1976).

In the termite *Macrotermes subhyalinus*, the soldiers' frontal glands secrete n-tricosane, n-pentacosane, 3- and 5-methylpentacosane, 5-methylheptacosane, (*Z*)-9-heptacosene and (*Z*)-9-nonacosene as major compounds. Although these are just the kind of hydrocarbons that are found on ant cuticle, the secretion is said to impair the healing of wounds in test ants and thus could represent a valuable supplement to the mechanical defence mechanism (Prestwich *et al.*, 1977).

In social wasps *Polistes exclamans* and *P. fuscatus*, the venom elicits alarm and attraction and *heterospecific* venom elicits an alarm response (Post, Downing & Jeanne, 1984). In *Apis mellifera* the Koshevnikov's gland, along with the setose membrane adjacent to the sting organ, produces a collection of aliphatic acetates including the main alarm pheromones isopentyl acetate (Boch, Shearer & Stone, 1962; Gunnison & Morse, 1968) and n-butyl acetate (Free *et al.*, 1983; Al-sa'ad, Free & Howse, 1985).

A great deal has been written on alarm pheromones of ants. Each subfamily of ant has developed its own strategy of glandular secretions to produce them. In myrmicine ants, the mandibular and pygidial gland secretions act as alarm pheromones. The mandibular glands frequently contain volatile alcohols and ketones. For example, 4-methyl-3-hexanol (X) and 4-methyl-3-hexanone in the mandibular gland secretion of *Tetramorium impurum* act as attractants for the workers (Pasteels *et al.*, 1980). In *Atta texana*, 4-methyl-3-heptanone acts as an alarm pheromone (Riley, Silverstein & Moser 1974). In *Pogonomyrmex barbatus* (McGurk, Frost & Eisenbraun 1966) and *P. badius* (Wilson, 1958) the ants when exposed for a few minutes to 4-methyl-3-heptanone found in the mandibular gland secretion carry pebbles in their mandibles and sometimes make digging movements with their legs. In *Manica mutica* (Fales *et al.*, 1972), (*E*)-4,6-dimethyl-4-octene-3-one [manicone, (XI)] functions as a powerful releaser of alarm behaviour. Hayashi & Komae (1977) indicated that β -pinene, limonene, α -pinene and camphene from the whole extract of *Pristomyrmex pungens* may act as alarm pheromones. In *Pheidole biconstricta*, the pygidial gland produces an alarm-defence secretion (Kugler, 1979). In *Novomessor cockerelli* and *N. albisetosus*, the pygidial gland secretes a strong smelling secretion which causes 'panic alarm' response in workers (Hölldobler, 1982). There is some concern at the unnaturally high concentrations used to test some synthesized mandibular gland compounds. Many substances will cause alarm actions in an ant colony at unphysiological concentrations. A careful study with *Myrmica* species did not reveal any alarm reaction to the

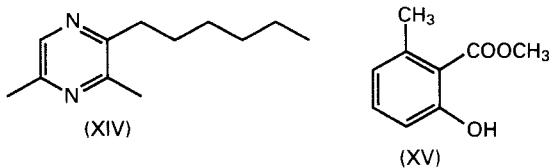
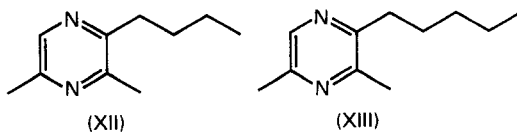
mandibular gland secretions. The main components of the secretion are 3-octanol and 3-octanone. 3-Octanol is an attractant for workers, 3-octanone increases the effect of 3-octanol, and 3-nonanone increase the linear speed of the ants (Morgan, Inwood & Cammaerts 1978; Cammaerts, Evershed & Morgan, 1981, 1983; Cammaerts *et al.*, 1985).

In formicine ants, alarm releasers appear to originate from mandibular, poison and Dufour glands. In the African weaver ant, *Oecophylla longinoda*, (Bradshaw, Baker & House 1979*a*) the mandibular gland of major workers contains multicomponent alarm pheromones, which release behavioural responses including alerting, attraction and biting. In addition to the mandibular gland, major workers use the poison and Dufour glands as sources of alarm pheromones (Bradshaw *et al.*, 1979*b*). They release formic acid from the poison gland and a mixture of hydrocarbons from the Dufour gland. Formic acid elicits a 'mass attack' response in other major workers; formic acid and Dufour gland secretions are considerably more effective than either secretion tested separately. These compounds act in combination with the mandibular gland secretions to form a complex alarm-defence system. In the slave-keeping ants, *Formica sanguinea*, *F. subintegra* and *F. pergandi*, Dufour and poison gland secretions are used against the slave species *F. subsericea* and *F. fusca*; formic acid from the poison gland and decyl, dodecyl and tetradecyl acetate from the Dufour gland (Regnier & Wilson, 1971) act as defensive and offensive weapons. It has variously been claimed that the undecane acts as an alarm substance (Regnier & Wilson, 1968, 1969; Ayre & Blum, 1971; Bergström & Löfqvist, 1970; Löfqvist, 1976) or as a spreading agent for the formic acid released from the poison gland (Regnier & Wilson, 1968; Löfqvist, 1976).

In the new world army ants (Dorylinae, tribe Ecitonini) *Eciton hamatum*, *Nomamyrmex esenbecki* and *Labidus praedator*, the detached heads of workers or soldiers or objects smeared with the substance from the crushed heads of soldiers were attacked by their nestmates when placed in the foraging column, while the remainder of the body evoked little or no response (Brown, 1960).

In *Aneuretus simoni*, the only living representative of the subfamily Aneuretinae, pygidial gland secretion caused aggressive alarm without having a repellent function (Traniello & Jayasuriya, 1981*a*).

In Ponerine ants, *Odontomachus troglodytes*, components of the mandibular gland secretion, 3-n-butyl-, 3-n-[pentyl-, and 3-n-hexyl-2,6-dimethylpyrazine (XII–XIV) released the full range of behaviour in workers (alerting, approach and attack) whereas



the fragile males retreated (Longhurst *et al.*, 1978). In *Gnamptogenys pleurodon*, methyl 6-methylsalicylate (XV) functions as an alarm pheromone (Duffield & Blum, 1975). In *Neoponera villosa* 4-methyl-3-heptanone acts as alarm pheromone (Duffield & Blum, 1973). To illustrate the economy of use of chemicals by insects both alkylpyrazines and methyl 6-methylsalicylate are found in the poison glands of some myrmicine ants, where they function as trail pheromones (see below).

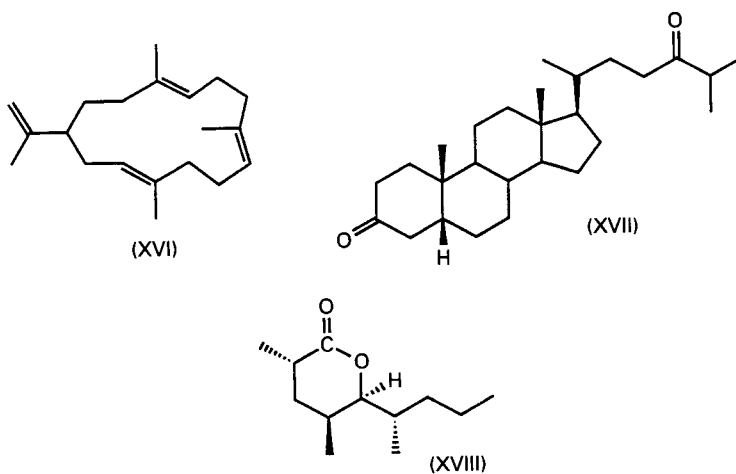
The dolichoderine ant *Iridomyrmex pruinosus* contain an anal gland (better known as pygidial gland) as the source of an alarm pheromone, 2-heptanone (Blum *et al.*, 1963).

(6) Trail pheromones

A trail pheromone is a chemical substance or mixture of substances applied to a surface by a first individual which is detected and followed by other individuals. The behaviour is best known in ants. When a foraging worker finds a food source, it returns to the nest laying broken streaks of scent trail to direct nestmates to follow the pathway to the food source, and as they return to the nest, they reinforce the chemical deposit. When the food source is exhausted, the returning workers do not reinforce the trail so that it evaporates away.

Trail pheromones are widely used by ants, some termites and some stingless bees and by at least one group of Lepidoptera. The existence of trail pheromones is known in many species because the behaviour is easily recognized, but there have been relatively few attempts at their isolation. Chemical aspects of known trail pheromones have been surveyed recently (Morgan, 1989).

In termites, the sternal glands, found in a number of species of several families situated on the 4th or 5th sternite, is the only known source of trail pheromones (Lüscher & Müller, 1960; Stuart, 1961*b*, 1963). Birch *et al.* (1972) identified nasutene [cembrene-A, (*E,E,E*)-isopropenyl-4,8,12-trimethylcyclotetradeca-4,8,12-triene, (XVI)] as the trail pheromone from the workers of the Australian nasute termite *Nasutitermes exitiosus*. The trail pheromone of the grass-feeding termite *Trinervitermes bettonianus* has also been identified as cembrene-A (McDowell & Oloo, 1984). Workers and both male and female alates produce the pheromone in the ratio, 1:62:1090 (12 μ g



total in female alates) respectively, and the compound is active at 0.5 ng/cm. Soldiers of *T. bettonianus* do not take part in active trail laying (Leuthold & Lüscher, 1974), while soldiers of *Nasutitermes costalis* lay trails and are responsible for the organization of foraging in this species (Traniello, 1981).

An aerial odour trail used by flying insects has been demonstrated in some bumblebees (von Frisch, 1967; Lindauer & Kerr, 1960). The labial gland secretion is used as a trail pheromone, and the scout bee that has located a food source deposits drops of the trail pheromone at specific intervals on foliage, twigs and other substrates on its way back to the nest. In stingless bees, Blum *et al.* (1970) identified neral and geranial (III, IV) as major components of the mandibular gland secretion used as the trail pheromone of *Trigona subterranea*.

In ants, the poison gland, Dufour gland, meta-tibial gland, hind-gut gland, rectal gland, Pavan's gland, pygidial gland or sternal gland, may be the source of trail pheromones, according to species, with rather distinct subfamily preferences. It is well known that foragers in ants lay scent trails on the ground which can be followed by other individuals (Forel, 1908; Goetsch, 1934; Carthy, 1950, 1951; 1952). When an ant is following such a trail it is guided primarily by the scent marks, although other orienting factors including visual stimuli, are sometimes involved (Goetsch, 1934; Sudd, 1959). Trail pheromones may be applied in mass-foraging recruitment, colony migration (Wilson, 1962) or initiation and guidance of slave-raids (Regnier & Wilson, 1971). Ant trail pheromones have been reviewed from a chemical viewpoint (Attygalle & Morgan, 1985).

Tandem running is a very primitive form of recruitment as observed in *Leptothorax acervorum* (Wilson, 1971) in which a scout ant, after finding a food source or a new nest site, leads nestmates one at a time, by keeping the recruited ant in close antennal contact with the leader ant. The recruited worker may invite nestmates to tandem following 'tandem calling behaviour' in which it extrudes the sting and releases a secretion from the poison gland (Möglich, Maschwitz & Hölldobler, 1974). Tandem running was also investigated in *Harpagoxenus sublaevis* (Buschinger & Winter, 1977).

Wilson (1959) showed that the Dufour gland is the source of the trail pheromone of *Solenopsis* species, which carry out mass-foraging. The secretion is a powerful attractant. It excites workers, draws them out of the nest and directs them toward the trail, while workers unable to reach the mass turn back without laying trails (Wilson, 1962). Vander Meer (1986) explained that for successful foraging by an ant exploring a new food source, its trail pheromone must first attract or recruit workers to the trail and secondly induce or initiate the workers to follow the trail. Thus the successful foraging for *s. invicta* involves steps of behaviour starting with recruitment, followed by an orientation primer, followed by orientation. 3-Ethyl-2,5-dimethylpyrazine has been identified as a venom-derived trail pheromone in a number of myrmicine ants (Morgan, 1989).

The trail pheromone of *Crematogaster* species originates from the tibial gland of the hind legs (Leuthold, 1968; Fletcher & Brand, 1968). A tube passes from the gland down to the foot, and the trail is laid from the feet, with the ant walking in a strange manner with its hind legs close together.

In formicine ants, the trail pheromones originate from the hind gut. In *Camponotus sericeus* a recruitment step is initiated by mechanical signals and motor patterns

involving tandem running, and the chemical trails secreted from the hind gut function only as orientation cues and do not release any recruitment effect (Hölldobler, Möglich & Maschwitz, 1974; Hölldobler, 1978). After formicine ants have located a food source a 'waggle' display to a recruiting ant inside the nest is required to induce nestmates to follow the trail (Hölldobler, 1971*b*, 1978; Möglich & Hölldobler, 1975; Traniello, 1977). *Oecophylla longinoda* workers employ multiple recruitment systems in which both the rectal and sternal gland secretions are used (Hölldobler & Wilson, 1978). The rectal gland secretes odour trails which cause (1) recruitment to new food sources, (2) recruitment to new terrain (foraging area), (3) emigration to new sites, and (4) long-range recruitment to repel intruders. In such cases, the trail pheromone is aided by tactile stimuli (mouth-opening, antennal contact and head wagging). The sternal gland secretion performs the short-range recruitment of nestmates to repel territorial intruders.

In Dolichoderine ants, Pavan's gland (sternal gland) is the source of the trail pheromone (Wilson & Pavan, 1959).

Ponerine ants utilize secretions from pygidial, poison and sternal glands as trail pheromones. For example *Leptogenys chinensis*, which feeds mainly on termites, lays trails from the pygidial and poison glands: the pygidial gland secretion is responsible for recruitment and orientation, while that from the poison gland is responsible for the orientation reaction (Maschwitz & Schönegege, 1977). *Onychomyrmex*, a genus belonging to the primitive ponerine tribe Amblyoponini, is the only genus that employs the sternal gland as the source of trail pheromones (Hölldobler, Engel & Taylor, 1982). The gland is absent in the two genera, *Cerapachys* and *Sphinctomyrmex* of the Cerapachyini tribe which utilize secretions from the poison and pygidial glands for trail communication.

In Ecitonine ants the hind gut and the pygidial gland are sources of trail pheromones. Blum & Portocarrero (1964) identified the hind gut as the source of trail pheromones in *Eciton* ants, but Hölldobler & Engel (1978) state that the pygidial gland is the source of the trail pheromone of *E. hamatum*. The army ant *Neivamyrmex nigrescens* workers employ the hind gut as the source of the trail pheromone (Watkins, 1964). Trails of the army ants are relatively non-volatile and can persist after deposition on the substrate for several days (Torgerson & Akre, 1970).

Aneuretus simoni, the only representative of the subfamily Aneuretinae, utilize the sternal gland as the source of the trail pheromone (Traniello & Jayasuriya, 1981*a, b*). The scout ants employ a motor display for recruiting nestmates to trail laying. The trail pheromone is employed by workers to locate food sources and during nest migration.

It has recently been shown that tent caterpillars, *Malacosomas* species, use trails to maintain aggregation, for exploration and to guide individuals to new food sources (Peterson, 1988). The steroid compound 5- β -cholestan-3,24-dione (XVII) has been identified as a component of the trail pheromone of *M. americanum* (Crump *et al.*, 1987).

(7) Territorial (home-range) pheromones

Chemicals by which animals mark and recognize their own territories (home range) for food gathering or defence (Cammaerts, Morgan & Tyler, 1977; Hölldobler & Wilson, 1977) are called home range marking pheromones. When the marked territory is defended against intrusion by other colonies or other species, it is called a territorial pheromone. Such pheromones appear to be widely used throughout the invertebrate and vertebrate animals, but as yet, few of the substances used for this purpose have been isolated.

In bees and wasps, particularly social bees, the use of chemical cues to mark foraging areas is not accurate, consequently, it is not significant where the insect forages over a vast area. Honey bee, *Apis mellifera*, workers crawl and deposit a 'footprint' substance which attracts other workers and stimulates them to enter the hive. Homecoming honeybees are also attracted by an odour in the hive (Butler, Fletcher & Walker, 1969). The same authors demonstrated the behaviour with workers of the wasp *Vespa vulgaris*. In the Costa Rican solitary bees, *Centris nitid* and *C. trigonoides subtarsata*, males use a tibial gland secretion to mark the boundaries of defended territories (not more than a metre and half in diameter from the flowering corms of *cusia grandis* (Williams *et al.*, 1984). Other *Centris* species mark their territories by the mandibular gland secretion (Vinson *et al.*, 1982).

The ant *Myrmica rubra* employs the Dufour gland secretion for marking its territory (Cammaerts, Morgan & Tyler, 1977). The secretion has a short-lived recruitment activity and a long-lasting territorial marking effect. In the formicine ant, *Oecophylla longinoda*, workers employ rectal gland secretion as a true territorial pheromone (Hölldobler & Wilson, 1977, 1978). Jaffé & Puche (1984) recorded that the metapleural gland of *Solenopsis geminata* produces a territorial pheromone.

(8) Surface pheromones

Surface pheromones are found on all members of the social insect colony. Such substances seem to be mainly adsorbed on the body surface, and perceived by direct contact or, at most over a very short distance (Shorey, 1973). They include recognition pheromones (caste-recognition; brood recognition), releasers of grooming and courtship behaviour and the secretions that stimulate food exchange. They are thought to be composed of a combination of species-specific odours and food sources. Rocca *et al.* (1983) identified α -pyrones [chiefly invictolide, (XVIII)] from the whole extract of queens of *Solenopsis invicta* which acts as queen recognition pheromone. Edwards & Chambers (1984) identified cembrene-A (XVI) in the Dufour gland secretions of fertile queens of *Monomorium pharaonis* and it may serve as a queen-recognition pheromone. There is also evidence that the cuticular hydrocarbons can also act as recognition pheromones (see, for example Bonavita-Cougourdan & Clément, 1987).

(9) Funeral pheromones

Chemical compounds are produced from dead ants that stimulate a live ant to remove a dead congener to a refuse pile outside the nest. The funeral pheromones are said to include saturated fatty acids, their esters and unsaturated fatty acids. When any object or living worker is daubed with these substances, they are treated as dead ants (Wilson *et al.*, 1958, Wilson, 1963; Matthews & Matthews, 1978).

VI. CONCLUSIONS

The system of dividing chemicals that modify behaviour into allelochemicals and pheromones and the subdivisions of these categories is one that has stood the test of expanding knowledge. Few primer pheromones are yet known, largely due to the lack of simple bioassays by which they can be recognized for isolation, and the larger time interval between receipt of the pheromone message and the production of the physiological effect. On the other hand, the short response time and the availability of

many good bioassays has led to the isolation and identification of a vast number of releaser pheromones, and a steadily growing number of them belong to social insects. The list of categories is clearly not complete and as behavioural knowledge grows, we can expect to see additions and subdivisions of the present list. In all cases the successful identification of pheromones depends upon the linking of biological (behavioural) information with chemical separation and identification methods (cf. Hummel & Miller, 1984). Little is yet known about the biosynthesis of pheromones, particularly in social insects, and their fate after detection by the recipient, but a start of these studies has been made (Prestwich & Blomquist, 1988).

VII. SUMMARY

1. Chemical communication plays an important part in the lives of insects, and particularly in lives of those that live in groups or social organizations.
2. Chemicals which are used in communication in the general sense are called semiochemicals, and there are a number of subdivisions recognized under this title.
3. Pheromones are a category of semiochemicals which are used for communication between individuals of the same species.
4. Pheromones are in turn subdivided into primer and releaser pheromones. The former produce a relatively long-lasting physiological change in the receiver, and the latter stimulate the receiver to some immediate behavioural response.
5. Far more is known about releaser pheromones at present because they are easier to study.
6. Nine categories of releaser pheromone are recognized here, used by both social and non-social insects.
7. Sex pheromones are widely used to bring the sexes together for mating, and they have been extensively studied in Lepidoptera.
8. Invitation pheromones, encouraging the species to feed or oviposit at an explored site, are not extensively known.
9. Aggregation pheromones are designed to bring individuals together into groups which may be temporary in sub-social insects, or permanent in social insects.
10. Dispersal or spacing pheromones are used by other species to reduce intraspecific competition for scarce resources.
11. Alarm pheromones are a broad and sometimes unclearly defined group which communicate alarm or attack, chiefly in colonial species.
12. Trail pheromones, applied to a surface by an individual, to be followed by another, are confined to Hymenoptera, Isoptera and a few Lepidoptera as far as is known.
13. Territorial and home range pheromones may be widely distributed, but as yet few of them have been recognized.
14. Surface and funeral pheromones are even less well known. Surface pheromones may play a large part in species or colony recognition.
15. We can expect the number and complexity of pheromones to be much greater in social insects, a part of the subject which until now has received relatively less attention.
16. As our understanding of the subject grows we may expect other categories to be added to this list.

REFERENCES

- AHMADI, A. & McCLELLAND, G. A. H. (1985). Mosquito-mediated attraction of female mosquitoes to a host. *Physiological Entomology* **10**, 251-255.
- AL-SA'AD, B. N., FREE, J. B. & HOWSE, P. E. (1985). Adaptation of worker honey bees (*Apis mellifera*) to their alarm pheromones. *Physiological Entomology* **10**, 1-14.
- ATTYGALLE, A. B. & MORGAN, E. D. (1985). Ant trail pheromones. *Advances in Insect Physiology* **18**, 11-30.
- AYRE, G. L. & BLUM, M. S. (1971). Attraction and alarm of ants (*Camponotus* spp.) by pheromones. *Physiological Zoology* **44**, 77-83.
- BERGSTRÖM, G. & LÖFQVIST, J. (1970). Chemical basis for odour communication in four species of *Lasius* ants. *Journal of Insect Physiology* **16**, 2353-2375.
- BERNDT, K. P. & NITSCHMANN, J. (1979). The physiology of reproduction in the pharaoh's ant *Monomorium pharaonis* L. The unmated queens. *Insectes Sociaux* **26**, 137-145.
- BIRCH, M. C. (1974). Aphrodisiac pheromones in insects. In *Pheromones* (ed. M. C. Birch), pp. 115-134. North-Holland, Amsterdam.
- BIRCH, M. C. & HAYNES, K. F. (1982). *Insect Pheromones*. Studies in Biology No. 147. Edward Arnold Ltd. London.
- BIRCH, A. J., BROWN, W. V., CORRIE, J. E. T. & MOOTE, B. P. (1972). Neocembrene-A, a termite trail pheromone. *Journal of the Chemical Society, Perkin Transactions I*, 2653-2658.
- BLUM, M. S. & PORTOCARRERO, C. (1964). Chemical releasers of social behaviour IV. The hindgut as the source of the odour trail pheromone in the neotropical army ant genus *Eciton*. *Annals of the Entomological Society of America* **57**, 793-794.
- BLUM, M. S., WARTER, S. L., MONROE, R. S. & CHIDESTER, J. C. (1963). Chemical releasers of social behaviour I. Methyl n-amyl ketone in *Iridomyrmex pruinosus* (Roger) (Formicidae: Dolichoderinae). *Journal of Insect Physiology* **9**, 881-885.
- BLUM, M. S., CREW, R. M., KERR, W. E., KEITH, L. H., GARRISON, A. W. & WALKER, M. M. (1970). Citral in stingless bees: isolation and function in trail laying and robbing. *Journal of Insect Physiology* **16**, 1637-1648.
- BOCH, R., SHEARER, D. A. & STONE, B. C. (1962). Identification of iso-amyl acetate as an active component in the sting pheromone of the honey bee. *Nature* **195**, 1018-1020.
- BONAVITA-COUGOURDAN, A. & CLÉMENT, J. L. (1987). Nestmate recognition: the role of cuticular hydrocarbons in the ant *Componotus vagus*. *Journal of Entomological Science* **232**, 1-10.
- BORDEN, J. H., CONN, J. E., FRISKIE, L. M., SCOTT, B. E., CHONG, L. J., PIERCE, H. D. JR & OEHLISCHLAGER, A. C. (1983). Semiochemicals for the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in British Columbia, Baited tree studies. *Canadian Journal of Forest Research* **13**, 325-333.
- BRADSHAW, J. W. S., BAKER, R. & HOWSE, P. E. (1979a). Multicomponent alarm pheromones in the mandibular glands of major worker of the African weaver ant, *Oecophylla longinoda*. *Physiological Entomology* **4**, 15-25.
- BRADSHAW, J. W. S., BAKER, R. & HOWSE, P. E. (1979b). Chemical composition of the poison apparatus secretions of the African weaver ant, *Oecophylla longinoda* and their role in behaviour. *Physiological Entomology* **4**, 39-46.
- BROWN, W. L. JR. (1960). The release of alarm and attack behaviour in some New World army ants. *Psyche* **66**, 25-27.
- BROWN, W. L. JR., EISNER, T. & WHITTAKER, R. H. (1970). Allomones and kairomones: transpecific chemical messengers. *Bioscience* **20**, 21-11.
- BUSCHINGER, A. (1968). Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hymenoptera, Formicidae). III. Kopula, Koloniegründung, Raubzüge. *Insectes Sociaux* **15**, 89-104.
- BUSCHINGER, A. (1972). Giftdrüsensekret als sexual pheromon bei der Ameise *Harpagoxenus sublaevis*. *Die Naturwissenschaften* **59**, 13-314.
- BUSCHINGER, A. (1983). Sexual behaviour and slave raiding of the dulotic ant, *Harpagoxenus sublaevis* (Nyl.) under field conditions (Hymenoptera: Formicidae). *Insectes Sociaux* **30**, 235-240.
- BUSCHINGER, A. & WINTER, V. (1977). Rekrutierung vom Nestgenossen mittels tandemlaufen bei sklavenraubzügen der dulotischen Ameise *Harpagoxenus sublaevis* (Nyl.). *Insectes Sociaux* **24**, 183-190.
- BUTENANDT, A. (1959). Geschlechtsspezifische Lockstoffe der Schmetterlinge. *Max-Planck Gesellschaft Jahrbuch*, 23-32.
- BUTLER, C. A. & FAIREY, E. M. (1964). Pheromones of the honey bee, biological studies of the mandibular gland secretion of the queen. *Journal of Apicultural Research* **3**, 65-76.
- BUTLER, C. A., CALLOW, R. K. & JOHNSTON, W. C. (1961). The isolation and synthesis of queen substance, 9-oxodec-trans-2-enoic acid, a honey bee pheromone. *Proceedings of the Royal Society B* **155**, 419-432.
- BUTLER, C. A., CALLOW, R. K. & CHAMPAN, J. R. (1964). 9-Hydroxydec-trans-2-enoic acid, a pheromone stabilizing honey bee swarms. *Nature* **201**, 733.

- BUTLER, C. A., FLETCHER, J. C. & WALTER, D. (1969). Nest-entrance marking with pheromones by the honey bee *Apis mellifera* L., and by a wasp *Vespa vulgaris* L. *Animal Behaviour* **17**, 142-147.
- CAMMAERTS, M. C., MORGAN, E. D. & TYLER, R. (1977). Territorial marking in the ant *Myrmica rubra* L. (Formicidae). *Biology of Behaviour* **2**, 263-272.
- CAMMAERTS, M. C., EVERSLED, R. P. & MORGAN, E. D. (1981). Comparative study of the mandibular gland secretion of four species of *Myrmica* ants. *Journal of Insect Physiology* **27**, 225-231.
- CAMMAERTS, M. C., EVERSLED, R. P. & MORGAN, E. D. (1983). The volatile components of the mandibular gland secretion of workers of the ants *Myrmica lobicornis* and *Myrmica sulcinodis*. *Journal of Insect Physiology* **29**, 659-664.
- CAMMAERTS, M. C., ATTYGALLE, A. B., EVERSLED, R. P. & MORGAN, E. D. (1985). The pheromonal activity of chiral 3-octanol for *Myrmica* ants. *Physiological Entomology* **10**, 33-36.
- CARTHY, J. D. (1950). Odour trails of *Acanthomyops fuliginosus*. *Nature* **166**, 154.
- CARTHY, J. D. (1951). The orientation of two allied species of British ants. II. Odour trail laying and following in *Acanthomyops (Lasius) fuliginosus*. *Behaviour* **3**, 304-318.
- CARTHY, J. D. (1952). The return of ants to their nest. *International Congress of Entomology 9th, Transactions*, 365-369.
- CARTHY, J. D. (1966). Insect communication. In *Insect Behaviour* (ed. P. T. Haskell), pp. 69-80. Symposia of the Royal Entomological Society of London, No. 3.
- CHIANG, H. C., HOLDAWAY, F. G., BRINDLEY, T. A. & NEISWANDER, C. R. (1960). European corn borer populations in relation to the estimation of crop loss. *Journal of Economic Entomology* **53**, 517-522.
- COLLINS, C. W. & POTTS, S. F. (1932). Attractants for the flying gypsy moth as an aid in locating new infestations. *US Department of Agriculture Technical Bulletin* **336**, 1-43.
- CONN, J. E., BORDEN, J. H., SCOTT, B. E., FRISKIE, L. M., PIERCE, H. D. JR. & OEHLISCHLAGER, A. C. (1983). Semiochemicals for the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in British Columbia, Field Trapping Studies. *Canadian Journal of Forest Research* **13**, 320-324.
- CORBET, S. A. (1971). Mandibular gland secretion of larvae of the flour moth *Anagasta kuehniella* contains an epideictic pheromone and elicits oviposition movements in a Hymenopteran parasite. *Nature* **232**, 481-484.
- CREWE, R. M. & VELTHUIS, H. H. W. (1980). False queens: a consequence of mandibular gland signals in worker honey bees. *Naturwissenschaften* **67**, 467-469.
- CRUMP, D., SILVERSTEIN, R. M., WILLIAMS, H. J. & FITZGERALD, T. D. (1987). Identification of trail pheromone of larva of eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *Journal of Chemical Ecology* **3**, 397-402.
- DETHIER, V. G., BROWN, I. B. & SMITH, G. N. (1960). The designation of chemicals in terms of the responses they elicit from insects. *Journal of Economic Entomology* **53**, 134-136.
- DITTRICK, L. E., JONES, R. L. & CHIANG, H. C. (1983). An oviposition deterrent for the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae), extracted from larval frass. *Journal of Insect Physiology* **29**, 119-121.
- DIXON, A. F. G. (1963). Reproductive activity of the sycamore aphid *Drepanosiphum platanoides* (Shrank) (Hymenoptera, Aphididae). *Journal of Animal Ecology* **32**, 33-48.
- DUFFIELD, R. M. & BLUM, M. S. (1973). 4-Methyl-3-heptanone: identification and function in *Neoponera villosa*. *Annals of the Entomological Society America* **66**, 1357.
- DUFFIELD, R. M. & BLUM, M. S. (1975). Methyl 6-methylsalicylate, identification and function in a ponerine ant (*Gnamptogenys pleurodon*). *Experientia* **31**, 466.
- EDWARDS, J. P. & CHAMBERS, J. (1984). Identification and source of a queen-specific chemical in the Pharaoh's ant, *Monomorium pharaonis* (L.). *Journal of Chemical Ecology* **10**, 1731-1747.
- EDWARDS, L. J., SIDDALL, J. B., DUNHAM, L. L., UDEN, P. & KISLOW, C. J. (1973). *Trans-β*-farnesene, alarm pheromone of the green peach aphid *Myzus persicae* (Sulzer). *Nature* **241**, 126-127.
- FABRE, J. H. (1914). Hochzeitsfluge der Nachtofenenaugen, pp. 80-86; Aus dem Liebesleben des Eichenspinners, pp. 86-92; Duft- und Geruchsinn der Insekten, pp. 92-98; in *Bilder aus der Insektenwelt*, Verlag Kosmos, Stuttgart (authorized translation in German of Fabre's *Souvenirs entomologiques*, Paris, Delagrave 1879, *Moers des Insects* and *La vie des Insects*).
- FALES, H. M., BLUM, M. S., CREWE, R. M. & BRAND, J. M. (1972). Alarm pheromones in the genus *Manica* derived from the mandibular gland. *Journal of Insect Physiology* **18**, 1077-1088.
- FLETCHER, D. J. C. & BLUM, M. S. (1983). The inhibiting pheromone of queen fire ants: effects of disinhibition on dealation and oviposition by virgin queens. *Journal of Comparative Physiology* **153**, 467-475.
- FLETCHER, D. J. C. & BRAND, J. M. (1968). Source of the trail pheromone and method of trail laying in the ant *crematogaster peringueyi*. *Journal of Insect Physiology* **14**, 783-788.
- FOREL, A. (1908). *The Sense of Insects*. Methuen, London.

- FREE, J. B. & FERGUSON, A. W. (1982). Transfer of pheromone from immature queen honey bees, *Apis mellifera*. *Physiological Entomology* **7**, 410-406.
- FREE, J. B., FERGUSON, A. W., SIMPKINS, J. R. & AL-SA'AD, B. N. (1983). Effect of honey bee Nasonov and alarm pheromone components on nest entrance behaviour. *Journal of Apicultural Research* **22**, 214-223.
- FREE, J. B., FERGUSON, A. W. & SIMPKINS, J. R. (1984). Influence of immature queen honey bees (*Apis mellifera*) on queen rearing and foraging. *Physiological Entomology* **9**, 387-394.
- GALY, N. E. (1962). Chemical mating attractants in the queen honey bee. *Science* **136**, 773-4.
- GOETSCH, Q. (1934). Untersuchungen über die Zusammenarbeit in Ameisenstaat. *Zeitschrift für Morphologie, Oekologie der Tiere* **28**, 319-401.
- GUNNISON, A. F. & MORSE, R. A. (1968). Source of the ether-soluble organics of stings of the honey bee, *Apis mellifera* (Hymenoptera: Apidae). *Annals of the Entomological Society of America* **61**, 5-8.
- HAYASHI, N. & KOMAE, H. (1977). The trail and alarm pheromones of the ant, *Pristomyrmex pungens* Mayr. *Experientia* **33**, 424-425.
- HILKER, M. & KLEIN, B. (1989). Investigation of oviposition deterrent in larval frass of *Spodoptera littoralis* (Boisd.). *Journal of Chemical Ecology* **15**, 929-938.
- HÖLLDOBLER, B. (1971a). Sex pheromone in the ant *Xenomyrmex floridanus*. *Journal of Insect Physiology* **17**, 1497-1499.
- HÖLLDOBLER, B. (1971b). Recruitment behaviour in *Camponotus socius* (Hymenoptera: Formicidae). *Zeitschrift für Physiologie* **75**, 123-142.
- HÖLLDOBLER, B. (1977). The behavioural ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behavioural Ecology and Sociobiology* **1**, 405-423.
- HÖLLDOBLER, B. (1978). Ethological aspects of chemical communication in ants. *Advances in the Study of Behaviour* **8**, 75-115.
- HÖLLDOBLER, B. (1982). Chemical communication in ants. New exocrine glands and their behavioural function. In *The Biology of Social Insects* (ed. M. D. Breed, C. D. Michener and H. E. Evans), pp. 312-317. Westview Press, Boulder, Colorado.
- HÖLLDOBLER, B. (1984). Evolution of Insect Communication. In *Insect Communication* (ed. T. Lewis), pp. 349-377. Academic Press, London, New York.
- HÖLLDOBLER, B. & ENGEL, H. (1978). Tergal and sternal glands in ants. *Psyche* **85**, 285-330.
- HÖLLDOBLER, B. & HASKINS, C. P. (1977). Sexual calling behaviour in primitive ants. *Science* **195**, 793-794.
- HÖLLDOBLER, B. & MASCHWITZ, U. (1965). Der Hochzeitsschwarm der Rossameise *Camponotus herculeanus* L. (Hym. Formicidae). *Zeitschrift für vergleichender Physiologie* **50**, 551-568.
- HÖLLDOBLER, B. & WILSON, E. O. (1977). Colony specific territorial pheromone in the African weaver ant. *Proceedings of the National Academy of Science, U.S.A.* **74**, 2072-2075.
- HÖLLDOBLER, B. & WILSON, E. O. (1978). The multiple recruitment system of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* **3**, 19-60.
- HÖLLDOBLER, B. & WILSON, E. O. (1983). Queen control of weaver ants (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **76**, 235-238.
- HÖLLDOBLER, B. & WÜST, M. (1973). Ein sexual pheromon bei der pharaoameise *Monomorium pharaonis* (L.). *Zeitschrift für Tierpsychologie* **32**, 1-9.
- HÖLLDOBLER, B., MÖGLICH, M. & MASCHWITZ, U. (1974). Communication by tandem running in the ant *Camponotus sericeus*. *Journal of Comparative Physiology*, **90**, 105-127.
- HÖLLDOBLER, B., ENGEL, H. & TAYLOR, R. W. (1982). A new sternal gland in ants and its function in chemical communication. *Naturwissenschaften* **69**, 20-91.
- HUMMEL, H. E. & MILLER, T. A. (eds.) (1984). *Techniques in Pheromone Research*, pp. 464. Springer-Verlag, Berlin.
- JAFFÉ, K. & PUCHE, H. (1984). Colony-specific territorial marking with the metapleural gland secretion in the ant *Solenopsis geminata* (Fabr.). *Journal of Insect Physiology* **30**, 265-270.
- KARLSON, P. & BUTENANDT, A. (1959). Pheromones (ectohormones) in insects. *Annual Review of Entomology* **4**, 39-58.
- KARLSON, P. & LÜSCHER, M. (1959). 'Pheromones' a new term for a class of biologically active substances. *Nature (London)* **183**, 55-56.
- KUGLER, CH. (1979). Alarm and defense, A function for the pygidial gland in the myrmicine ant, *Pheidole biconstricta*. *Annals of the Entomological Society of America* **72**, 532-536.
- LAW, J. H. & REGNIER, F. E. (1971). Pheromones. *Annual Review of Biochemistry* **40**, 533-48.
- LEUTHOLD, R. H. (1968). A tibial gland scent-trail and trail-laying behaviour in the ant *Crematogaster ashmeadi* Mayr. *Psyche* **75**, 233-248.

- LEUTHOLD, R. H. & LÜSCHER, M. (1974). An unusual caste polymorphism of the sternal gland and its production of trail pheromone in the termite *Trinervitermes bettonianus*. *Insectes Sociaux* **21**, 335-342.
- LEWIS, T. (1984). The element and frontiers of insect communication. In *Insect Communication* (ed. T. Lewis), pp. 1-27. 12th Symposium of the Royal Entomological Society of London. Academic Press, London.
- LINDAUER, M. & KERR, W. E. (1960). Communication between the workers of stingless bees. *Bee World* **41**, 29-41, 65-71.
- LLOYD, J. E. (1983). Bioluminescence and communication in insects. *Annual Review of Entomology* **28**, 131-160.
- LÖFQVIST, J. (1976). Formic acid and saturated hydrocarbons as alarm pheromones for the ant *Formica rufa*. *Journal of Insect Physiology* **21**, 1331-1346.
- LONGHURST, C., BAKER, R., HOWSE, P. E. & SPEED, W. (1978). Alkylpyrazines in ponerine ants: their presence in three genera, and caste specific behavioural responses to them in *Odontomachus troglodytes*. *Journal of Insect Physiology* **24**, 833-8327.
- LÜSCHER, M. & MÜLLER, B. (1960). Ein spürbildendes sekret bei termiten. *Naturwissenschaften* **47**, 503.
- MARKL, H. (1967). Die verstandigung durch stridulationssignal bei Blattschneiderameisen. I. Die biologische Bedeutung der Stridulation. *Zeitschrift für vergleichende Physiologie* **57**, 299-330.
- MARKL, H. (1973). The evolution of stridulatory communication in ants. *Proceedings of the 7th International Congress of the International Union for the Study of Social Insects, 1973*, pp. 258-265.
- MASCHWITZ, U. (1964). Gefahrenalarmstoffe and Gefahrenalarmierung bei sozialen Hymenoptera. *Zeitschrift für Vergleichende Physiologie* **47**, 596-655.
- MASCHWITZ, U. & SCHÖNEGGE, P. (1977). Recruitment gland of *Leptogenys chinensis*. *Naturwissenschaften* **64**, 584-590.
- MATTHEWS, R. W. & MATTHEWS, J. R. (1978). *Insect Behaviour*. John Wiley & Sons, New York.
- McDOWELL, P. G. & OLOO, G. W. (1984). Isolation, identification and biological activity of trail-following pheromone of termite *Trinervitermes bettonianus* (Sjöstedt) (Termitidae: Nasutitermitinae). *Journal of Chemical Ecology* **10**, 835-851.
- McGURK, D. J., FROST, J. & EISENBRAUN, E. J. (1966). Volatile compounds in ants; identification of 4-methyl-3-heptanone from *Pogonomyrmex* ants. *Journal of Insect Physiology* **12**, 1435-1441.
- MELL, R. (1928). *Biologie und systematik der chinesischen Sphingiden*. Friedlander, Berlin.
- MÖGLICH, M. & HÖLLDOBLER, B. (1975). Communication and orientation during foraging and emigration in the ant *Formica fusca*. *Journal of Comparative Physiology* **101**, 275-288.
- MÖGLICH, M., MASCHWITZ, U. & HÖLLDOBLER, B. (1974). Tandem calling: a new signal in ant communication. *Science* **186**, 1076-1047.
- MORGAN, E. D. (1989). Insect trail pheromones: a perspective of progress. In *Isolation and Chromatography of Insect Hormones and Pheromones* (ed. A. R. McCaffery and I. D. Wilson) Plenum Press, London (in the press)
- MORGAN, E. D. & MANDAVA, N. B. (1988). *Handbook of Natural Pesticides, Insects*, vol. iv, part A and vol. iv, part B, *Pheromones*. CRC Press, Boca Raton.
- MORGAN, E. D., INWOOD, M. R. & CAMMAERTS, M. C. (1978). The mandibular gland secretion of the ant, *Myrmica scabrinodis*. *Physiological Entomology* **3**, 107-114.
- NAULT, L. R., MONTGOMERY, M. E. & BOWERS, W. S. (1976). Ant-aphid association: role of aphid alarm pheromone. *Science* **192**, 1349-1350.
- NORDLUND, D. A. & LEWIS, W. J. (1976). Terminology of chemical-releasing stimuli in intra-specific and inter-specific interactions. *Journal of Chemical Ecology* **2**, 211-220.
- NORRIS, M. J. (1954). Sexual maturation in the desert locust (*Schistocerca gregaria* (Forsk.) with special reference to the effects of grouping. *Anti-locust Bulletin*, No. 18, 44 pp.
- NORRIS, M. J. (1964). Accelerating and inhibiting effects of crowding on sexual maturation in two species of locusts. *Nature* **203**, 784-785.
- OTTE, D. (1977). Communication in Orthoptera. In *How Animals Communicate* (ed. T. A. Sebeok), pp. 334-361. Indiana University Press, Bloomington.
- PASSERA, L. (1980). La fonction inhibitrice des reines de la forme *Plagiolepis pygmaea* Latr.; rôle des pheromones. *Insectes Sociaux* **27**, 212-225.
- PASTEELS, J. M., VERHAEGHE, J. C., BRAEKMAN, J. C., DALOZE, D. & TURSCH, B. (1980). Caste-dependent pheromones in the head of the ant *Tetramorium caespitum*. *Journal of Chemical Ecology* **6**, 467-472.
- PETERSON, S. C. (1988). Chemical trail marking and following by caterpillars of *Malacosoma neustria*. *Journal of Chemical Ecology* **14**, 287-301.
- PETERSON-BRAUN, M. (1977). Untersuchungen zur sozialen organisation der pharaoameise *Monomorium pharaonis* L. (Hymenoptera: Formicidae). II. Die Kastendeterminierung. *Insectes Sociaux* **24**, 303-318.

- PITMAN, G. B. & VITÉ, T. P. (1969). Aggregation behaviour of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to chemical messengers. *Canadian Entomologist* **101**, 143-149.
- PITMAN, G. B., VITÉ, J. P., KINZER, G. W. & FENTIMAN, A. F. JR. (1969). Specificity of population-aggregating pheromones in *Dendroctonus*. *Journal of Insect Physiology* **15**, 363-366.
- POST, D. C., DOWNING, H. A. & JEANNE, R. L. (1984). Alarm response to venom by social wasps *Polistes exclamans* and *P. fuscatus* (Hymenoptera: Vespidae). *Journal of Chemical Ecology* **10**, 1425-1433.
- PRESTWICH, G. D. & BLUMQUIST, G. J. (eds) (1988). *Pheromone Biochemistry*, pp. 565. Academic Press, New York.
- PRESTWICH, G. D., BIERL, B. A., DEVILBISS, E. D. & CHAUDHURY, M. F. B. (1977). Soldier frontal glands of the termite *Macrotermes subhyalinus*; morphology, chemical composition, and use in defence. *Journal of Chemical Ecology* **8**, 579-590.
- PROKOPY, R. J. (1972). Evidence for a marking pheromone deterring repeated oviposition in apple maggot-flies. *Environmental Entomology* **1**, 336-337.
- REGNIER, F. E. & WILSON, E. O. (1968). The alarm-defence system of the ant *Acanthomyops claviger*. *Journal of Insect Physiology* **14**, 955-970.
- REGNIER, F. E. & WILSON, E. O. (1969). The alarm-defence system of the ant *Lasius alienus*. *Journal of Insect Physiology* **15**, 893-898.
- REGNIER, F. E. & WILSON, E. O. (1971). Chemical communication and 'propaganda' in slave-maker ants. *Science* **172**, 267-269.
- RENWICK, J. A. A. & RADKE, C. D. (1980). An oviposition deterrent associated with frass from feeding larvae of the cabbage looper, *Trichoplusia ni* (Lepidoptera: Noctuidae). *Environmental Entomology* **9**, 318-320.
- RENWICK, J. A. A. & RADKE, C. D. (1981). Host plant constituents as oviposition deterrents for the Cabbage looper, *Trichoplusia ni*. *Entomologia experimentalis et applicata* **30**, 201-204.
- RILEY, R. G., SILVERSTEIN, R. M. & MOSER, J. (1974). Biological responses of *atta texana* to its alarm pheromone and the enantiomer of the pheromone. *Science* **183**, 760-762.
- ROBACKER, D. C. & HENDRY, L. B. (1977). Neral and geranial: components of the sex pheromone of the parasitic wasp, *Itopectis conquisitor*. *Journal of Chemical Ecology* **3**, 563-577.
- ROCCA, J. R., TUMLINSON, J. H., GLANCEY, B. M. & LÖFGREN, C. S. (1983). The queen recognition pheromone of *Solenopsis invicta*, preparation of (*E*)-6-(1-pentyl)-2H-pyran-2-one. *Tetrahedron Letters* **24**, 1889-1892.
- RUTTNER, F., KOENIGER, N. & VEITH, H. J. (1976). Queen substance bei eierlegenden Arbeiterinnen der Hönigbiene (*Apis mellifica* L.). *Naturwissenschaften* **63**, 434.
- SALT, G. (1937). The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts. *Proceedings of the Royal Entomological Society of London*, ser. B **122**, 57-75.
- SHOREY, H. H. (1973). Behavioural responses to insect pheromones. *Annual Review of Entomology* **18**, 349-379.
- SIMPSON, J. (1963). Queen perception by honey bee swarms. *Nature* **199**, 94-95.
- STUART, A. M. (1961*a*). Studies on the communication of alarm in the termite *Zootermopsis nevadensis* (Hagen), Isoptera. *Physiological Zoology* **36**, 85-96.
- STUART, A. M. (1961*b*). Mechanism of trail-laying in two species of termites. *Nature* **189**, 419.
- STUART, A. M. (1963). Origin of the trail in the termites *Nasutitermes corniger* and *Zootermopsis nevadensis* (Isoptera). *Physiological Zoology* **36**, 69-84.
- SUDD, J. H. (1959). Interaction between ants on a scent trail. *Nature* **183**, 1588.
- TORGERSON, R. & AKRE, R. (1970). The persistence of army ant chemical trails and their significance for the Ecitonine-Ecitonine association (Formicidae: Ecitonini). *Melandria* **5**, 1-28.
- TRANIELLO, J. F. A. (1977). Recruitment behaviour, orientation and the organization of foraging in the carpenter ant *Camponotus pennsylvanicus* De Geer (Hymenoptera: Formicidae). *Behavioural Ecology and Sociobiology* **2**, 61-79.
- TRANIELLO, J. F. A. (1981). Enemy deterrence in the recruitment strategy of termites: Soldier-organized foraging in *Nasutitermes costalis*. *Proceedings of the National Academy of Science, U.S.A.* **78**, 1976-1979.
- TRANIELLO, J. F. A. & JAYASURIYA, A. K. (1981*a*). Chemical communication in the primitive ant *Aneuretus simoni*. The role of the sternal and pygidial glands. *Journal of Chemical Ecology* **7**, 1023-1033.
- TRANIELLO, J. F. A. & JAYASURIYA, A. K. (1981*b*). The sternal gland and recruitment communication in the primitive ant *Aneuretus simoni*. *Experientia* **37**, 46-47.
- VANDER MEER, R. K. (1986). The trail pheromone complex of *Solenopsis invicta* and *Solenopsis richteri*. In *Fire Ants and Leaf Cutting Ants, Biology and Management* (ed. C. S. Löfgren and R. K. Vander Meer), pp. 201-210. Westview Press, Boulder and London.
- VARGO, E. L. & FLETCHER, D. J. C. (1986). Evidence of pheromonal queen control over the production of male and female sexuals in the fire ant *Solenopsis invicta*. *Journal of Comparative Physiology A* **159**, 741-749.

- VET, L. E. M. & VAN DER HOEVEN, R. (1984). Comparison of the behavioural response of two *Leptopilina* species (Hymenoptera: Eucolidae), living in different microhabitats, to kairomone of their host (Drosophilidae). *Netherlands Journal of Zoology* **34**, 220-227.
- VINSON, S. B., WILLIAMS, H. J., FRANKIE, G. W., WHEELER, J. W., BLUM, M. S. & COVILLE, R. E. (1982). Mandibular glands of male *Centris adani*, their function in scent marking and territorial behaviour (Hymenoptera: Anthophoridae). *Journal of Chemical Ecology* **8**, 319-327.
- VITÉ, J. P. & PITMAN, G. B. (1968). Bark beetle aggregation effects of feeding on the release of pheromones in *Dendroctonus* and *Ips*. *Nature* **218**, 169-170.
- VON FRISCH, K. (1967). *The Dance Language and Orientation of Bees*. Harvard University Press (Belknap), Cambridge, Massachusetts.
- WATKINS, J. (1964). Laboratory experiments on the trail following of army ants of the genus *Neivamyrmex* (Formicidae: Dorylinae). *Journal of the Kansas Entomological Society* **37**, 22-28.
- WHEELER, D. E. & NIJHOUT, H. F. (1984). Soldier determination in *Pheidole bicarinata*: inhibition by adult soldiers. *Journal of Insect Physiology* **30**, 127-133.
- WHITTAKER, R. H. & FEENY, P. P. (1971). Allelochemicals. Chemical interactions between species. *Science* **171**, 757-770.
- WILLIAMS, H. J., VINSON, S. B., FRANKIE, G. W., COVILLE, R. E. & IVIE, G. W. (1984). Morphology, chemical contents and possible function of the tibial gland of males of the Costa Rican solitary bees *Centris nitida* and *Centris trigonoides subtarsata* (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society* **57**, 150-54.
- WILSON, E. O. (1958). A chemical releaser of alarm and digging behaviour in the ant *Pogonomyrmex badius* (Latrielle). *Psyche* **65**, 41-51.
- WILSON, E. O. (1959). Source and possible nature of the odour trail of fire ants. *Science* **129**, 643-654.
- WILSON, E. O. (1962). Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). I. The organization of mass-foraging. *Animal Behavior* **10**, 134-147.
- WILSON, E. O. (1963). Pheromones. *Scientific American* **208**, 123-132.
- WILSON, E. O. (1971). *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- WILSON, E. O. & BOSSERT, W. H. (1963). Chemical communication among animals. *Recent Progress in Hormone Research* **19**, 673-716.
- WILSON, E. O. & PAVAN, M. (1959). Source and specificity of chemical releasers of social behaviour in the dolichoderine ants. *Psyche* **66**, 70-76.
- WILSON, E. O., DURLACH, N. I. & RETH, L. M. (1958). Chemical releasers of necrophoric behaviour in ants. *Psyche* **65**, 108-114.