netic data, in our understanding of the solar origin of magnetic fields near the orbit of the earth. The existence of a very-large-scale coherent pattern of solar magnetic fields, both across the surface of the sun and out into interplanetary space, is an extremely important finding. It promises to open new directions of research in the fields of solar activity, solar terrestrial relationships, and stellar magnetic fields.

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Ant Venoms, Attractants, and Repellents

Secretions are used by ants in attack and defense and as chemical messengers in their social organization.

G. W. K. Cavill and Phyllis L. Robertson

Venoms, attractants, and repellents are glandular secretions which enable an animal to kill or paralyze the prey that forms its food or the food of its young; to convey messages to its fellows concerning food sources, mating, and the presence of its enemies; and to discourage or prevent those enemies from interfering with its social pattern.

General observations on insect secretions are by no means novel. But it is only in the last decade, with the development of more modern techniques in chromatography and spectroscopy, in bioassay and tissue culture, that research workers have acquired some of the analytical methods needed for fundamental studies on the small, even infinitesimal, amounts of these substances. In recent reviews, Beard (*1*) has discussed insect venoms and toxins, Roth and Eisner (*2*) have considered the defensive secretions or repellents of arthropods, and Karlson and Butenandt (*3*) have discussed the insect pheromones—that is, communication secretions. More recently, Wilson and Bossert (*4*) have considered chemical communication among animals. It now seems appropriate to make a critical examination of venoms, attractants, and repellents within one specific family, the Formicidae; to assess the present level of knowledge about their source, chemical constitution, and function; and, against this background, to consider possible lines for future development.

In using the terms *venom, attractant,* and *repellent* we are able to indicate the primary function of the secretion under consideration. But whatever its primary function, other, secondary functions may also be involved which are brought into play either deliberately or automatically. For example, a sting-bearing ant will normally use its venom offensively to kill the prey it hunts down for food (Fig. 1), but if the nest is attacked the ant may use its venom defensively to repel the intruder. Again, in the presence of an enemy, an ant may produce an alarm secretion which, at low level, may act as an attractant to members of its own nest, but, at higher concentration, may have the secondary function of stimulating them to aggressive or retreat behavior, while also repelling the foe (*4*). These are limitations to our basic classification of secretions as venoms, attractants, and repellents. The terms indicate primary function only, and convey no information concerning any secondary function the secretion may possess; they constitute broad, general categories and are not mutually exclusive.

Ant Relationships

In using ants as subjects for research on venoms, attractants, and repellents, we are dealing with a group of insects in which the production of these secretions has become of prime importance. Grounds for such an opinion are to be found in the evolutionary relationship of ants to other insects, in the characteristics of the order to which ants belong, and in the lines of specialization which have developed within the group itself.

Ants (family Formicidae) belong to the order Hymenoptera of the class Insecta, an order which has originated near the peak of the insect evolutionary tree (Fig. 2). Imms states (*5*), "If the Hymenoptera be judged by their behaviour, they must be regarded as including the highest members of their class. Structurally the majority of their species have attained an advanced degree of specialization which is only surpassed by the Diptera." In general, members of the Hymenoptera are notable for extreme mobility both on the ground and in the air, for the widespread adoption of parasitic modes of existence during development, for the use of the ovipositor as a sting, and for the evolution of social existence. In the family Formicidae, dependence on a functional sting reaches a maximum and is then lost, while social existence is developed to the greatest diversity and the greatest efficiency known in the Hymenoptera.

Within the Formicidae a remarkably wide range of habits is displayed (*6, 7*), which is significant in the present context because at least some habit differences can be correlated directly with changes from group to group in the rela-

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tive importance of secretions, in their functions, and in their chemical nature. Foraging, feeding, and nesting habits, for example, are of this type. The Ponerinae and the Myrmeciinae, two of the basic subfamilies, are solitary foragers, in general are carnivorous feeders, and are equipped with powerful stings. They are ground dwellers, living in colonies that tend to be small and to show little caste differentiation. The Cerapachyinae and Dorylinae are also sting-bearing, ground-dwelling, carnivorous feeders, but the former have developed a specialized type of larval feeding, while a group-raiding method of foraging has reached a peak in the Dorylinae. The Pseudomyrmicinae show an early tendency to forsake the ground, to become arboreal, and to feed omnivorously on plant and animal materials.

Ants of the more advanced subfamily Myrmicinae follow odor trails in foraging, are also equipped with stings, and in many cases feed on plant materials. Their colonies tend to be large and show striking caste differentiation. But the highly evolved Dolichoderinae have become rather uniform in their habits of odor trailing, feeding, and nesting, and they have ceased to depend on the use of a sting for offense or defense. The Formicinae, generally accepted as constituting the most advanced subfamily, have the most diverse habits of all. Their foraging may be either solitary or along odor trails, and they may live in underground galleries, in mound nests, or in trees. They no longer use a sting, yet they are strongly protected by a secretion produced by the principal sting gland.

In the phylogenetic tree (Fig. 2), biological information such as the foregoing is coordinated with paleontological and morphological evidence to produce a general picture of evolutionary relationships within, and about, the Formicidae. This picture is built on the views of Wheeler (*6, 8*), Clark (*9*), and later workers such as Jeannel, Berland, Bernard (see *10, 11*), and Creighton (*7*). These views have been modified somewhat by Brown and Eisner (*12*), in the light of additional modern morphological studies.

Thus, ants have been chosen as experimental material for research on secretions because they belong to an insect order which is one of the most highly evolved in structure and behavior. Within this order their superfamily has attained peak development of those structures used for producing and ejecting venom. The superfamily has attained a similar level of development of social behavior, which is reflected in the production, for defense and communication, of a wide range of repellents and attractants.

The Exocrine System of Ants

Venoms, attractants, and repellents are the product of exocrine—that is, ducted—glands, which are generally ectodermal in origin, varying in complexity from single cells to zoned structures composed of glandular regions and storage sacs. The best-known, classical studies of specific exocrine glands in ants are those of Forel (*13*) and Janet (*14*). Recently, the entire exocrine system has been studied in the dolichoderine *Iridomyrmex humilis* (*15*), in three species of Ponerinae (*16*), and in *Myrmecia gulosa* (Myrmeciinae) (*17*).

The following components of the exocrine system in *Myrmecia gulosa* (Fig. 3) and in representatives of other ant subfamilies are of particular significance in relation to secretion studies: (i) The mandibular glands are a pair of sacs lying against the exoskeleton of the head between the sockets of the mandibles and the antennae, each sac opening in the base of a mandible. Biological tests indicate that their secretion acts as an alarm substance. (ii) The maxillary glands are associated with the mouthparts, but their function in the context of this discussion has not been determined. (iii) The pharyngeal glands are two clusters of strap-like lobes, opening into the pharynx near the mouth and having a digestive function. (iv) The salivary (or labial) glands are the adult successors of the larval silk glands. Each consists of a glandular filament free in the cavity of the prothorax, a salivary reservoir, and a duct uniting with its fellow at the back of the head to open in the labium. (v) The metasternal glands form two large clusters of gland cells opening into cavities of the exoskeleton of the metathorax, said by Tulloch (*18*) to play a part in determining nest odor, but regarded by later workers as of unknown function. (vi) The venom glands are a pair of filaments free in the cavity of the gaster, uniting and passing into a single, cuticular storage sac which supplies the base of the sting with venom. (vii) Dufour's gland (the accessory gland) is a single, tubular gland forming part of the venom apparatus and running into the base of the sting beside the duct from the venom sac. In the Hymenoptera in general, its secretion is thought to function as a sting lubricant (*11*), but in at least one group of ants it is used as an odor-trail substance (*19*). (viii) The dorsal abdominal glands open through the intersegmental membrane of the 6th and 7th abdominal segments. They may be analogous to the Nasanoff, or scent, glands of the bee, but in ants their function is unknown. (ix) The anal glands have not been recorded in primitive subgroups, but in highly evolved ants they may become the major glands of the gaster. They are thought to be primarily defensive in function. However, their secretion also produces alarm reactions in ants of both the same and other species (*20*).

The components of the exocrine gland system vary in their relationships from group to group of the Formicidae. For example, the venom apparatus of the bull ant, *Myrmecia gulosa* (Myrmeciinae), has a generalized pattern (*21*) which has much in common with that of other Hymenoptera, such as wasps, bees, and parasitic ichneumons. In the ponerine genera *Rhytidoponera, Bothroponera,* and *Amblyopone,* the venom apparatus is somewhat similar, but foreshadows the structural relationship in the Myrmicinae by an increase in the development of Dufour's gland.

In the Myrmicinae, with the enlargement of Dufour's gland there is a corresponding decrease in the development of the venom sac. This change in relationship is reflected in the change from carnivorous feeding on prey killed by sting-ejected venom to feeding on plants at sites marked by odor trails, generally secreted by Dufour's gland.

In the Dolichoderinae, the development of the venom glands and reservoir, and also of Dufour's gland, is overshadowed by the development of anal glands, which are not components of the venom gland complex at all. Their enlargement emphasizes the basic importance of their accepted function of alarm and defense (*6*) in the Dolichoderinae. In these ants, as in the Myrmicinae, foraging depends on the laying of odor trails, but here another gland has taken over the function. This is Pavan's gland, or the ventral gland (*15*), which may well be homologous with the third gland of the ichneumon venom apparatus (*22*).

In the Formicinae, the balance of venom-apparatus components alters again in a different direction. The venom reservoir is enlarged to become one of the major organs of the gaster; the development of Dufour's gland remains comparable to that in the lower ants, but the sting mechanism is no longer functional, and no anal glands have been reported.

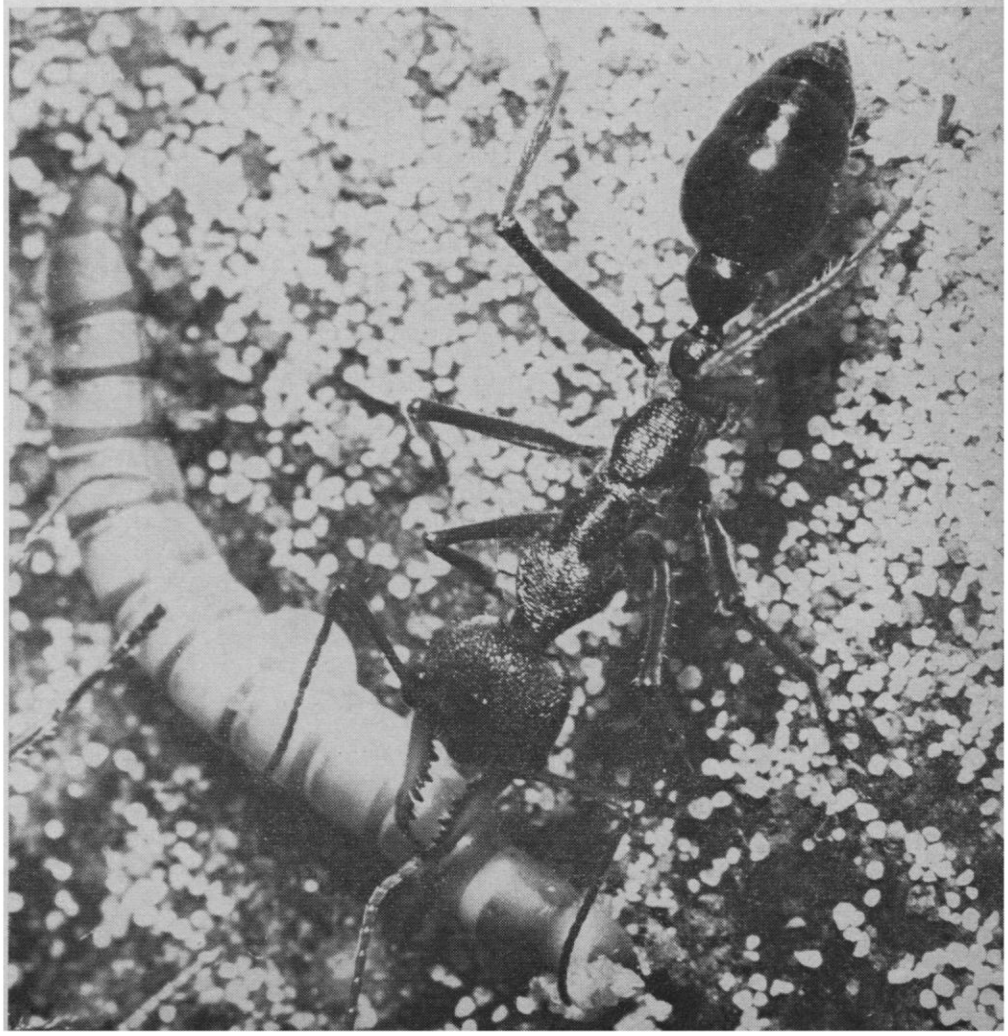
Venoms

Knowledge of the secretion of venoms by ants extends back at least to the 17th century, when the dry distillation of ants, possibly of the wood ant, *Formica rufa,* gave an acid subsequently characterized as formic. This may well be the first recorded chemical investigation of any insect secretion (*23*). Two centuries later, Forel (*13*) considered the production of formic acid by ants, and Melander and Brues (*24*) estimated the quantity per body weight in four species of Formicinae. At the same time, these authors noted its absence from six *Eciton* species (Dorylinae) and from three species of Myrmicinae. More recently, Stumper (*25*) examined 49 species of Formicinae, recording the presence of formic acid in every case. The presence of formic acid appears to characterize the subfamily Formicinae rather than the family Formicidae as a whole. Formic acid is secreted by the venom gland of the Formicinae, is stored in the venom reservoir, and is used offensively to incapacitate prey and defensively to repel intruders. Nevertheless, by virtue of the degeneration of the sting in the Formicinae and the substitution of spraying as a method of application, it falls somewhat outside Beard's definition (*1*) of a venom as "the poisonous matter which certain animals secrete and communicate by biting or stinging."

More typical venoms are found among species of the primitive subfamilies, where the sting mechanism is highly developed. But the collecting of sting-bearing ants in quantity and the extracting of their venom present many practical difficulties; these were emphasized in the course of our work on Australian bull ants of the genus *Myrmecia* (*21*). These are large ants, up to 2 centimeters long, which excavate nests, containing as many as 2000 individuals, in dry, stony ground in areas of tree roots and large rocks. The ants, which are extremely agile and pugnacious, are collected in cooled glass jars fitted with baffle lids. They are obtained at a rate of no more than 200 to 300 per collector per day. Mass-production methods for obtaining venom by electric shock, which have been developed successfully for the honey bee, *Apis mellifera* (*26*), appear not to be applicable to *Myrmecia* species. Instead, the venom reservoir is dissected out of the gaster of each ant, and the pure venom is then drained from it directly (*21*).

The venoms of sting-bearing ants which have been studied in recent years can be classified broadly as proteinaceous

Fig. 1. Workers of the bull ant, *Myrmecia gulosa* (Fabr.), attacking a meal worm. [A. Woods, School of Biological Sciences, University of New South Wales]



and nonproteinaceous. Venoms isolated from members of the subfamilies Myrmeciinae (*21*), Ponerinae (*17*), Dorylinae (*27*), and Pseudomyrmicinae (*28*) appear to be proteinaceous, although only those of the bull ants (Myrmeciinae) have been studied in any detail. The isolation of histamine from the venom of the red bull ant, *Myrmecia gulosa,* relates it to the venom of the honey bee, whereas the venom of the common wasp, *Vespa vulgaris,* contains not only histamine but also serotonin. In addition to the above physiologically active amines, the venom of the European hornet, *Vespa crabro,* contains acetylcholine (*1*). This and other quaternary bases have been found previ-

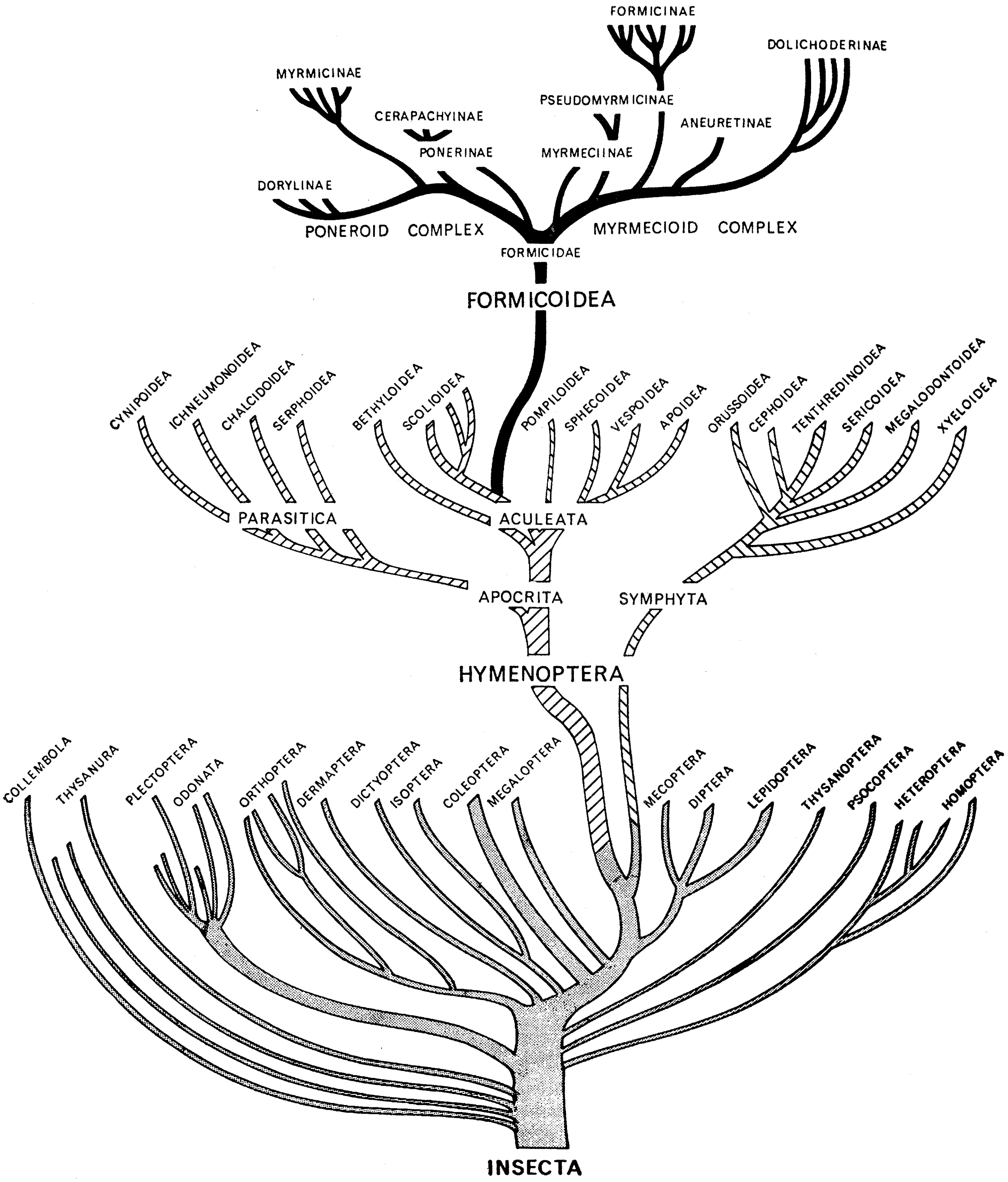


Fig. 2. Phylogenetic relationships of ants (Formicidae, Formicoidea).

ously in association with the amines in many invertebrate venoms (29). The venom of *Vespa vulgaris* also yields the low-molecular-weight peptide known as wasp kinin. None of the kinins, which have in common a variety of potent pharmacological properties (30), have been identified in bull ant venoms, although the latter do exhibit kinin-like activity (31). The amines, quaternary bases, and kinins produce pain, a function generally associated with venoms.

Myrmecia gulosa venom also exhibits hyaluronidase activity. Hyaluronidases, together with phospholipases and other enzymes, are known in the venoms of many invertebrates, where they may assist in the breakdown of host tissue and in the spreading of toxic factors. Finally, from *M. gulosa* venom, a heat-labile, hemolytic protein fraction has been characterized (21) which may correspond to the protein fraction mellitin known to be toxic in the venom of the honey bee (32). However, the specific toxins in bull ant venoms have not yet been determined, although the general characteristics that they have in common with known proteinaceous venoms are clear.

Of the nonproteinaceous venoms, that of the fire ant, *Solenopsis saevissima* (Myrmicinae), is the most extensively studied (33). The active principle derived from the venom gland is an amine, possibly $C_{35}H_{73}N$. A carbonyl compound has been detected in the accessory gland. The amine, which readily forms a hydrochloride, is responsible for the insecticidal (34) and hemolytic (35) activity of the venom. Further information on the structure of these constituents is awaited with interest.

Attractants and Repellents

Melander and Brues (24), in their discussion on the chemical nature of insect secretions, referred to "products of two kinds: defensive malodorous highly volatile liquids developed principally to repel predacious enemies and alluring sweet scented, or sweet tasting, fluids used to attract the two sexes of a species, or the individuals of a community. . . ." These odorous exocrine-gland secretions are the ones which we recognize as repellents and attractants. They differ specifically from venoms in that they originate from different glands; in the Formicidae they are known to be produced in mandibular or anal glands, or even in the accessory gland of the venom apparatus. Their function in relation to members of other species is primarily defensive rather than offensive, and their mode of delivery is by oozing or spraying, not by injection.

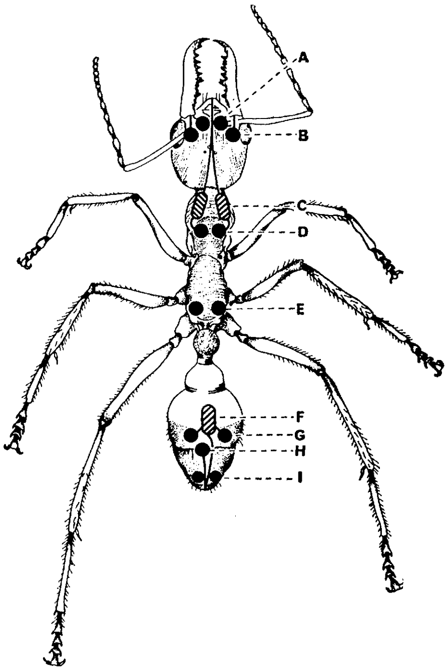


Fig. 3. Exocrine gland system of the bull ant, *Myrmecia gulosa* (Fabr.), subfamily Myrmeciinae. (*A*) Pharyngeal glands; (*B*) mandibular glands; (*C*) salivary reservoirs; (*D*) salivary glands; (*E*) metasternal glands; (*F*) venom reservoir; (*G*) venom glands; (*H*) accessory gland; (*I*) dorsal abdominal glands.

Pavan, in 1952, observed that iridomyrmecin (Fig. 4) isolated from the anal glands of the cosmopolitan Argentine ant, *Iridomyrmex humilis,* possessed insecticidal activity (36). This observation has prompted much of the current interest in the source, constitution, and function of odorous exocrine-gland secretions. It is only recently that the chemistry of these secretions has been investigated. The terpenoid ketone methylheptenone (Fig. 4) has been isolated (37) from the Australian meat ant, *Iridomyrmex detectus,* while iridomyrmecin has been established (38) as a member of the chemically interesting cyclopentanoid monoterpenes. It is primarily the defensive secretions, such as iridomyrmecin, obtainable in relatively large amounts, that have been characterized to date. The known secretions are listed in Table 1.

Reference must again be made to formic acid, which, by reason of its glandular origin and function, we have accepted as an atypical venom within the Formicinae. Of the simple aliphatic acids, both formic and acetic acid have been reported (2) to be defensive secretions—that is, repellents—in a wide range of arthropods. Formic acid has also been noted from two species of the Myrmicinae, *Myrmica rubida* and *M. riginodus* (39). Another myrmicine ant, *Myrmicaria natalensis,* has yielded a mixture of acetic, propionic, and isovaleric acids, together with some isobutyric acid (40).

While relatively simple aliphatic aldehydes, saturated and unsaturated, constitute the major components of the defensive secretions of stink bugs (41), only one of these, hex-2-enal, has been obtained from an ant, the myrmicine *Crematogaster africana* (42). On the other hand, terpenoid aldehydes and ketones are widespread among the Dolichoderinae (43). Quite recently, too, the aliphatic ketone heptan-2-one has been identified as an alarm secretion in *Iridomyrmex pruinosus* (44). This finding is of particular interest, since this is the first nonterpenoid secretion obtained from the Dolichoderinae. Previously, tridecan-2-one and undecane had been characterized in the Formicinae from the mandibular glands of two *Lasius* species (45).

Contemporary studies in Italy and Australia have resulted in the isolation of a variety of terpenoid constituents (43, 46). Of these, the cyclopentanoid monoterpenes (see Fig. 4), which are structurally related to nepetalactone, the physiologically active principle of the catmint plant, *Nepeta cataria* (47), are of major chemical, as well as biological, interest. The iridolactones, iridomyrmecin and isoiridomyrmecin, and the dialdehydes, iridodial and dolichodial, have now been described from a wide range of dolichoderine ants (43). Further, the terpenoid ketones—2-methylhept-2-en-6-one, 2-methylheptan-4-one, and 4-methylhexan-2-one—are found in association with dialdehydes.

The pattern of structural relations noted for dolichoderine ant extractives supports a biogenetic scheme of the type originally proposed by Sir Robert Robinson for the cyclopentanoid monoterpenes. He noted (48) that iridodial may arise from a Michael-type condensation of a terminally oxidized citronellal, and such oxidations are known to occur in the metabolism of terpenoids in animals (49). The biogenetic scheme proposed (43) for the dolichoderine ant extractives extends this original suggestion, in that citral, rather than citronellal, may be regarded as the basic unit (see Fig. 4). Thus, through simple chemical transformations (oxidation, reduction, and the reverse aldol reaction), citral would be converted into the volatile ketones—methylheptenone, methylheptanone, and methylhexanone—which are found in association with the insect cyclopentanoid monoterpenes. A stereospecific reduction of citral into L-citronellal, followed by a terminal oxidation and Michael addition (see *48*), would yield iridodial. This compound occupies a key position in the overall pattern, being readily transformed into the iridolactones, or into dolichodial. The biogenesis of the plant cyclopentanoid monoterpenes may involve a similar path, whence oxidation of the enol-lactol form of iridodial would yield nepetalactone.

The occurrence of dolichodial in ants, and of the structurally identical anisomorphal in phasmids (*50*)—two groups of insects which are widely separated phylogenetically—is of considerable interest. This and further observations suggest that the ability to synthesize terpenoids may be widespread among the Insecta. Again, the mandibular secretion of a formicine ant, *Lasius fuliginosus*, contains a sesquiterpenoid derivative, dendrolasin (*51*) (Fig. 5), which, biogenetically, may be derived from farnesal, the C_{15} aldehyde corresponding to citral (*52*).

However, the acyclic monoterpenoids citral and citronellal (Fig. 4) have not as yet been isolated from the Dolichoderinae, although citral is obtained from the mandibular glands of *Atta sexdens* (Myrmicinae) (*53*) and a mixture of citronellal and citral has been isolated from the mandibular secretion of *Acanthomyops claviger* (Formicinae) (see *2*). Incorporation of labeled acetate and of mevalonic acid, by feeding experiments with *Acanthomyops claviger* and injection in *Anisomorpha buprestoides*, indicates that the biosynthesis of citronellal and citral in the ants, and of anisomorphal in phasmids, follows the classical terpene biogenetic route (*54*).

Table 1. Odorous secretions of the Formicidae.

Compound*	Source	Reference
	Aliphatic	
	Formicinae:	
Formic acid	*Camponotus, Cataglyphis,* *Colobopsis, Formica,* *Lasius, Plagiolepis,* *Polyergus* spp. (49 spp. of these genera)	(*25*)
	Myrmicinae:	
Formic acid	*Myrmica rubida,*	(*39*)
	Myrmica riginodus	(*39*)
Acetic, propionic, isovaleric,and isobutyric† acids	*Myrmicaria natalensis*	(*40*)
trans-2-Hexenal	*Crematogaster africana*	(*42*)
	Dolichoderinae:	
Heptan-2-one	*Iridomyrmex pruinosus*	(*44*)
	Formicinae:	
Tridecan-2-one and undecane	*Lasius umbratus,*	(*45*)
	Lasius bicornis	(*45*)
	Terpenoid	
	Dolichoderinae:	
2-Methylhept-2-en-6-one (methylheptenone)	*Iridomyrmex detectus,*	(*37*)
	Iridomyrmex conifer,	(*58*)
	Iridomyrmex nitidiceps,	(*59*)
	Tapinoma nigerrimum	(*60*)
2-Methylheptan-4-one (propyl isobutyl ketone)	*Tapinoma nigerrimum*	(*60*)
4-Methylhexan-2-one (methylhexanone)	*Dolichoderus clarki*	(*61*)
	Myrmicinae:	
Citral	*Atta sexdens rubropilosa*	(*53*)
	Formicinae:	
Citronellal and citral	*Acanthomyops claviger*	(*62*)
	Myrmicinae:	
Limonene	*Myrmicaria natalensis*	(*40*)
	Dolichoderinae:	
Iridodial	*Iridomyrmex detectus,*	(*58, 63*)
	Iridomyrmex conifer,	(*58*)
	Iridomyrmex nitidiceps,	(*61*)
	Iridomyrmex rufoniger,	(*61*)
	Tapinoma nigerrimum	(*60*)
Iridomyrmecin	*Iridomyrmex humilis*	(*38, 64*)
Isoiridomyrmecin	*Iridomyrmex nitidus*	(*58, 65*)
Dolichodial	*Dolichoderus clarki;* additional *Dolichoderus* and *Iridomyrmex* spp.	(*59, 66*)
	Formicinae:	
Dendrolasin	*Lasius fuliginosus*	(*51, 52*)

* As total extraction procedures have been used in many cases, the glandular origin of these compounds is not necessarily known. † Trace amount.

Ant Behavior Patterns

In examining the proteinaceous and nonproteinaceous substances which ants use as venoms, and the aliphatic and terpenoid constituents which they use as attractants and repellents, consideration has been given to the system of exocrine glands from which the compounds originate. But, to carry understanding of ant secretions to the level now required, it is necessary to have concise information not only on their chemical nature and glandular origin but also on the functions they serve.

Although the compounds enumerated in the previous section and in Table 1 are grouped broadly as venoms, attractants, and repellents according to their primary functions, few of them have been subjected to detailed functional analysis. It is recognized that they play a major part in determining behavior. But research on ant behavior has tended to develop in isolation from research on ant chemistry, and has dealt little with chemically known substances.

Only during the past 10 to 15 years has particular attention been given to the influence which exocrine gland secretions exert in the shaping of behavior patterns in ants. It is now recognized that secretions play leading roles in the alarm behavior of ants, in foraging, in trail following, in group raiding and nomadism, and in the numerous processes involving care of the brood and the establishment of new colonies. Each of these activities is set in train by an initial stimulus, either physical or chemical, which leads to a complicated pattern of behavior representing the end product of a series of genetically fixed reactions. The initial stimulus is often a secretion.

The same secretion, or additional ones, may be produced at other stages in the course of the activity. Up to the present, laboratory studies of ant behavior have generally been based on the analysis of physical responses to whole gland secretions. It is clear that understanding of behavior patterns will be further advanced by resolution of the whole secretions into their chemical components. It will then become possible to pinpoint key components having an overriding effect on behavior, and to determine whether, for any one behavior pattern, there is only one such component or whether there are a number, acting successively or in concert.

Table 2 does not give an exhaustive analysis of the available information on ant behavior [this has been reviewed in detail by Wilson (*19*)]. Instead it indicates the present level of our knowledge on the interrelationship of behavior pattern, secretion, and gland, and the type of information on which this knowledge is based.

Conclusion

The Formicidae, a highly evolved family of social insects, produce secretions for offense, defense, and communication from a system of exocrine glands extending throughout the body. The most conspicuous of these are the mandibulars and salivaries, opening in the head, the metasternals in the thorax, and the complex of glands—venom, anal, Pavan's, and dorsal abdominal—in the gaster. Their secretions are produced as liquids or vapors and propelled along ducts, passing to the exterior or into body cavities such as the alimentary canal. The glands vary, from group to group of Formicidae, in their morphological development and their relationships to each other. These differences, which are reflected in group habit changes, can be correlated broadly with chemical differences in the compounds the glands secrete.

The venoms of the more primitive subfamilies—Myrmeciinae, Ponerinae, Dorylinae, and Pseudomyrmicinae—are in general proteinaceous, and correspond to the venoms of wasps and bees rather than to the secretions of higher ants. The venoms of the more highly evolved Myrmicinae are too inadequately known for generalization. In the further highly evolved subfamily, the Dolichoderinae, the venom apparatus is reduced or atrophied, and its place is taken by anal glands which produce volatile alarm and

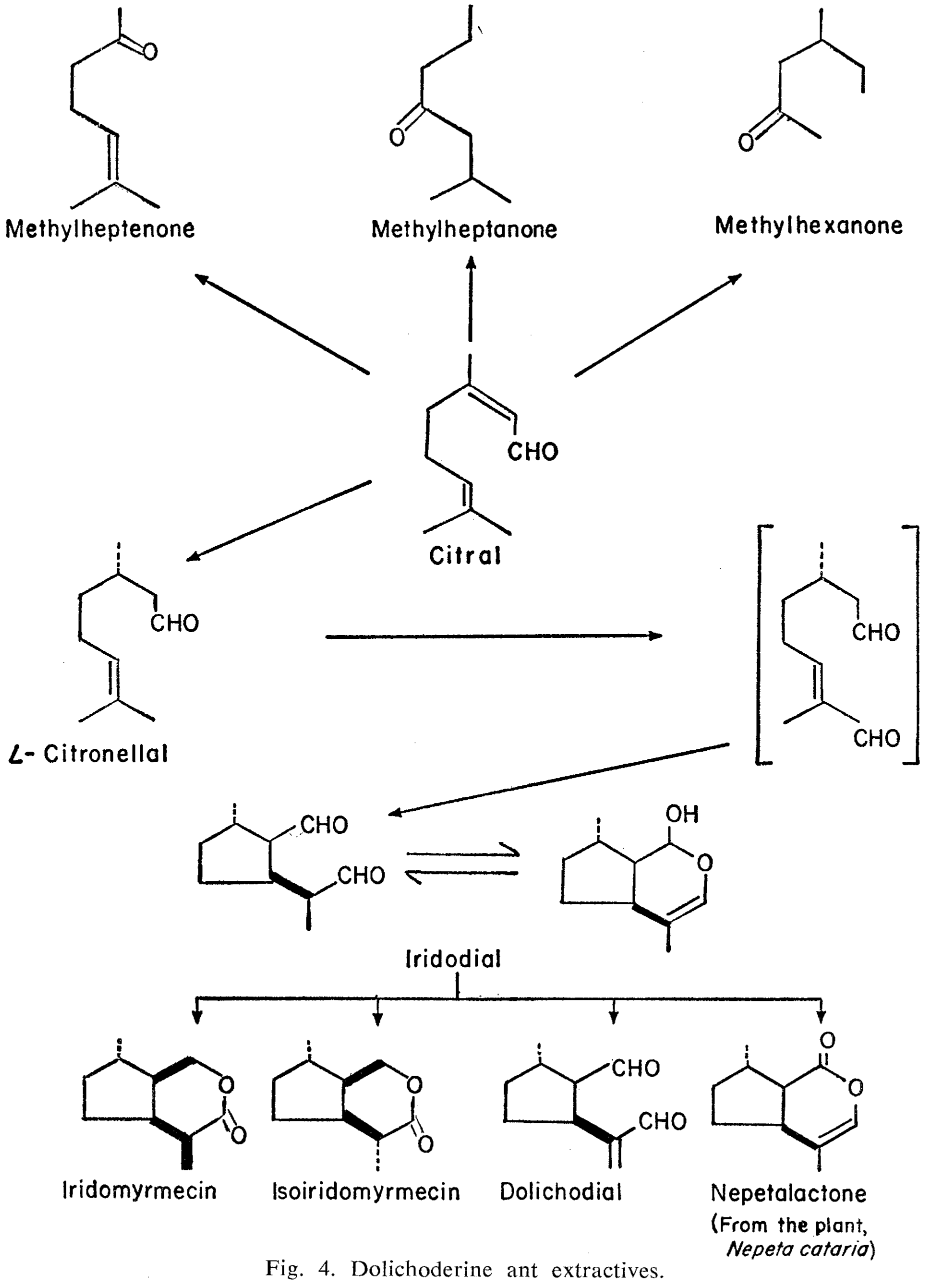
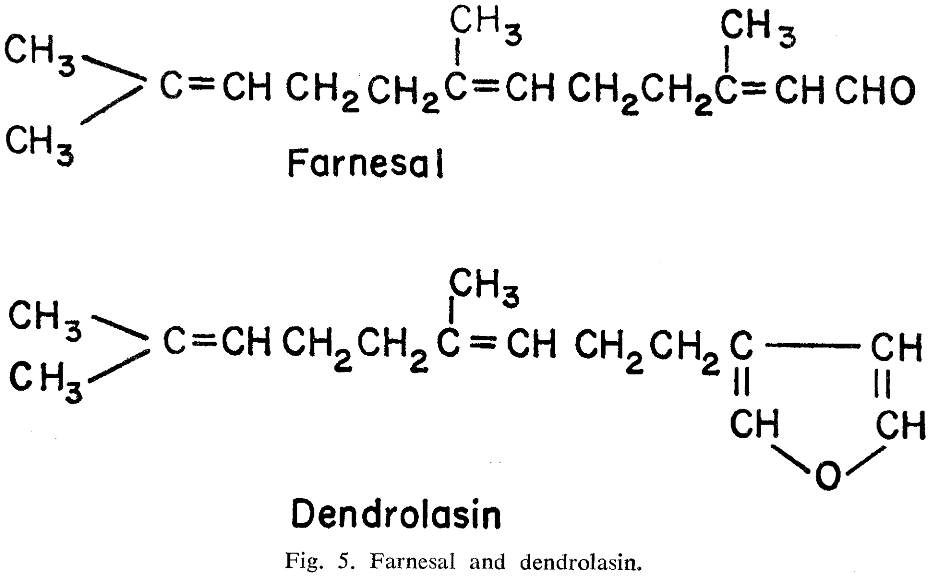


Fig. 4. Dolichoderine ant extractives.



$$\begin{matrix}CH_3\\CH_3\end{matrix}\!\!>C{=}CH\,CH_2CH_2\overset{CH_3}{\overset{|}{C}}{=}CH\,CH_2CH_2\overset{CH_3}{\overset{|}{C}}{=}CH\,CHO$$

Farnesal

$$\begin{matrix}CH_3\\CH_3\end{matrix}\!\!>C{=}CH\,CH_2CH_2\overset{CH_3}{\overset{|}{C}}{=}CH\,CH_2CH_2\begin{array}{ccc}C & \text{——} & CH\\ \| & & \|\\ CH & & CH\\ & \diagdown O \diagup & \end{array}$$

Dendrolasin

Fig. 5. Farnesal and dendrolasin.

Table 2. Ant behavior patterns.

Species	Subfamily	Behavior	Substance	Origin	Type of evidence*	Reference
Myrmecia gulosa	Myrmeciinae	Alarm frenzy		Mandibular glands	*A, F*	(*17*)
Eciton hamatum; *Nomamyrmex esenbecki;* *Labidus praedator*	Dorylinae	Alarm frenzy		Heads of workers	*B*	(*67*)
Pogonomyrmex badius	Myrmicinae	Alarm frenzy		Mandibular glands	*B, F*	(*68*)
Tapinoma sessile; *Liometopum occidentale;* *Monacis bispinosa*	Dolichoderinae	Alarm frenzy		Anal glands	*B, F*	(*20*)
Tapinoma nigerrimum	Dolichoderinae	Alarm frenzy	Methylheptenone and propyl isobutyl ketone†	Anal glands	*C, F*	(*20*)
Acanthomyops claviger	Formicinae	Alarm frenzy	Citronellal and citral	Heads, mandibular glands	*A, E, F*	(*62*)
Myrmecia gulosa	Myrmeciinae	Stinging	Proteinaceous venom	Venom reservoir	*D, E, F*	(*21*)
Solenopsis saevissima var. *richteri*	Myrmicinae	Stinging	An amine, possibly $C_{35}H_{73}N$	Venom reservoir	*E, F*	(*34*)
Solenopsis xyloni	Myrmicinae	Stinging	An amine	Venom	*E, F*	(*69*)
Leptogenys diminuta; *L. purpures;* *Onychomyrmex* spp.	Ponerinae	Group raiding			*D*	(*70*)
Cerapachys spp.; *Phyracaces* spp.; *Sphinctomyrmex* spp.	Cerapachyinae	Group raiding			*D*	(*70*)
Eciton spp.	Dorylinae	Group raiding		Venom reservoir	*A*	(*24*)
Eciton spp.	Dorylinae	Nomadism		Nomadism depends on brood secretions (gland unknown)	*B, D, F*	(*71*)
Pheidole ecitonodora; *Ph. antillensis.*	Myrmicinae	Odor-trail following			*A*	(*6*)
Solenopsis saevissima; *S. geminata;* *S. xyloni;* *Pheidole fallax*	Myrmicinae	Odor-trail following		Dufour's (accessory) gland	*B, F*	(*19, 55*)
Atta texana	Myrmicinae	Odor-trail following		Venom reservoir	*B, D, F*	(*56*)
Iridomyrmex humilis; *I. pruinosus;* *Monacis bispinosa*	Dolichoderinae	Odor-trail following		Pavan's (ventral) gland	*B, F*	(*20*)

* Types of evidence on which records are based: *A*, detection by odor; *B*, behavioral reactions to natural secretion; *C*, behavioral reactions to synthetic secretions; *D*, field observations; *E*, chemical characterization; *F*, morphological studies. † These substances, known from the anal gland of *T. nigerrimum*, produced "alarm frenzy" in *T. sessile*.

defense secretions instead of venoms. In the third highly evolved subgroup, the Formicinae, the venom glands secrete large quantities of formic acid. Here the substitution of a single carbon compound for the proteinaceous-type venoms of the more primitive groups is a remarkable chemical simplification in the evolutionary pattern.

The subfamily Myrmicinae occupies an anomalous, but in some ways a key, position in the current picture of research on formicid secretions. In morphology and habits it appears to lie somewhere between the primitive and the truly advanced subfamilies, containing elements of both and being more diverse than either. The venom of one myrmicine species has been characterized chemically, and total extractions of ants of two other species have resulted in identification of several products, including simple aliphatic acids, an unsaturated aldehyde, and a monoterpene. Much more work is necessary in this group before chemical patterns can be established.

So far, attractants and repellents have been studied principally in the Dolichoderinae and Formicinae. Of the attractants, the alarm substances are the best known chemically. They are produced in relatively large amounts by the anal glands of the Dolichoderinae and the mandibular glands of the Formicinae. The known alarm secretions are oxygenated aliphatic or terpenoid compounds of relatively low molecular weight (~150 ± 50) and high volatility. Presumably, such factors as molecular size, shape, and polarity are of major significance in the functioning not only of these alarm substances but of the odorous secretions as a whole.

As yet, nothing is known of the chemistry of a second group of attractants, the odor-trail substances, although their behavioral functions and effects are well known. These substances are produced by the ventral gland in some species of dolichoderine ants (*20*), and by either Dufour's gland (*55*) or the venom gland in certain Myrmicinae (*56*).

It is also within the highly evolved subfamilies that the defensive secretions, or repellents, have been characterized. The chemically interesting cyclopentanoid monoterpenes are produced in the anal glands of the Dolichoderinae, in association with the terpenoid ketones (see Fig. 4). The terpenoid alarm secretions from the mandibular glands of the Formicinae may also function secondarily as repellents (*4*). The terpenoid lactones and ketones have good "knockdown" insecticidal activity (*57*), a factor ensuring their efficiency in defense.

Up to the present, behavioral studies have been able to define a particular pattern of behavior, and perhaps point to the gland which controls it. Chemical research has characterized many secretions which the glands produce. But in only a few cases has a concerted effort been made to trace both the glandular origin and the behavioral function of a chemically known secretion. A major objective in future investigations should be the building up of coordinated information of this type on source, constitution, and function.

In conclusion, we would ask where further major gaps lie in our knowledge of ant venoms, attractants, and repellents. In particular, the secretions involved in development and reproduction represent an avenue of research as yet scarcely touched. These secretions help to set the general pattern of worker care of the brood, just as they set the pattern of the mating flights of sexual forms, which precede the establishment of new colonies. The substances involved may vary considerably in nature and origin, and knowledge of at least some of them may open up new fields of interest for insect control.

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