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VOLATILE MARKING SECRETIONS FROM THE LABIAL GLAND OF NORTH EUROPEAN *PYROBOMBUS* D. T. MALES (HYMENOPTERA, APIDAE)

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SUMMARY

The volatile secretions produced by the labial gland in male bumble-bees, *Bombus* Latr., belonging to the subgenus *Pyrobombus* D. T., have been studied in six species : *B. cingulatus* Wahlb., *B. hypnorum* L., *B. jonellus* K., *B. pratorum* L., *B. lapponicus* Fabr. and *B. scandinavicus* Friese. Totally, 181 specimens have been analyzed. The secretions, which are used for marking different objects along the flight-route, have been analyzed by capillary gas chromatography and combined capillary gas chromatography/mass spectrometry. Isoprenoids and fatty acid derivates together make up the secretions. The former group of compounds dominates the marking secretions from the species studied, with the exception of *B. scandinavicus*. The compositions of the secretions are characteristic for each species.

RÉSUMÉ

Les sécrétions volatiles de marquage de la glande labiale des mâles *Pyrobombus* D. T. (Hymenoptera, Apidae) d'Europe du Nord.

Les sécrétions volatiles de la glande labiale chez les bourdons mâles *Bombus* Latr., appartenant au sous-genre *Pyrobombus* D. T., ont été étudiées chez six espèces : *B. cingulatus* Wahlb., *B. hypnorum* L., *B. jonellus* K., *B. pratorum* L., *B, lapponicus* Fabr. et *B. scandinavicus* Friese. Au total, 181 spécimens ont été analysés. Les sécrétions, qui servent à marquer différents objets sur le trajet du vol territorial, ont été soumises à la chromatographie en phase gazeuse (colonne capillaire) et à l'analyse combinée par chromatographie en phase gazeuse et spectrométrie de masse. Les sécrétions sont composées d'isoprénoïdes et de dérivés d'acides gras. Les isoprénoïdes sont les composés dominants, sauf chez l'espèce *B. scandinavicus*. Les compositions des sécrétions sont caractéristiques pour chaque espèce.

INTRODUCTION

The large and diverse subgenus *Pyrobombus* D. T. has a holarctic distribution. About twentyfive species are recognized in the western hemisphere (MILLIRON, 1971) and nine in western Europe. Six species occur in Fennoscandia, *B. cingulatus* Wahlb., *B. hypnorum* L., *B. jonellus* K., *B. pratorum* L., *B. lapponicus* Fabr. and *B. scandinavicus* Friese.

The marking secretions of the males originate from the cephalic part of the labial gland (KULLENBERG *et al.*, 1973). The results from the nineteen species of *Bombus* already reported shows that the mixture of components forms a species-specific secretion (BERGSTRÖM *et al.*, 1973; BERGSTRÖM and SVENSSON, 1973 *a, b*; CALAM, 1969; KULLENBERG *et al.*, 1970).

The perfume is used by the males when they make their route-flights. Along the route the males stop at different places and mark leaves, twigs, grass, etc. with their perfume. The different elements of behaviour performed during the route-flight activities are found to be species-specific (HAAS, 1949; SVENSSON, unpubl.).

Species of the subgenus *Pyrobombus* emerge early from their hibernation quarters and form small colonies which reach their maximum size early in the season (FREE and BUTLER, 1959; WÓJTOWSKI, 1963). Several authors have discussed a double generation for some species (ALFKEN, 1913; MEIDELL, 1968; HOBBS, 1967). HOBBS (1964) has suggested that *Pyrobombus* is a link between the primitive group *Odontobombus* Krüger (pocket-makers) and *Anodontobombus* Krüger (pollenstorers), based on brood-rearing studies.

In this study we report new analytical results from *B. cingulatus, B. hypnorum* and *B. pratorum* and compare and summarize the studies on the chemical composition of the marking secretions of north European species within the subgenus *Pyrobombus*. The secretions of *B. hypnorum* and *B. pratorum* are compared from two different populations, about 1.300 kilometers apart.

MATERIAL AND METHODS

Taxonomy and distribution.

B. cingulatus was earlier treated, except by its author, as a subspecies of *B. hypnorum* until REINIG (1936) re-established its specific rank. A similar taxonomic confusion earlier existed between *B. pratorum* and *B. jonellus*, the latter being regarded as a subspecies. From southern Europe, the three closely allied species *B. pratorum, B. brodmannicus* Vogt and *B. pyrenaeus* Pér., form another such relationship. Recently, TKALCU (1973) demonstrated their specificity. Earlier studies on *B. lapponicus* (SVENSSON, 1973) showed that males of the two allegged subspecies could be distinguished, both by morphological criteria and by the composition of the marking secretion. In later studies on specimens from nests, where the males could be used as reference to the identification

of queens, differences between the queens were found (SVENSSON, to be publ.). On account of morphological, physiological and behavioral characteristics, the two Fennoscandian subspecies of *B. lapponicus* were raised to the rank of full species, viz. *B. lapponicus* and *B.* « *scandinavicus* ». The nomenclature of *B. scandinavicus* remains uncertain until the status of the south European forms of *B.* « *lapponicus* » is established.

The species studied are all widely distributed in an East-West direction except *B. scandinavicus* which seems to exhibit an European boreo-alpine distribution. The distribution of species studied in Fennoscandia is shown by LØKEN (1973).

B. hypnorum and *B. pratorum* are both common in the whole of Fennoscandia, likewise *B. jonellus* which is, however, more abundant in the northern parts. *B. cingulatus* is restricted to the northern coniferous forests and *B. lapponicus* and *B. scandinavicus* are most often found in and close to alpine and subalpine areas. *B. scandinavicus* does not seem to occur in the adjacent coniferous forests.

The taxonomic literature consulted for identification during the early studies was : ELFVING (1960), KNECHTEL (1955), RICHARDS (1927) and later LØKEN (1973). The subgeneric classification follows RICHARDS (1968).

Collection of the bees.

The bees were collected in the northern part of Sweden. Torne Lappmark (in the vicinity of Abisko and Kiruna) and on Öland, an island in the southern Baltic. A full account of the collection data together with the chemical analysis is given in Table I. The males were collected on different occasions during their flight period and usually during several years. The preparation of the bees for chemical analysis has been discribed earlier (BERGSTRÖM and SVENSSON, 1973 *a*). After analysis the bees analyzed are pinned, labelled and kept at the Department of Entomology, Uppsala University.

Analysed material.

The marking secretion emanates from the labial gland (cf. KULLENBERG *et al.*, 1973), the cephalic part of which occupies more than half the volume of the head, see figure 1 *a*. Whole heads, decapitated alive, were put in hexane or diethylether and glands were also prepared and put in hexane. Glands from living individuals were analyzed in a fresh state. On these occasions a part of the glands was sufficient for the direct chemical analysis, see figure 1 *b*. *B. lapponicus* and *B. scandinavicus* males have been studied individually in order to get an absolute correlation between the chemical composition of the secretion and the morphology (cf. BERGSTRÖM and SVENSSON, 1973 *a*; SVENSSON, 1973).

Analytical techniques.

The techniques employed in these analyses have been described earlier (STÄLLBERG-STENHAGEN, 1972; BERGSTRÖM, 1973 and STÄLLBERG-STENHAGEN *et al.*, 1973). Introduction of volatile material into the gas chromatograph was made via a pre-column system. Glass capillary columns were used, both unpolar Silicone columns (OV-101 and SE-30) and polar FFAP columns. Both direct coupled capillary gas chromatography/mass spectrometry, using a LKB 2091 instrument, and separate capillary gas chromatography (flame ionization detector) were employed. In the identification we rely to a large extent on data accumulated in our laboratory from a number of reference compounds. In the analyses thin layer chromatographic preseparation was applied together with comparative olfactory examination of extract and fractions. Original analytical data regarding the objects reported here are kept at the Ecological Station on Öland.

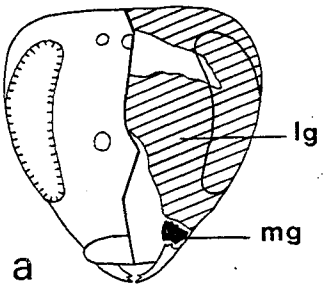

FIG. 1. — The position *(a)* and the general appearance of a part of the labial gland's cephalic part *(b)* of a *Bombus lapponicus* male. mg : mandibular gland; lg : labial gland. Scale in 1 *b* : 0.1 mm (SEM-photo 1 *b* : L. Ågren).

FIG. 1. — Position *(a)* et apparence générale d'une partie de la région céphalique *(b)* de la glande labiale du mâle de *Bombus lapponicus*. mg : glande mandibulaire; lg : glande labiale. Echelle en 1 *b* : 0,1 mm.

RESULTS OF CHEMICAL ANALYSES

Bombus cingulatus Wahlberg.

Figure 2 shows a typical capillary gas chromatogram (total ion current detection) of the volatile components from a minor part of the labial gland of one *B. cingulatus* male. The two larger peaks, components 1 and 2, are identified as 2,3-dihydro-6-*trans*-farnesol and all-*trans*-farnesol, respectively. These identifications are based on capillary gas chromatographic retention indices, relative to straight chain saturated hydrocarbons, and mass spectra. The data were compared with those of reference compounds. 2,3-dihydro-6-*trans*-farnesol was synthesized stereospecifically earlier (STÄLLBERG-STENHAGEN, S., et *al.*, 1972).

Material of this species has been collected in northern Sweden and analysed both in 1974 and 1975, see Table I, with very good agreement between the separate analyses.

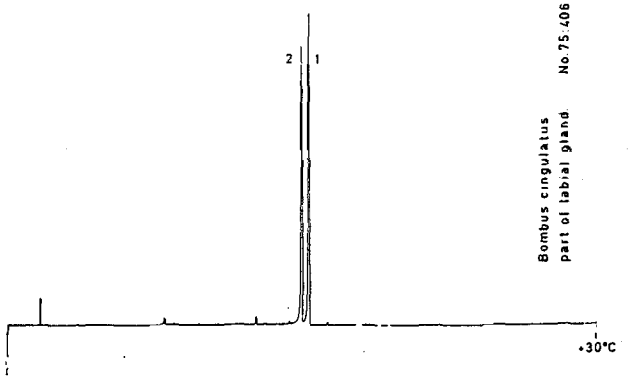

FIG. 2. — Capillary gas chromatogram showing volatile compounds from a part of the labial gland of a *Bombus cingulatus* male.

FIG. 2. — Chromatogramme en phase gazeuse sur colonnes capillaires des composés volatils d'une partie de la glande labiale d'un mâle *Bombus cingulatus*.

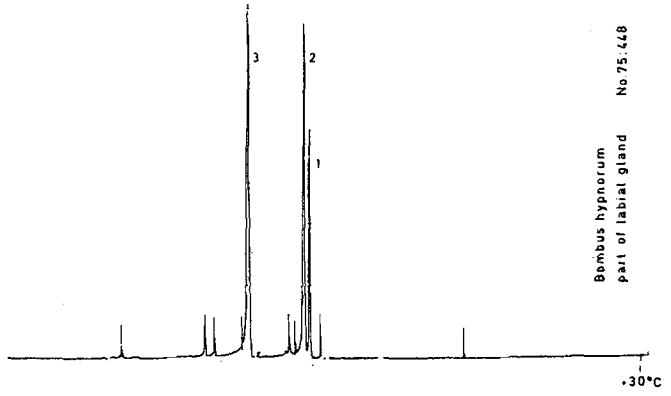

FIG. 3. — Capillary gas chromatogram which shows the major components from a part of the labial gland of a male *Bombus hypnorum*.

FIG. 3. — Chromatogramme en phase gazeuse sur colonnes capillaires montrant les constituants majeurs d'une partie de la glande labiale d'un mâle *Bombus hypnorum*.

Some minor components have also been identified. Thus, two isomers of farnesene are present in the secretion and also minor amounts of 2,3-dihydro-6-*trans*-farnesal and dodecanol.

B. hypnorum Linnaeus.

This species was analysed on several occasions in 1966 and in 1968-1972 and 1975 with material collected on Öland and in 1973 and 1975 on material collected at Abisko, see Table I. A variation in the proportion of the major diterpenic components has been noted. This variation seems to be in time rather

TABLE I. — Collection data and chemical analysis performed of *Pyrobombus* species studied. CGC, capillary gas chromatography; GC/MS, capillary gas chromatography/mass spectrometry; TLC, thin layer chromatography.

TABLEAU I. — Ensemble des données et méthodes d'analyse utilisées pour l'étude des diverses espèces de *Pyrobombus*. CGC : chromatographie en phase gazeuse sur colonnes capillaires; GC/MS : chromatographie en phase gazeuse/spectrométrie de masse; TLC : chromatographie en couche mince.

Species	Locality	Date of collection	Number of individuals	Analytical methods
B. cingulatus	T. Lpm. Laxforsen	22/7 1974	1	CGC; GC/MS
»	»	»	1	CGC; GC/MS
»	»	»	1	CGC; GC/MS
»		31/7 1974	1	CGC; GC/MS
»	»	5/8 1975	1	GC/MS
»	»	5/8 1975	4	GC/MS
H. hypnorum	T. Lpm. Abisko	26/7 1973	2	CGC
»	»	31/7 1973	1	CGC
»	»	25/8 1975	1	GC/MS
»	Öl. Torslunda	1966	2	GC/MS
»	»	1968	3	GC/MS
»	»	1969	5	GC/MS
»	»	1970	2	GC/MS
»	»	1971	5	CGC
»	»	1972	18	CGC
»	»	1975	1	GC/MS
B. jonellus	T. Lpm. Abisko	26/8 1975	7	GC/MS
»	» Laxforsen	5/8 1975	1	GC/MS
»	(from Bergström and Svensson,	1973 *b*)	5	CGC; GC/MS
B. lapponicus	T. Lpm. Laxforsen	5/8 1975	1	GC/MS
»	»	5/8 1975	1	CGC; GC/MS
»	(from Bergström and Svensson,	1973 *a*)	24	CGC; GC/MS
B. scandinavicus	T. Lpm. Abisko	10/8 1975	1	GC/MS
»	»	19/7 1973	10	TLC
»	»	31/7 1973	6	TLC
»	(from Bergström and Svensson,	1973 *a*)	10	CGC; GC/MS
B. pratorum	T. Lpm Abisko	11/7 1972	1	GC/MS
»	» Låktatjåkka	4/8 1973	3	CGC
»	Öl. Torslunda	1965	28	GC/MS
»	»	1967	5	GC/MS
»	»	1968	1	GC/MS
»	»	1969	11	GC/MS
»	»	1971	14	CGC
»	»	18/7 1976	1	GC/MS
»	»	11/8 1976	1	GC/MS

than depending on place of collection. There are no marked differences between the compositions of secretions from Öland and Abisko.

The major component is all-*trans*-geranylcitronellol (see chromatogram from part of the labial gland in figure 3) component 3. In a few of the analyses all-*trans*-geranylgeranyl acetate has been found to be a major component. Minor components identified are a hexadecenol (component 1) and hexadecanol

(component 2). A preliminary account of the results of analyses of this and some other species was published in 1970 (KULLENBERG *et al.*, 1970).

B. jonellus Kirby.

Results from analyses of this species have been reported earlier (BERGSTRÖM and SVENSSON, 1973 *b*). Some additional analyses were performed, see Table I. The major volatile marking substances of *B. jonellus* are 2,3-dihydro-6-*trans*-farnesol with the corresponding aldehyde as a minor component. Figure 4

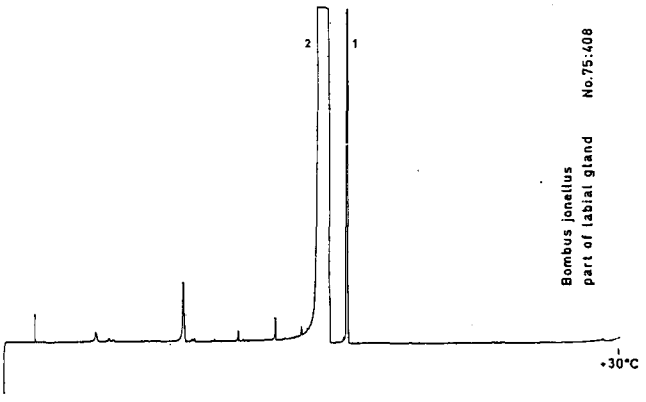

FIG. 4. — Capillary gas chromatogram of volatile compounds from a part of a labial gland of a *Bombus jonellus* male.

FIG. 4. — Chromatogramme en phase gazeuse sur colonnes capillaires des composés volatils d'une partie d'une glande labiale d'un mâle *Bombus jonellus*.

shows the proportion between these compounds in the natural secretion. The gas chromatogram was obtained from a small part of one labial gland. Material of this species was collected in the northern part of Sweden (see (Table I).

B. lapponicus Fabricius and *B. scandinavicus* Friese.

These two species have also been treated in detail in a earlier publication (BERGSTRÖM and SVENSSON, 1973 *a*). There we demonstrated the large and constant difference between the marking secretions of the two forms *lapponicus* and *scandinavicus* and put the question whether these forms should be recognized as separate species.

B. lapponicus is dominated by geranylcitronellol (component 2) see capillary gas chromatogram in figure 5. Hexadecanol (component 1), is present in appreciable amounts and octadecyl acetate and eicosyl acetate as minor components. *B. scandinavicus*, capillary gas chromatogram in figure 6, has a hexadecenyl acetate as the major constituent (component 2). In addition it has as minor components hexadecanol (component 1) and hexadecyl acetate (component 3).

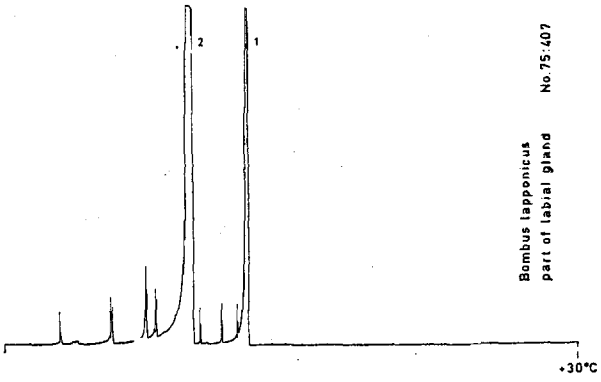

FIG. 5. — Capillary gas chromatogram of volatile compounds from the labial gland of a *Bombus lapponicus* male.

FIG. 5. — Chromatogramme en phase gazeuse sur colonnes capillaires des composés volatils de la glande labiale de mâles *Bombus lapponicus*.

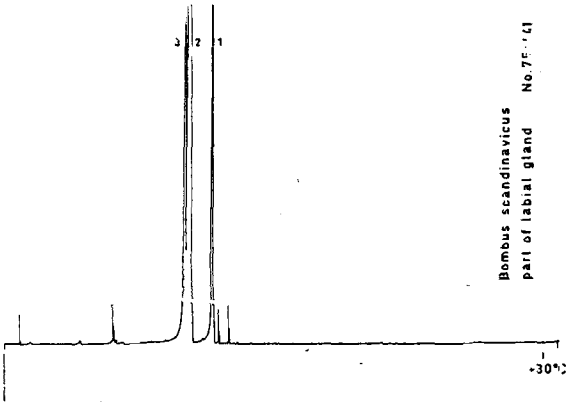

FIG. 6. — Capillary gas chromatogram of volatile compounds from the labial gland of a *Bombus scandinavicus* male.

FIG. 6. — Chromatogramme en phase gazeuse sur colonnes capillaires des composés volatils de la glande labiale de mâles *Bombus scandinavicus*.

B. pratorum Linnaeus.

B. pratorum has been analysed on several occasions, starting in 1965, 1967-1969 and again in 1971 and 1976 with material collected on Öland (see Table I). Invariably, smaller amounts of volatile material have been found in this species than in the other species investigated.

B. pratorum is a species rich in isoprenoid components. Thus the secretion contains geraniol, geranyl acetate, citronellol, citronellyl acetate, all-*trans*-farnesol (main component), all-*trans*-farnesyl acetate, geranylgeraniol and geranylgeranyl acetate. Preliminary results on this species were given in an earlier

TABLE II. — Volatile components (dominant components in bold figures) of the labial gland secretion in six species of *Pyrobombus*. The numbers correspond to the major components in figures 2-7. Minor components are indicated by ×.

TABLEAU II. — Constituants volatils (le ou les constituants dominants sont entourés par un cercle) de la sécrétion de la glande labiale chez six espèces de *Pyrobombus*. Les numéros correspondent aux constituants majeurs des figures 2-8. Les constituants mineurs sont indiqués par un ×.

	ISOPRENOIDS	Geraniol	Citronellol	Geranyl acetate	Citronellyl acetate	Farnesene isomers	All-*trans*-farnesol	2,3-Dihydro-6-*trans*-farnesol	» -al	All-*trans*-farnesyl acetate	Geranylgeraniol	Geranylcitronellol	Geranylgeranyl acetate	ACETOGENINS	Dodecanol	Hexadecenol	Hexadecanol	Hexadecenyl acetate	Hexadecyl acetate	Octadecenol	Octadecyl acetate	Eicosenyl acetate
B. cingulatus						×	**2**	**1**	×						×							
B. hypnorum												**3**	×			**1**	**2**					
B. jonellus								**2**	**1**													
B. lapponicus												**2**					**1**				×	×
B. scandinavicus																	**1**	**2**	**3**			
B. pratorum		×	×	×	×	×	**1**			**2**	×		**5**				**3**			**4**		

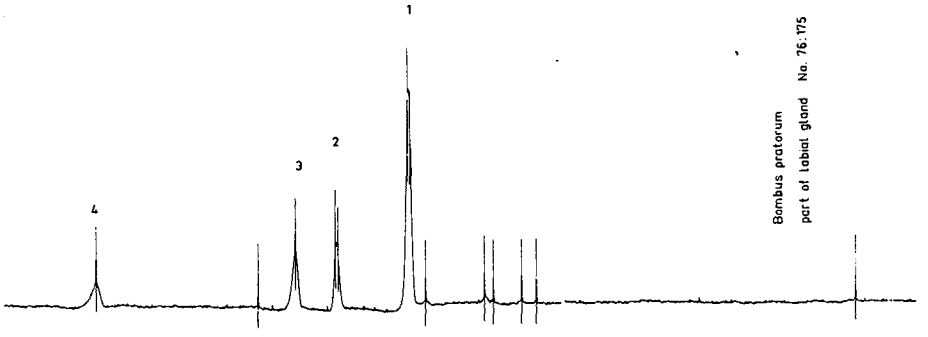

FIG. 7. — Capillary gas chromatogram of volatile compounds from the labial gland of a *Bombus pratorum* male.

FIG. 7. — Chromatogramme en phase gazeuse sur colonnes capillaires des composés volatils de la glande labiale de mâles *Bombus pratorum*.

report (KULLENBERG *et al.*, 1970). A variation in the proportion between the isoprenoid components during the season has been noted. This is also true for some other species but the phenomenon has not yet been studied systematically. Thus in *B. pratorum* geranylgeranyl acetate and traces of geranylgeraniol seem to be present in the marking secretion towards the end of the season but absent at the beginning of the flight period. In figure 7 a capillary gas chromatogram of volatile material from a part of the labial gland of an individual (collected 11 Aug. 1976) is shown. The main component (n° 1) was identified as all-*trans*-farnesol. The corresponding acetate (n° 2) is present together with hexadecanol (n° 3) and a octadecenol (n° 4) in appreciable amounts.

B. pratorum was also collected at Abisko (see Table I) in 1972 and 1973. The results of analyses show a large degree of similarity between material from the two populations.

DISCUSSION

The present report gives the results from analysis of the marking secretions of 6 species of the subgenus *Pyrobombus*. This enables us to make some comparisions between them. Inside this group all species, with the exception of *B. scandinavicus*, have sesqui- or diterpenes as their major components. Only a few non-isoprenoid compounds are present. The analytical findings have been summarized in Table II. It is clear from an inspection of this table that all secretions are species-specific. *B. scandinavicus* stands out particularly by its total absence of isoprenoid compounds and *B. pratorum* by its very complex secretion. The resemblance in habitus between *B. cingulatus* and *B. hypnorum* has no chemical correspondence. Instead there is a great chemical resemblance between *B. hypnorum* and *B. lapponicus*. These two species are morphologically well separated and use different heights above the ground when performing their route-flights (KULLENBERG, personal communication; SVENSSON, unpubl.). When studying the genitalia of *Pyrobombus* males, KRÜGER (1942) concluded : « Die Unterschiede in den männlichen Genitalanhängen sind bei allen untersuchten Arten so gering dass sie *nicht als isolierend Faktoren* für die Artentstehung in Betracht kommen können ». If this is so, that the similar features of the genitalia could permit successful copulations, the isolation will be maintained in another way. Regarding the males, the cephalic marking secretions are supposed to function as territory recognition marks, territorial flight stimulators and copulation excitants (BRINGER, 1973; KULLENBERG, 1956, 1973; KULLENBERG and BERGSTRÖM, 1975). The species-specific perfume and route-flight behaviour may function as a part of the isolation mechanism. It seems as if the morphologically closely related species has evolved a larger difference in the composition of the secretion than the well separated species.

Up to now results have been reported by us for 18 species. These represent 8 subgenera. In addition, Calam has reported on *B. ruderarius* Müll. From the

genus *Psithyrus* Lep., cuckoo-bumblebees, six species have been analyzed. They were also found to have a similar species specific composition of the marking secretion as in the genus *Bombus* (KULLENBERG *et al.*, 1970). With this background one can say that the members of the subgenus *Pyrobombus* fall into the general picture of species-specific marking secretions made up of different combinations of acetogenins (fatty acid derivatives) and isoprenoids (terpenes). A comparison between the subgenera *Pyrobombus* and *Bombus* Latr. (s. s.) for instance, reveals that while members of the latter group predominantly seem to have evolved the acetogenic way of biosynthesis, the *Pyrobombus* group with the exception of *B. scandinavicus* utilizes mainly the isoprenoids pathway.

If we consider the generic division of *Bombus* proposed by Tkalců (1972, 1974 and in several other papers), *Pyrobombus* is regarded as a genus and divided into several subgenera. In Fennoscandia three subgenera are represented, viz., *Pyrobombus* (s. s.), *Melanobombus* D.-T. and *Cullumanobombus* Vogt. With this background, three further species are added to the genus *Pyrobombus* already chemically analysed, *P. (Pyrobombus) soroeensis* Fabr., *P. (Melanobombus) lapidarius* L. and *P. (Cullumanobombus) cullumanus* K. (KULLENBERG *et al.*, 1970). These three species, compared with the six species treated in this paper (*Pyrobombus* subgenus *Pyrobombus*, sensu Tkalců), coincide as regards the main groups of chemical compounds with the isoprenoid-group, except for *lapidarius* which has chosen the acetogenic way as in *scandinavicus*.

Thus, there seems to be a relationship regarding the biosynthesis of volatile substances — with some exceptions — inside a certain subgenus/genus.

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