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TAXONOMIC POTENTIAL OF THE CHEMICAL CONSTITUENTS IN THE CEPHALIC MARKING SECRETIONS OF *BOMBUS* AND *PSITHYRUS* SPECIES (HYMENOPTERA, APIDAE) : A NUMERICAL TAXONOMIC STUDY

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SUMMARY

A tentative study of the chemotaxonomic potential of the cephalic marking secretions of *Bombus* and *Psithyrus* species is presented, using numerical taxonomy methods. Thirty one chemical compounds previously reported by other authors were used as taxonomic characters for a sample of 13 species of *Bombus* and 6 of *Psithyrus*. The species of these two genera appeared mixed in those dendrograms which include the whole sample, thus suggesting a selection of *Psithyrus* for similarity to *Bombus* in order to improve their ability for parasitization, rather than phyletic relationships between both genera.

Cluster analysis of *Bombus* species showed a quite clean discrimination between the two classical sections *Odontobombus* and *Anodontobombus* and, in some cases, the results were consistent with classical classification at lower levels, for example, in the species of the *Terrestribombus* group.

INTRODUCTION

The classification, systematics and evolutionary relationships of bumblebees *(Bombus)* and their parasitic species of cuckoobumblebees *(Psithyrus)* have been the object of considerable recent research. Nevertheless, some major questions still remain unresolved (*cf.* PEKKARINEN *et al.*, 1979), and additional analysis appears to be necessary.

These problems have been approached using different criteria such as wing venation (PLOWRIGHT and STEPHEN, 1973), colour variation (PEKKARINEN, 1979), enzyme constitution (PEKKARINEN *et al.*, 1979 ; PEKKARINEN, 1979 ; PAMILO *et* *al.*, 1978, 1981, 1984 ; OBRECHT and SCHOLL, 1981), mouthpart morphometry (PEKKARINEN, 1979), etc.

In a recent paper, BLUM (1981) drew attention to the possible use of the chemical constituents of the exocrine secretions of eusocial insects as a potential source of taxonomic information. Among other examples, he pointed out the cephalic marking secretion of male *Bombus* and *Psithyrus* species as a practical case.

The purpose of the present communication is to assess the extent of Blum's qualitative suggestion on the two cited genera, using numerical taxonomy methods, whose reliability in other areas is well established. Therefore, this study should be regarded as preliminary and part of a more general project concerned with the application of numerical taxonomy to the possible taxonomic value of the chemical composition of insect semiochemicals of related species. These types of studies are, to the best of our knowledge, very scarce (cf. BELLÉS *et al.*, 1985).

The chemical composition of the volatile compounds present in the secretions of the labial gland of male bumblebees has been investigated by KULLENBERG *et al.* (1970) for 13 species of the genus *Bombus* and 6 species of the genus *Psithyrus*. Almost simultaneously, CALAM (1969) reported a similar study for a smaller sample (4 species of *Bombus* and 1 species of *Psithyrus*). The results of both groups were in fairly good agreement.

The Swedish research group has also reported more exhaustive analysis for some species (BERGSTRÖM *et al.*, 1973, 1973 a, 1973 b ; SVENSSON and BERGSTRÖM, 1977, 1979), and the results have been summarized and commented upon by BERGSTRÖM *et al.* (1981).

MATERIALS AND METHODS

Operative taxonomic units (O.T.U.'s)

Cluster analysis was based upon the taxonomical and chemical data reported by KULLENBERG *et al.* (1970) which cover the most representative sample of the two genera under study, *i.e.*, 13 species of *Bombus* (one of them divided into two forms) and 6 species of *Psithyrus*.

Bombus species are listed in table 1, assuming the two classical sections *Anodontobombus* and *Odontobombus* (*cf.* KRUGER, 1917 ; FRISON, 1927), and the system of subgenera proposed by RICHARDS (1968). The species of *Psithyrus* are (our code number in parenthesis) : *barbutellus* (Kirby) (15), *bohemicus* (Seidl) (16), *campestris* (Panzer) (17), *globosus* Eversman (18), *rupestris* (Fabricius) (19), and *sylvestris* (Lepeletier) (20).

TABL. 1. — *Classification of* Bombus *species included in the cluster analysis.*

Section	Subgenus	Species	Code number
Anodontobombus	*Cullumanobombus*	*cullumanus* Kirby	1
	Pyrobombus	*hypnorum* (Linnaeus)	2
		pratorum (Linnaeus)	3
	Melanobombus	*lapidarius* (Linnaeus)	4
	Kallobombus	*soroeensis* (Fabricius)	5
	Bombus	*lucorum* (Linnaeus) « Dark » form	6
		lucorum (Linnaeus) « Blonde » form	7
		patagiatus Nylander	8
		sporadicus Nylander	9
		terrestris (Linnaeus)	10
Odontobombus	*Thoracobombus*	*agrorum* (Fabricius)	11
		muscorum (Linnaeus)	12
	Megabombus	*hortorum* (Linnaeus)	13
	Subterraneobombus	*subterraneus* (Linnaeus)	14

Characters

Chemical constituents in the cephalic marking secretions reported by KULLENBERG *et al.* (1970) and accounting for the cluster analysis are summarized in table 2. Two slightly different sets of qualitative characters, defined by the presence or absence of each chemical constituent, were used. The first character set is composed of the series of thirty-one compounds originally reported (see table 2). The second one is based on the same list, except for the compound hexadecen-1-ol, which is split into three isomers according to the three double bond positional isomers (7,8- ; 9,10- and 11,12-hexadecen-1-ol, respectively) reported by KULLENBERG *et al.* (1970). In this set, *Bombus hypnorum* and *Psithyrus sylvestris* are omitted from the O.T.U.'s list since there is no indication in the original reference as to the identity of the specific isomers present in their secretions.

Similarity coefficient

The widely employed Jaccard coefficient (*cf.* SOKAL and SNEATH, 1973) has been chosen as similarity measure, because it seems to be the most appropriate for the type of characters utilized. It neglects the similarity due to a common absence of a particular character on the two O.T.U.'s compared, and, conversely, it takes into account only those simultaneously present in both O.T.U.'s.

The use of other coefficients, which consider the overall matching (either by presence or absence), appears in this case to be inadequate, as it would lead to a false high degree of similarity between most of the O.T.U. pairs.

Clustering method

Starting from the dissimilarity matrix, hierarchical classifications or dendrograms have been computed, using the weighted pair-group clustering method (*cf.* SOKAL and SNEATH, 1973 ; CUADRAS, 1981).

TABL. 2. — *Volatile compounds found in the cephalic marking secretions of male bumblebees and cuckoobumblebees* (data from KULLENBERG *et al.*, 1970). The species are numbered according the code indicated in Table 1 (*Bombus* species : 1-14) and in the text (*Psithyrus* species : 15-20). The presence or absence of each compound in these species is represented by « 1 » or « 0 », respectively.

Compounds	Species																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Geraniol	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Citronellol	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Geranyl acetate	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Citronellyl acetate	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
all-*trans*-Farnesol	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
(-)-2, 3-Dihidrofarnesol	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
all-*trans*-Farnesyl acetate	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
2, 3-Dihydrofarnesyl acetate	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Geranylgeraniol	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Geranylcitronellol	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Geranylgeranyl acetate	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tetradecan-1-ol	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1
Hexadecen-1-ol *	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1
Hexadecan-1-ol	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Octadecen-1-ol	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0
Eicosen-1-ol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Tetradecyl acetate	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hexadecyl acetate	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Octadecenyl acetate	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Octadecyl acetate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eicosyl acetate	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Docosyl acetate	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ethyl decanoate	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ethyl dodecanoate	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Ethyl tetradecenoate	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1
Ethyl hexadecenoate	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ethyl hexadecadienoate	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ethyl hexadecatrienoate	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetradecanal	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1
Hexadecanal	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Nonadecene	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

* Double bond position. — *Bombus agrorum* : 7, 8 ; *B. lapidarius* : 9, 10 ; *Psithyrus bohemicus* : 11, 12.

RESULTS AND DISCUSSION

The four dendrograms obtained are depicted in Figs. 1-4. In order to discuss the results more conveniently, we will consider separately dendrograms including the species of *Bombus* and *Psithyrus* mixed (Figs. 1-2) and those only including *Bombus* species (Figs. 3-4).

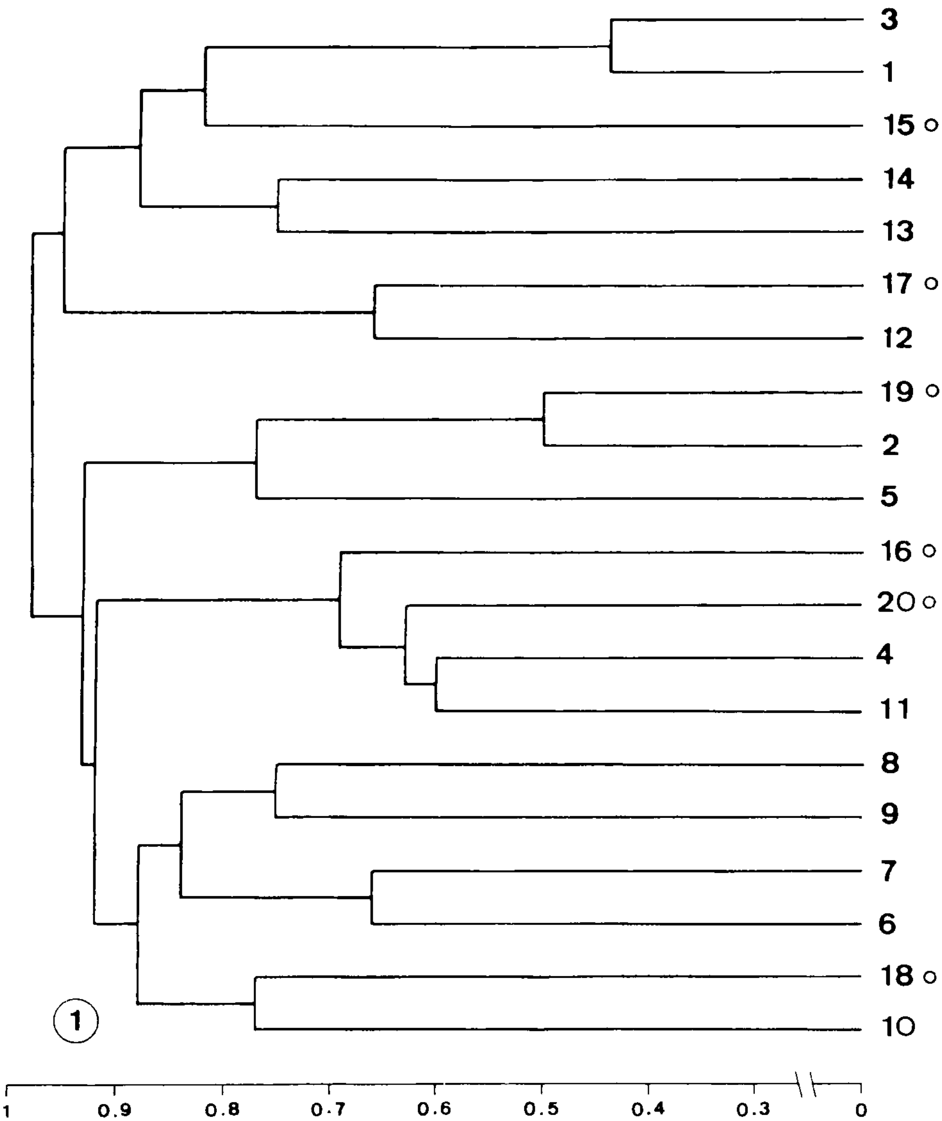

FIG. 1. — *Dendrogram obtained for* Bombus *and* Psithyrus *species.*

(See the code number corresponding to each species in table 1. Those belonging to the genus *Psithyrus* are indicated by open circles).

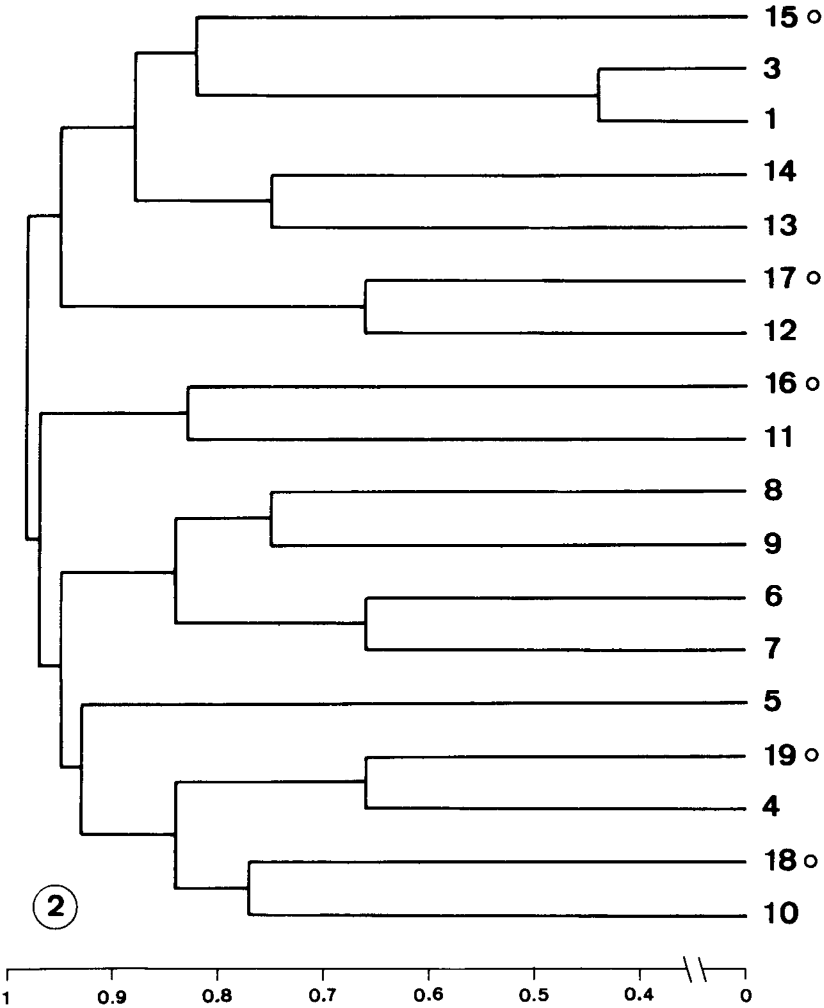

FIG. 2. — *Dendrogram obtained for* Bombus *and* Psithyrus *species considering the various isomers of hexadecen-1-ol.*

(Abbreviations as in figure 1. *Bombus hypnorum* (2) and *Psithyrus sylvestris* (20) have been omitted since there is no data available on the identity of the specific isomers of that compound in these species).

Cluster analysis of Bombus *and* Psithyrus *species*

The difference between the two dendrograms (Figs. 1-2) arises from the distinction between either the various isomers of hexadecen-1-ol (Fig. 2) or their absence (Fig. 1), as stated above.

The most striking conclusion to be derived from both dendrograms is that the species of both genera, *Bombus* and *Psithyrus,* appear « mixed », in strong opposition to other phenograms such as those based upon enzymatic constitution (PEKKARINEN *et al.*, 1979 ; PAMILO *et al.*, 1981 ; OBRECHT and SCHOLL, 1981) or wing venation (PLOWRIGHT and STEPHEN, 1973). Thus the marking secretions studied in this work seem to reflect a selection of *Psithyrus* for similarity to *Bombus* in order to improve their ability for parasitization, rather than phyletic relationships between both genera. For instance *Psithyrus rupestris,* which is known to parasitize *Bombus lapidarius,* appears in dendrogram 2 (Fig. 2) to be very close to this species. Such a kind of « proximity » is in agreement with the observations made by CEDERBERG (1979) who found that *P. rupestris* recognized the specific marking secretion of its host, *B. lapidarius.*

Cluster analysis of Bombus *species*

In the sample studied, the two great groups into which the genus *Bombus* is currently divided, *i.e. Odontobombus* and *Anodontobombus* appear to be well separated in both dendrograms, with only minor inconsistencies (*B. lapidarius* in dendrogram 4, and *B. agrorum* in dendrogram 3).

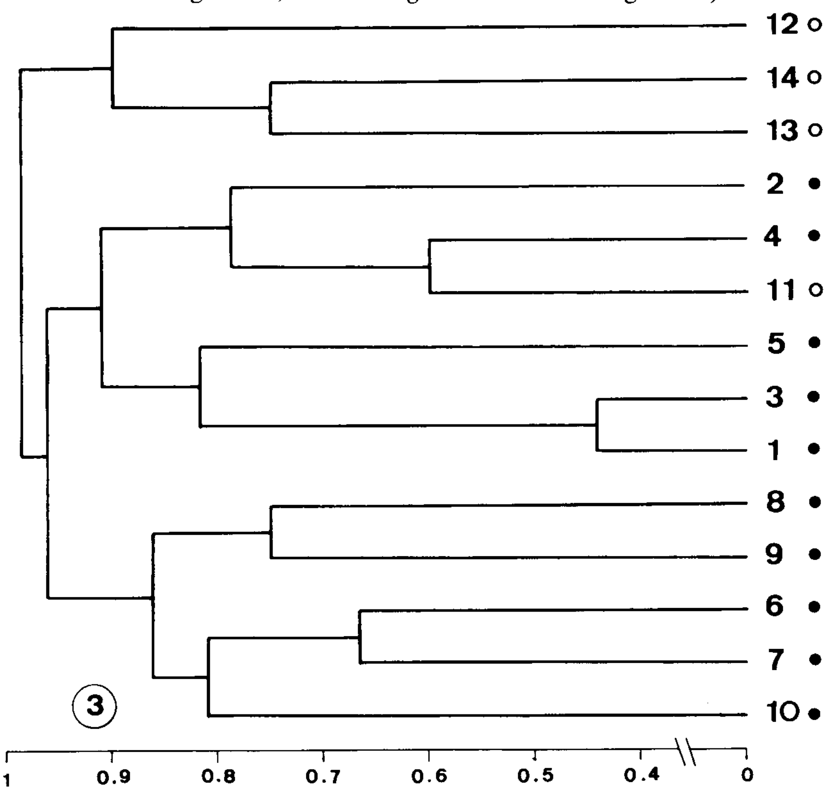

FIG. 3. — *Dendrogram obtained for* Bombus *species.*
Those belonging to the *Anodontobombus* section are indicated by black circles and those of *Odontobombus* by open circles.
(See the code number corresponding to each species in table 1).

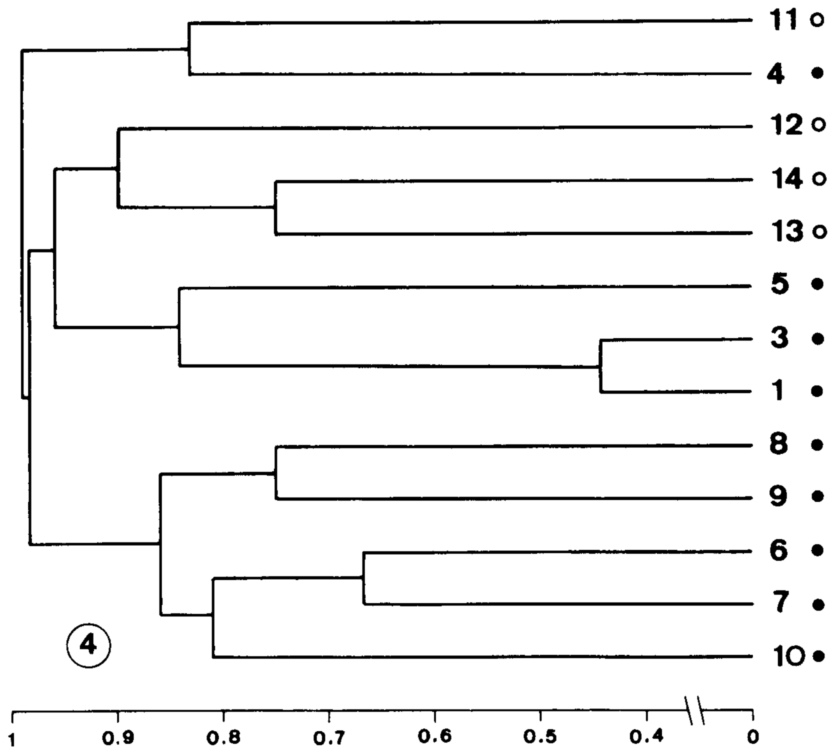

FIG. 4. — *Dendrogram obtained for* Bombus *species considering the various isomers of hexadecen-1-ol.* (Abbreviations as in figure 3. *Bombus hypnorum* (2) has been omitted since there is no data available on the identity of the specific isomers of that compound in this species).

Where subgeneric divisions are concerned, the separation achieved is less clean. *Bombus agrorum* and *B. muscorum,* which belong to the same subgenus, *Thoracobombus,* appear quite separate in both dendrograms. The same inconsistency is found in the case of *Bombus (Pyrobombus) hypnorum* and *B. (P.) pratorum,* although the subgenus *Pyrobombus,* in spite of its apparently homogeneous morphology, shows a notable heterogeneity as demonstrated in studies concerning allozyme constitution (PEKKARINEN *et al.*, 1979), numerical taxonomic analysis of wing venation (PLOWRIGHT and STEPHEN, 1973) and mouth-part morphometrics (MEDLER, 1962).

Nevertheless, all the species of *Bombus s. str.* studied *(patagiatus, sporadicus, terrestris* and both « dark » and « blonde » forms of *lucorum)* coincide at the same cluster in both dendrograms, and even the grouping at species level is also satisfactory. This result agrees with the generalized view that considers these species as very closely related and clearly isolated from other congeneric groups, and which even have been combined under a separate subgenus *Terrestribombus* Vogt (*cf.* RICHARDS, 1968 ; BERGSTRÖM *et al.*, 1973).

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RÉSUMÉ

POTENTIEL TAXONOMIQUE DES CONSTITUANTS CHIMIQUES
DES SÉCRÉTIONS CÉPHALIQUES DE MARQUAGE DES ESPÈCES
DE *BOMBUS* ET DE *PSITHYRUS* : ETUDE DE TAXONOMIE NUMÉRIQUE

On a étudié par la taxonomie numérique le potentiel chimiotaxonomique des sécrétions céphaliques de marquage chez les espèces de *Bombus* et de *Psithyrus*. On a utilisé la « weighted pair-group clustering method » (SOKAL and SNEATH, 1973) comme technique de taxonomie numérique. Trente et un composés chimiques isolés à partir de ces sécrétions et précédemment mentionnés par d'autres auteurs ont été pris comme caractères taxonomiques pour un échantillon de 13 espèces de *Bombus* et de 6 espèces de *Psithyrus* (Tabl. 1 et 2). Les espèces de *Bombus* étudiées sont : *cullumanus* Kirby, *hypnorum* (Linnaeus), *pratorum* (Linnaeus), *lapidarius* (Linnaeus), *soroeensis* (Fabricius), *lucorum* (Linnaeus) (y compris les deux formes « foncée » et « blonde »), *patagiatus* (Nylander), *sporadicus* (Nylander), *terrestris* (Linnaeus), *agrorum* (Fabricius), *muscorum* (Linnaeus), *hortorum* (Linnaeus) et *subterraneus* (Linnaeus). Les espèces de *Psithyrus* sont : *barbutellus* (Kirby), *bohemicus* (Seidl), *campestris* (Panzer), *globosus* (Eversman), *rupestris* (Fabricius) et *sylvestris* (Lepeletier).

Des dendrogrammes ont été calculés pour l'ensemble de l'échantillon et pour les espèces de bourdons seules (Fig. 1 et 2). La conclusion la plus frappante est que les espèces des deux genres, *Bombus* et *Psithyrus*, apparaissent mélangées. Les résultats semblent donc indiquer une sélection des psithyres favorisant la ressemblance avec les bourdons, pour améliorer leur capacité à les parasiter, plutôt que des relations phylétiques entre les deux genres.

Les dendrogrammes des espèces de bourdons montrent une discrimination très nette entre les deux groupes classiques *Odontobombus* et *Anodontobombus* (Fig. 3 et 4). On a trouvé de petites incohérences dans les sous-genres *Pyrobombus* et *Thoracobombus* en ce qui concerne la séparation au niveau spécifique. Par contre toutes les espèces de *Bombus s.str.* (groupe *Terrestribombus)* semblent être bien classées selon la classification taxonomique usuelle.

ZUSAMMENFASSUNG

DIE LEISTUNGSFÄHIGKEIT DER CHEMISCHEN BESTANDTEILE
DER MARKIERUNGSSEKRETE AUS DEN KOPFDRÜSEN VON *BOMBUS*-
UND *PSITHYRUS*-ARTEN (HYMENOPTERA, APIDAE) IN DER TAXONOMIE :
EINE NUMERISCH-TAXONOMISCHE STUDIE

Es wird von einer versuchsweisen numerisch-taxonomischen Studie über die chemo-taxonomische Leistungsfähigkeit der Markierungssekrete aus den Kopfdrüsen von *Bombus*- und *Psithyrus*-Arten, berichtet. Als numerisch-taxonomische Technik wurde die gewichtete Paar-Gruppen-Methode benutzt. Als

taxonomische Merkmale wurden 31 chemische Verbindungen eingesetzt, die in Arbeiten früherer Autoren aus diesen Sekreten isoliert worden waren. Das Probenmaterial bestand aus 13 *Bombus*-Arten und 6 *Psithyrus*-Arten (Tab. 1 und 2).

Von *Bombus* wurden folgende Arten untersucht : *cullumanus* (Kirby) ; *hypnorum* (Linnaeus) ; *pratorum* (Linnaeus) ; *lapidarius* (Linnaeus) ; *soroeensis* (Fabricius) ; *lucorum* (Linnaeus) (einschließlich die beiden Formen « dunkel » und « blond ») ; *patagiatus* (Nylander) ; *sporadicus* (Nylander) ; *terrestris* (Linnaeus) ; *agrorum* (Fabricius) ; *muscorum* (Linnaeus) ; *hortorum* (Linnaeus) und *subterraneus* (Linnaeus). Von *Psithyrus* waren es folgende Arten : *barbutellus* (Kirby) ; *bohemicus* (Seidl) ; *campestris* (Panzer) ; *globosus* (Eversman) ; *rupestris* (Fabricius) und *sylvestris* (Lepeletier).

Dendrogramme wurden für den ganzen Probenumfang und für die *Bombus*-Arten allein berechnet (Fig. 1 und 2). Das auffälligste Ergebnis der ersteren Analyse ist, daß die Arten beider Gattungen gemischt erschienen. Demnach geben diese Resultate offenbar eher eine Selektion von Psithyrus auf Grund ihrer Ähnlichkeit mit Bombus wieder, die ihre Fähigkeit zur Parasitierung verbessern soll, als eine phyletische Beziehung zwischen beiden Gattungen.

Die Dendrogramme der *Bombus*-Arten zeigten eine klare Unterscheidung zwischen den beiden klassischen Sektionen *Odontobombus* und *Anodontobombus* (Fig. 3 und 4). Hinsichtlich der Trennung auf dem Niveau der Art wurden kleinere Widersprüche bei den Untergattungen *Pyrobombus* und *Thoracobombus* gefunden. Anderseits erschienen alle Arten von *Bombus s.str.* (Gruppe *Terrestribombus*) gut klassifiziert entsprechend der üblichen taxonomischen Anordnung.

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