

AN EXAMINATION OF BIOCHEMICAL POLYMORPHISM IN ANTS

Robin M. Crewe (Department of Entomology, University of Natal,
Pietermaritzburg, South Africa).

In any discussion of biochemical polymorphism, two problems have to be dealt with if the discussion is to be meaningful. Firstly, a clear definition of what one means by polymorphism has to be given, and secondly, one has to restrict oneself to some particular aspect of biochemical variation in order to make the study feasible.

A universally accepted definition of polymorphism is difficult to obtain, as a perusal of the Royal Entomological society symposium on "Insect Polymorphism" reveals (Kennedy *et al.*, 1961). In general, polymorphism is taken to refer to discontinuous genetic variation within a population which produces discontinuous phenotypes (Mayr, 1970). This definition excludes the discontinuous variation found in the castes of ants from being classed as true polymorphism, and this variation has been referred to as polyphenism by Mayr (1963). Wilson (1971) suggests that it is possible to define polymorphism in a special sense for the social insects, as meaning "the coexistence of two or more functionally different castes within the same sex". This definition is justified in his view, because it is not confused with the genetic usage of the word polymorphism. While this may be true for Wilson's allometric studies of the exoskeleton of the female castes, it can give rise to confusion when studying the occurrence and biosynthesis of biological chemicals which may be present in both sexes and in the different female castes. It would seem that the most useful course to follow would be to discard any mention of biochemical polymorphism, and to talk in terms of sex specific secretions in males and females, and caste specific secretions in castes (queens and workers) of the females. Furthermore, it should be accepted that the males are not regarded as a caste as Michener (1961) has suggested. Thus what we originally called biochemical polymorphism has been resolved into firstly differences which arise as a result of sexual dimorphism, and secondly the differences which arise as a result of the differentiation of the female castes.

Since the biochemical composition of any organism is immensely complicated, some group of biological chemicals has to be selected in order to determine whether they are sex specific or caste specific. Intuitively, a group of compounds would be chosen which was not involved in primary metabolism, but was the end-product of a metabolic pathway (secondary substances as defined by Alston, 1965). Pheromones would appear to be an ideal group for such a study, since they are end-products of metabolic pathways, and are likely to be characteristic of the organism in which they are synthesised. Thus in this paper, the biochemical differences which might exist between pheromones as a result of sexual dimorphism and caste differentiation will be discussed.

Law *et al.* (1965) were the first to suggest the possibility of a

pheromonal distinction between the castes and between the sexes of ants. Two of the species they studied were subsequently shown to exhibit no differentiation in the terpenoid products of their mandibular glands (Regnier and Wilson, 1968 and 1969), while the third species, Pheidole fallax, appears to exhibit caste specificity of pheromones between the major and minor workers. The only other direct investigation of pheromone variability was that of Brand et al. (1973). In their paper they identified "caste-specific compounds" in the heads of male carpenter ants. While understanding their reluctance to use the term biochemical polymorphism, I think they erred in using the term "caste-specific" since this overlooks the distinctions between castes within a sex and sexual dimorphism. While these two papers have been provocative in that they suggested that the variation in the composition of exocrine products might be significant in understanding the functions and evolutionary development of pheromones, they did not define clearly enough the framework within which the variation takes place. By examining the composition and distribution of pheromones in terms of sexual dimorphism and caste differentiation, the underlying causes of the pheromonal variation may be revealed.

The data that is available is presented in Table 1 and is limited to those studies in which the sexes and castes of the various species were tested for the presence of pheromones. Many studies of formicid pheromones have been omitted because only the pheromones of the workers were analysed. However, using this limited evidence, some generalisations can be made.

In the case of the alarm pheromones produced in the mandibular glands of species in the genera Crematogaster, Atta, Pogonomyrmex, Acanthomyops and Lasius (see Table 1 for all data) there appears to be neither sex specificity nor caste specificity, although in the case of Acanthomyops and Lasius, the mandibular gland secretions of the queens have not been investigated, and in the case of Pogonomyrmex, the male mandibular glands also remain uninvestigated.

The mandibular gland secretions of the five species of Camponotus studied by Brand et al. (1973), show marked sex specificity, and it is interesting to note that these secretions are swarming releasers for the females, a function very different from that of the alarm pheromones found in the mandibular glands of the other ant species.

While sex specificity in mandibular gland secretions is remarkable, since the gland is common to both sexes, in the case of Dufour's gland and poison gland secretions it is to be expected, since these glands are associated with the sting which is confined to the females. In the case of the Dufour's gland secretion of Pheidole fallax, the expected sex specificity is associated with caste specificity, since Law et al. (1965) have shown that the secretions from this gland of the major and minor workers differ. Similarly in Xenomyrmex floridanus (Hölldobler, 1971) there appears to be caste specificity in that the queens have a reduced Dufour's gland, while the worker Dufour's gland is hypertrophied. Whether caste specificity occurs in the Dufour's gland

secretions of Acanthomyops claviger or Lasius alienus is not known, since the secretion from the queens has not been analysed.

In the poison gland secretions of X. floridanus there is the expected sex specificity, together with caste specificity, but in this case caste specificity seems to be the reverse of that in the Dufour's gland i.e. the females have large poison glands and the workers poison glands are relatively small.

Finally, the tibial gland trail pheromone of Crematogaster exhibits sex specificity, but apparently no caste specificity.

Of the glands listed in Table 1, the mandibular glands and probably the tibial glands are the only integumentary glands (Wheeler, 1910), and as such are the only ones present in both sexes and all the female castes. Where the mandibular glands are the source of alarm pheromone secretions, there is neither sex specificity nor caste specificity. Where the mandibular gland secretion functions in a sexual context as in Camponotus, there seems to have been a selective pressure for the production of sexually dimorphic secretions. Similarly in the case of the tibial glands, it appears that only the queens and workers have a trail pheromone. This is not surprising in view of the fact that the males are generally not involved in the colonial organisation.

Dufour's gland and the poison gland, which are reproductive glands (Wheeler, 1910), produce secretions which exhibit the expected sex specificity. This is in contrast to the secondary sex specificity which has arisen in the mandibular gland secretions of the species of Camponotus. The sex specificity in Camponotus is particularly interesting because it involves a differentiation in the secretion of a gland which is common to both sexes. It indicates clearly that the evolution of mandibular gland secretions in a number of Formicine genera has been vastly different (compare Camponotus with Lasius and Acanthomyops), and these differences may be important in trying to understand the different modes of social organisation found in ants. A similar, but more complicated situation, is found in the mandibular gland secretions of the honeybees which exhibit not only sex specificity but caste specificity as well (Blum, 1970).

Similarly, the evolution of pheromonal differences in the castes of Pheidole fallax may have important consequences in social organisation. In this species the trail pheromone is produced in the Dufour's gland of the minor workers, while the major workers produce skatole from the poison gland. In this case the differences between the worker castes seem to have developed as a result of division of labour (Polyethism) in the social milieu. A similar situation seems to have developed in Xenomyrmex floridanus, although in this case the differentiation seems to have been as a result of the reproductive functions of the queens and the necessity for trail-laying in the workers. The interesting behavioural work on Xenomyrmex needs to be substantiated by chemical analysis of the secretions of its glands, since, as Hölldobler points out, the situation may be confused by pheromonal parsimony (Blum, 1970).

Besides the possibility that pheromonal parsimony may blur

the caste specificity of pheromones (e. g. in Xenomyrmex the same compound might act as a trail pheromone in the workers and as a sex pheromone in the queens), the factors which determine caste polyethism and age polyethism (Wilson, 1971) may be responsible for caste specificity in some pheromones. The case of Pheidole fallax would seem to be a particularly good example of the caste specificity of pheromones occurring in conjunction with caste polyethism. Although the variation of pheromone composition with age (age polyethism) has been shown to occur in the case of sting and mandibular gland secretions of honeybees (Boch and Shearer, 1966 and 1967), there is no evidence that such variation occurs during the aging of ants, thus this would seem to be a fruitful area for investigation.

In summary, pheromones which are common to both sexes and all castes, usually have functions unrelated to mating or polyethism, and are generally involved in producing alarm responses. Those pheromones which either facilitate mating or are important in polyethism, would seem to be sex specific or caste specific.

Table 1 - The glandular source, function and differentiation with respect to sex and caste of a number of formicid enocrine secretions

Species	Nature of Pheromone	Sex specific	Caste specific	Reference
<u>A. Mandibular glands</u>				
<u>Atta texana</u>	alarm	No	No	Moser <u>et al</u> 1968
<u>Crematogaster peringueyi</u>	alarm	No	No	Crewe <u>et al</u> 1970
<u>C. ashmeadi</u>	alarm	No	No	
<u>C. clara</u>	alarm	No	No	Crewe - unpub. data
<u>Pogonomyrmex badius</u>	alarm	?	No	
<u>Acanthomyops claviger</u>	alarm	No	?	Wilson 1971
<u>Lasius alienus</u>	alarm	No	?	Wilson 1971
<u>Camponotus noveboracensis</u>				
<u>C. pennsylvanicus</u>				
<u>C. nearcticus</u>	swarm releaser	Yes ♂	-	Brand <u>et al</u> 1973
<u>C. rasilis</u>				
<u>C. subbarbatus</u>				
<u>B. Dufour's Gland</u>				
<u>Pheidole fallax</u>	trail substance	Yes ♀	Yes	Law <u>et al</u> 1965

Table 1 - continued

Species	Nature of Pheromone	Sex specific	Caste specific	Reference
<u>A. claviger</u>	alarm	Yes ♀	?	Regnier & Wilson 1968
<u>L. alienus</u>	alarm	Yes ♀	?	Regnier & Wilson 1969
<u>Xenomyrmex floridanus</u>	trail pheromone	Yes ♀	Yes	Holldobler 1971
C. <u>Poison Gland</u>				
<u>X. floridanus</u>	sex pheromone	Yes ♀	Yes	Holldobler 1971
<u>P. fallax</u>	defensive secretion	Yes ♀	Yes	Law <u>et al</u> (1965)
D. <u>Tibial Gland</u>				
<u>Crematogaster peringueyi</u>	trail substance	Yes ♀	No	Unpub. data

♂ ♀ - These symbols indicate the sex in which the secretion is localised. In the case of the females this can be either queens or workers.

LITERATURE CITED

- ALSTON, R. E. (1965) Comparison of the importance of basic metabolites, secondary compounds and macromolecules in systematic studies. Lloydia 28, 300-312.
- BLUM, M. S. (1970) The chemical basis of insect sociality. In "Chemicals controlling insect behaviour" Ed. M. Beroza, (Academic Press, New York, p. 61-94)
- BOCH, R. and SHEARER, D. A. (1966) Iso-pentyl acetate in stings of honeybees of different ages. J. apicult. Res. 5: 65-70.
- BOCH, R. and SHEARER, D. A. (1967) 2-Heptanone and 10-hydroxy-trans-dec-2-enoic acid in the mandibular glands of worker honey bees of different ages. Z. vergl. Physiol. 54: 1-11
- BRAND, J. M., DUFFIELD, R. M., MacCONNELL, J. G., BLUM, M. S. and FALES, H. M. (1973) Caste-specific compounds in male carpenter ants. Science, N. Y. 179: 388-389
- CREWE, R. M., BRAND, J. M., FLETCHER, D. J. C. and EGGERS, S. H. (1970) The mandibular gland chemistry of some South African species of Crematogaster (Hymenoptera: Formicidae). J. Ga. ent. Soc. 5: 42-47
- HOLLDOLBLER, B. (1971) Sex pheromone in the ant Xenomyrmex floridanus. J. Insect Physiol. 17: 1497-1499
- KENNEDY, J. S., ed. (1961) Insect polymorphism. Symp. R. ent. Soc., Lond. No. 1: 1-115
- LAW, J. H., WILSON, E. O. and McCLOSKEY, J. A. (1965) Biochemical polymorphism in ants. Science, N. Y. 149: 544-545
- MAYR, E. (1963) Animal species and evolution. (Belknap Press, Harvard University Press, Cambridge. 797 pp.)
- MAYR, E. (1970) Populations, species and evolution. (Belknap Press, Harvard University Press, Cambridge. 453 pp.)
- MICHENER, C. D. (1961) Social polymorphism in Hymenoptera. Symp. R. ent. Soc., Lond. No. 1: 43-56
- MOSER, J. C., BROWNLEE, R. C. and SILVERSTEIN, R. (1968) Alarm pheromones of the ant Atta texana. J. Insect Physiol. 14: 529-535
- REGNIER, F. E. and WILSON, E. O. (1968) The alarm-defense system of the ant Acanthomyops claviger. J. Insect Physiol. 14: 955-970
- REGNIER, F. E. and WILSON, E. O. (1969) The alarm-defense system of the ant Lasius alienus. J. Insect Physiol. 15: 893-898
- WHEELER, W. M. (1910) Ants, their structure, development and behaviour (Columbia University Press, New York. 663 pp.)
- WILSON, E. O. (1971) The Insect Societies. (Belknap Press, Harvard University Press, Cambridge. 548 pp.)