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Research papers

Chemistry of the postpharyngeal gland secretion and its implication for the phylogeny of Iberian *Cataglyphis* species (Hymenoptera: Formicidae)

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Summary. A comparative morphological and chemical study of six endemic species of *Cataglyphis* from the Iberian Peninsula: *C. ibericus*, *C. rosenhaueri*, *C. hispanicus*, *C. humeya*, *C. velox* and *C. floricola* and the Moroccan species *C. bombycinus* is described. The morphological study relied primarily on genitalia characteristics, whereas the chemical study concentrated on the postpharyngeal gland constituents. Cladograms based on the morphological and chemical data were performed using Ward's method. The dendrogram based on morphological features revealed that the Iberian *Cataglyphis* can be classified into three species groups *albicans*, *altisquamis* and *emmae*. The same pattern occurred when the dimethylalkanes constituents of the postpharyngeal gland were utilised as character states, with a slight displacement of species within the *altisquamis* group. However, when the complete hydrocarbon blend was utilised major discrepancies in the dendrograms occurred. *Cataglyphis velox* proved to be very similar to *C. bombycinus*, whereas *C. floricola* clustered with the other two species of the *altisquamis* group. Based on the geographical distribution and paleontological data (Tinaut 1993) it is assumed that *C. floricola* recently invaded the Iberian Peninsula. Based on the chemical findings we postulate that chemical character displacement occurred in *C. floricola* as a result of its sympatry with *C. velox* after the former colonized the Iberian Peninsula. We further discuss the possible reason for the different dendrograms obtained when only the dimethylalkanes are considered and its implication for the communicative role of the postpharyngeal gland secretion in these ants.

Key words. postpharyngeal gland – phylogeny – hydrocarbons – chemotaxonomy – Hymenoptera – *Cataglyphis*

Introduction

The extensive identification of exocrine products in insects has opened the way for their use in taxonomy, classification, and often for reconstructing phylogenies. Defensive secretions, for example were used in phylogenetic studies of various insect groups including staphylinid beetles (Steidle & Dettner 1993), chrysomelid leaf beetles (Pasteels 1993), and fire ants of the genus *Solenopsis* (Brand *et al.* 1973; Vander Meer 1986). Sex pheromones were used in the classification and evolution of tortricide moths (Roelofs & Brown 1982). Dufour's gland constituents served as character states for the reclassification of lactone producing bees (Cane 1983a) and of andrenid bees (Cane 1983b). The cephalic secretion of male bumble bees was used for numerical taxonomy studies (Belles *et al.* 1987), and even for the distinction between colour morphs within a species (Bergström *et al.* 1973). Cuticular hydrocarbons were likewise used in the classification of beetles (Jacob 1979; Page *et al.* 1990), *Drosophila* species from the *Drosophila virilis* group (Bartelt *et al.* 1986), and termites (Bagnères *et al.* 1990; Kaib *et al.* 1991). The concordance between chemical and morphological data that generally occurs makes these chemicals a good tool in taxonomy. Some precautions however should be taken in chemotaxonomic analyses, in particular with respect to the biological role of the secretions utilized. The use of defensive secretions is relatively reliable since they need not be species specific, and therefore are not subjected to selective pressures to diversify. Any changes in their chemistry may thus be the consequence of speciation, provided they remain pungent.

On the other hand, secretions that are used for communication may be subjected to continuous selective pressures to diversify, as they have to be species specific, and often must also exhibit individual compositions. Moreover, any changes in the chemical composition of pheromones may result in the formation of a behavioural barrier, leading to a quick fixation within the population. The selection for chemical diversity is accentuated in closely related sympatric species. This may result in two sympatric species which might be phylogenetically related, but exhibit disparate secretionary compositions, while their more distant relatives, being allopatric, retained the ancestral composition. In the present paper we have used the hydrocarbon constituents of the postpharyngeal gland for the classifica-

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tion and the assessment of the phylogenetic relationship of several *Cataglyphis* species.

The study of hydrocarbons in ants has focused primarily on their role in intra- and interspecific communication. Several lines of evidence suggest that these substances are involved in nestmate recognition (Bonavita-Cougourdan *et al.* 1987; Morel *et al.* 1988; Henderson *et al.* 1990; Nowbahari *et al.* 1990). More recently the role of the glandular secretion in modifying the aggressive behaviour of ants was established in the formicine ant *Cataglyphis niger* (Soroker *et al.* 1994), and in the myrmicine species *Manica rubida* (Hefetz *et al.* 1996). Using the glandular hydrocarbons, it was further demonstrated that the gland serves as a storage organ, and that the unified colonial odor is achieved by constant exchanges of secretions through trophallaxis and mutual grooming, constituting therefore a "Gestalt-organ" (Soroker *et al.* 1994; Vienne *et al.* 1995).

Cataglyphis is a genus with a wide geographic distribution including various ecosystems ranging from deserts to temperate regions around the Mediterranean basin. This distribution has resulted in a large generic diversity which complicates the study of their phylogeny. Taxonomic studies of this genus using essentially morphological and anatomical traits (Santschi 1929; Wehner 1983; Agosti 1990; Wehner *et al.* 1994) have proved insufficient leaving unresolved problems. The few chemotaxonomic studies performed (Hefetz & Lenoir 1992; Keegans *et al.* 1992) relied mostly on Dufour's gland secretion, and aimed at separating different species within this genus.

Six endemic species of *Cataglyphis* exist in the Iberian Peninsula representing the highest diversity of this genus in Europe. However, only a few studies pertaining to their phylogenetic relationships have been published (Tinaut & Plaza 1989; Tinaut 1990a, b, 1993). In this study we present a complete chemical analysis of the postpharyngeal gland content in these six Iberian species. We also include the analysis of the Moroccan species *C. bombycinus* since it has implication on the understanding of the phylogenetic relationship among the Iberian species, and points to ecological constraints that may have influenced the chemical evolution of the glandular secretion.

Materials and methods

Ants

Six species of *Cataglyphis* were collected in May 1994 in Andalucia (South Spain): *C. velox* at Almodovar, *C. ibericus* at Guadix, *C. rosenhaueri* at Baena, *C. hispanicus* at Cordoba, *C. humeya* at Trevelez, and *C. floricola* at Donàna. The seventh species, *C. bombycinus*, was collected in the area of Mhamid (Southeast Morocco).

Morphological studies

For the morphological studies we selected principally characters of the male genitalia. Other characters (*i.e.*, characters 1, 2, 9, 10) were selected because of their suggested evolutionary history (according to Agosti 1990, 1994a,b) and presumed implications for the phylogeny of the genus.

The character states used in the present work are the following:

1. Mandible with an apical tooth and a straight masticatory border without teeth (0), mandible pointed and only with an apical tooth (1).
2. Discoidal cell vestigial (0), or absent (1).
3. Shape of sagitta ventral face straight or lightly concave (0), lightly convex (1) or sharply convex (2).
4. Ventral face of sagitta with teeth (0) or without teeth (1).
5. Teeth in more than half sagitta ventral face (0) or occupying less than half (1).
6. Sagitta with antero-dorsal process absent (0) or present (1).
7. Volsella curved (0) or straight (1).
8. Basal process in the stipe absent (0), or present (1).
9. Proportion of the maxillary palps of males: 5 similar to 6 (0), 5 smaller than 6 (1).
10. Polymorphic workers (0), monomorphic workers (1).
11. Small process in the basis of the volsella (0 = absent, 1 = present).
12. Process in the basis of the volsella rounded (0) or pointed (1).
13. Volsella smooth (0) or with edges in the middle (1).
14. Edges of the volsella small (0) or well developed (1).

Chemical studies

For the chemical analyses, two colonies per species were collected and individuals were immediately stored at −20°C until dissection. The postpharyngeal glands from about thirty ants of each species were dissected in chilled distilled water and immediately immersed in pentane for extraction. Chemical analysis of the samples was conducted primarily by coupled gas chromatography/mass spectrometry (Fisons MD800 quadrupole). The samples were run on a 30 m × 0.32 mm DB-5 fused silica capillary column that was temperature programmed from 100°C to 300°C at 3°C/min with an initial hold of 3 min. The various compounds were identified according to retention indices and to known fragmentation patterns, which enable structure assignments even of complex mixtures of branched hydrocarbons (Doolittle *et al.* 1995 and references cited therein) as well as by comparing their spectra to published spectra (McLafferty & Stauffer 1989; Bagnères *et al.* 1991). Position of the double bonds was elucidated by alkylthiolation using dimethyl disulfide (DMDS) (Vincenti 1987). For alkylthiolation, 10 µl of the extract were mixed with 50 µl of carbon disulfide, 50 µl DMDS, and 5 µl of iodine solution (60 mg in 1 ml ether) and heated to 60°C for 12h. The excess of iodine was destroyed with 50–100 µl aqueous sodium thiosulfate solution (0.5 g in 10 ml H_2O). After addition of 300 µl pentane and 50 mg sodium chloride the organic layer was separated, concentrated, according to the known procedure (Klimetzek *et al.* 1989), and submitted to GC/MS analysis.

Statistical analyses of the chemical profiles for the different species were done using normalized chromatograms, considering the largest peak of each spectrum as 100%. Each chromatogram was further divided into four sections while assigning a value to each peak according to its relative intensity (values of 1–4 for peaks ranging from 0 to 25%, 25–50%, 50–75% and 75–100% respectively).

Morphological and chemical patterns of the different species were analysed separately using an ascendant hierarchical classification (Statistica software under Windows). We used the Ward's method and amalgamation distances to measure the similarity between the species on the basis of the assigned values.

Results

Morphological studies

The status of the character states investigated in the various *Cataglyphis* species presented in Table 1, and the hierarchical analysis conducted using the morphological character states in Figure 1A, revealed three assemblies of species. These corresponded to the species groups classified according to Agosti (1990): The *albicans* group (*C. ibericus* and *C. rosenhaueri*), the *al-*

Table 1 List of morphological characters used for constructing the hierarchical analysis of the *Cataglyphis* species studied. The numbers in the list correspond to the character descriptions in Materials and methods. Species abbreviation is as follows: **RO** *C. rosenhaueri*; **IB** *C. ibericus*; **HU** *C. humeya*; **VE** *C. velox*; **HI** *C. hispanicus*: **FL** *C. floricola*; **BO** *C. bombycinus*

Characters	Species						
	RO	IB	HU	VE	HI	FL	BO
1	0	0	0	0	1	0	0
2	0	1	0	0	0	0	1
3	0	0	2	2	2	1	1
4	1	1	0	0	0	0	0
5	1	1	0	0	0	1	0
6	1	1	0	0	0	0	0
7	0	0	1	1	1	1	1
8	0	0	0	0	0	1	1
9	1	1	0	0	0	0	0
10	1	1	0	0	0	1	0
11	0	0	1	1	0	0	0
12	0	0	1	0	0	0	0
13	0	0	1	1	0	0	0
14	0	0	0	1	0	0	0

tisquamis group (*C. humeya*, *C. hispanicus* and *C. velox*), and the *emmae* group (*C. floricola* and *C. bombycinus*). The degree of similarities between groups and within groups was assessed using the amalgamation distances calculated before clustering (Table 2). The results of the clustering and the calculated distances confirmed that the Spanish species *C. floricola* is phylogenetically related to the Moroccan desert species *C. bombycinus*. It is also apparent that *C. ibericus* and *C. rosenhaueri* are distinct from all other species, but that the differences between these two species are nevertheless as great as the differences between *C. humeya* and *C. velox* which also cluster together. The distance between the other two species that cluster closely together, *C. floricola* and *C. bombycinus*, is larger then that of the former two couples (1.73 for *bombycinus-floricola* as compared to 1.00 for *ibericus-rosenhaueri* or 1.41 for *humeya-velox*).

Chemical studies

The postpharyngeal gland secretions of the seven *Cataglyphis* species studied contained altogether 241 hydrocarbons ranging from C_{13} to C_{35} (Table 3). These included *n*-alkenes (27 substances), *n*-alkanes (20 substances), monomethylalkanes (92 substances), dimethylalkanes (95 substances), and trimethylalkanes (8 substances). The chemical profiles of the secretion revealed species specificity that was expressed both in the identity of the major products and the presence or absence of minor constituents. Of the total number of compounds identified, only 20 were common to all species, all of which were *n*-alkanes or monomethylalkanes. It is noteworthy that within the dimethylalkanes none of the compounds were omnipresent. Another interesting feature of the secretions was that in all species the complex of monomethylnonacosane was dominant. In four species they comprised the major constituents, in two other species they were of secondary importance, and only in *C. humeya* they were present in moderate amounts. Some products seemed to be characteristic of the group and contributed largely to its specification. For instance, the two species from the *albicans* group possessed dimethylalkanes which were absent or rarely present in species of the two other groups. These included high amounts of dimethylheptacosanes (3, 7-DiMe C_{27}; 3, 11-DiMe C_{27}; 3, 13-DiMe C_{27}), and dimethylnonacosanes (11, 17-DiMe C_{29}; 3, 15-DiMe C_{29}; 3, 13-DiMe C_{29}; 3, 7-DiMe C_{29}). In contrast, *C. floricola* and *C. bombycinus* differed from the three species of the *altisquamis* group in the presence of large quantities of 11 and 13-Me C_{30} and of 9, 13-DiMe C_{29}, and 11, 15-DiMe C_{31}. We are certainly aware that variation of the stereochemical configuration of chiral branched hydrocarbons in different species may open another facette of diversity, however, up to now it proved to be impossible to separate enantiomers or even diastereomers of the questionable compounds. We, thus, deal with positional isomers, only.

Figure 1B, C gives the results of the hierarchical analyses conducted using the assigned values for all identified hydrocarbon (Fig. 1B), or based only on the relative occurrence of the dimethylalkanes (Fig. 1C). There were some discrepancies when the cluster based on all hydrocarbon constituents of the secretion was compared to the cluster based on the morphological data obtained. The association of *C. rosenhaueri* and *C. ibericus* remained unchanged, but *C. velox* was separated from the *altisquamis* group and clustered with *C. bombycinus*, while *C. floricola* became associated with two of the *altisquamis* species group, *C. hispanicus* and *C. humeya*. In order to resolve the reason for this discrepancy we repeated the hierarchical analysis for each class of compounds separately. Out of these, the cluster based on the dimethylalkanes matched, with minor differences, the cluster based on the morphological data (Fig. 1C). The associations of the species group remained the same, with a minor displacement in the *altisquamis* group where, unlike the relationship projected by the morphological characteristics, *C. humeya* was more similar to *C. hispanicus* than to *C. velox*. The similarity between the species, based on the dimethylalkanes constituents only, was further evaluated using the amalgamation distances before clustering (Table 2). The congruency between the hierarchical arrangement of the species using morphology or chemistry was 81%. Thus, in the majority of comparisons the degree of similarity between the various species according to their morphology matched that obtained on the basis of the dimethylalkanes constituents of the postpharyngeal gland.

Discussion

The chemical analysis of the postpharyngeal gland secretion of the species studied revealed a complex, species specific mixture of hydrocarbons dominated by mono- and dimethylalkanes. Species specificity is re-

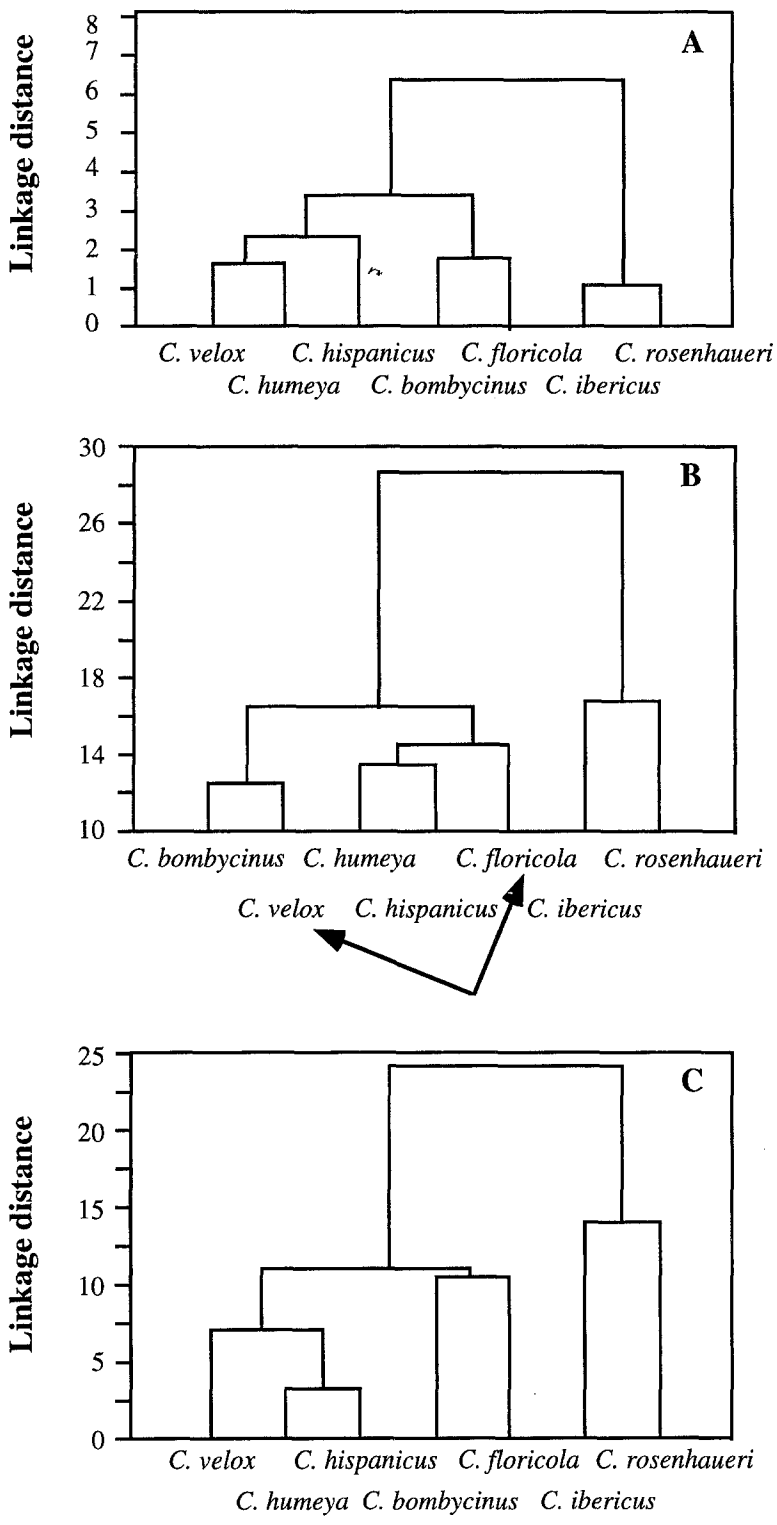

Fig. 1 Dendrogram representing possible phylogenetic relationships between six *Cataglyphis* species that are endemic to the Iberian Peninsula and of the Moroccan desert species *C. bombycinus*. Cluster analyses were based on morphological character states (**A**); total hydrocarbons composition of the postpharyngeal gland secretion (**B**); the dimethylalkane constituents of the gland (**C**). Analyses were carried out on the basis of the values attributed to the morphological and chemical characters using Ward's method for clustering

flected in the identity of the major constituents as well as the idiosyncratic occurrences of minor components. This secretionary pattern is similar to that found in other ant species (Vander Meer *et al.* 1989; Bagnères & Morgan 1991; Hefetz *et al.* 1992; Soroker *et al.* 1995). This is, however, the first chemical study of the postpharyngeal gland that encompasses several species of the same genus which are also endemic to a small geographic region (*e.g.*, Iberian Peninsula), enabling a test of their use in chemosystematics.

The morphological studies confirmed earlier studies concerning the phylogenetic associations between the species (Tinaut & Plaza 1989; Agosti 1990; Tinaut 1990a,b, 1993). Three generic groups emerged from the

Table 2 Amalgamation distances, calculated before clustering, based on the similarities of the morphological characters (right upper side of the table) and dimethylalkanes constituents of the postpharyngeal gland secretion (left lower side of the table) **RO** *C. rosenhaueri*; **IB** *C. ibericus*; **HU** *C. humeya*; **VE** *C. velox*; **HI** *C. hispanicus*; **FL** *C. floricola*; **BO** *C. bombycinus*

DiMe alkanes	Morphology						
	RO	IB	HU	VE	HI	FL	BO
RO	--	1.00	3.61	3.61	3.32	2.45	3.00
IB	13.82	--	3.74	3.74	3.46	2.65	2.83
HU	14.53	14.42	--	1.41	2.00	2.65	2.45
VE	14.76	14.39	5.57	--	2.00	2.65	2.45
HI	15.13	14.70	3.74	6.86	--	2.24	2.00
FL	15.62	15.39	8.43	10.39	8.31	--	1.73
BO	16.46	16.25	8.12	9.75	8.25	10.34	--

cluster analysis: *albicans* group including *C. ibericus* and *C. rosenhaueri*; *altisquamis* group including *C. humeya*, *C. hispanicus* and *C. velox*; and a third group including *C. floricola* and the Moroccan species *C. bombycinus* which reflect the proximity between the *emmae* group and *bombycinus* group. Two interesting points, which are relevant to the following chemotaxonomic analysis, emerged from the morphological study. *Cataglyphis ibericus* and *C. rosenhaueri* cluster distinctively apart from all other species, indicating that they are morphologically very similar to each other and rather different from all other endemic Iberian species. Indeed, they were for a long time considered as two colour types within the same species (Tinaut & Plaza 1989). The statistical analysis presented here demonstrates that the amalgamation distance (based on morphology alone) between *C. ibericus* and *C. rosenhaueri* is the same as between *C. humeya* and *C. velox*. Since the latter two species are considered "good species", we conclude that *C. ibericus* and *C. rosenhaueri* are also two distinct species. This conclusion is supported by the chemical data that revealed a similar clustering pattern, but an even higher segregation between *C. ibericus* and *C. rosenhaueri*. The larger differences in the chemical profiles may be the consequence of the number of characters used and their scoring for constructing the hierarchical analysis, but may also indicate that the rate of changes at the chemical levels were higher than at the morphological level. Since in *C. ibericus* hydrocarbons seem to be involved in nestmate recognition (Dahbi *et al.* 1996), there may have been stronger selection pressure for chemical diversification than for morphological diversification.

The second feature that stems from the dendrogram based on the morphology is the association of *C. floricola* with the North African species *C. bombycinus*. This corroborates other biological and paleogeographical data (Tinaut 1993), that suggest that *C. floricola* invaded the Iberian Peninsula only recently. The distribution of *C. floricola* is restricted to the area of the Guadalquivir Delta in the Iberian Peninsula, and it is postulated that it belonged primarily to the North African ancestral population of *C. emmae* that was isolated during the formation of the Mediterranean Sea.

Two cluster analyses were performed based on the postpharyngeal gland constituents, resulting in two different dendrograms. The use of all hydrocarbons in the hierarchical analysis led to the same general dendrogram that was obtained with the morphological data, except for the location of *C. velox* and *C. floricola*. The first clustered with *C. bombycinus*, whereas the second clustered with the *altisquamis* group. These shifts disappeared when only the dimethylalkanes were considered, and the chemical dendrogram matched that constructed based on morphology. We interpret these findings as an indication that ecological constraints may have shaped the chemistry of the postpharyngeal gland secretion of *C. floricola* after it invaded the Iberian Peninsula. We further postulate that this selective pressure operated differently on the different classes of compounds in the secretion.

The morphological data suggest that both *C. floricola* and *C. bombycinus* belonged to the same ancestral population, and therefore it is reasonable to assume that the glandular secretion of the extant *C. bombycinus*, but not that of the colonizing *C. floricola*, reflects the glandular composition of the ants from the ancestral North African population. Since the hydrocarbon profile of *C. bombycinus*, is very similar to that of *C. velox*, as revealed by the cluster analysis, we can further postulate that sympatry with *C. velox* may have selected for changes in the glandular composition in *C. floricola*. Indeed, among the three species (*C. velox*, *C. humeya* and *C. hispanicus*) that inhabit the presumed geographic region of *C. floricola* colonization (which according to today's distribution of the species was limited to the Guadalquivir depression in the Iberian Peninsula) *C. velox* is the closest species, geographically and ecologically, to *C. floricola*, albeit they occupy different habitats within this region (Tinaut & Plaza 1989). Based on these findings we hypothesize that when *C. floricola*, or its ancestral form, colonized the Iberian Peninsula it still possessed an ancestral chemical profile similar to that of *C. velox*. Assuming that the secretion acts as a signal, selection pressure would induce a fast change in the chemical signature of the newly invading *C. floricola*. Consequently the glandular composition became distinct from that of *C. velox* (its sympatric competitor) and from that of *C. bombycinus* (its ancestral species). These two latter species, on the other hand, did not change drastically and, due to their original chemical similarity, clustered together. The presumed changes in *C. floricola* rendered its secretionary composition more similar to that of *C. hispanicus*, explaining why it clustered within the *altisquamis* group. Since *C. floricola* is allopatric with either *C. hispanicus* or *C. humeya*, the changes in the glandular chemistry of *C. floricola* were not selected against. A similar chemical character displacement has been suggested for the hydrocarbon components of Dufour's gland in *C. nodus* and *C. niger* (Hefetz & Lenoir 1992).

It is interesting to note that when the cluster analysis is performed using the dimethylalkanes only, this chemical character displacement is not expressed. A possible explanation for the apparent lack of plasticity

Table 3 Postpharyngeal gland hydrocarbons in six *Cataglyphis* species which are endemic of the Iberian Peninsula (**RO** *C. rosenhaueri*; **FL** *C. floricola*; **IB** *C. ibericus*; **HI** *C. hispanicus*; **HU** *C. humeya*; **VE** *C. velox*) and in one *Cataglyphis* species of the Moroccan desert (**BO** *C. bombycinus*). **Me**, **DiMe**, **TriMe** monomethylalkanes, dimethylalkanes and trimethylalkanes, respectively

Compound	RO	IB	HI	HU	VE	FL	BO
n-Alkanes							
C_{13}	1	1	1	0	0	1	0
C_{14}	1	1	1	0	0	0	0
C_{15}	1	1	1	1	1	1	0
C_{16}	1	0	1	1	1	0	0
C_{17}	1	1	0	0	0	1	0
C_{18}	1	1	0	1	0	1	0
C_{19}	1	1	1	1	0	1	0
C_{20}	1	1	0	1	0	1	0
C_{21}	0	0	1	0	0	1	0
C_{22}	0	0	1	0	0	1	0
C_{23}	1	1	1	1	1	1	1
C_{24}	0	0	1	0	0	1	0
C_{25}	1	1	4	1	1	4	3
C_{26}	0	1	1	1	1	1	1
C_{27}	2	1	2	4	2	4	2
C_{28}	0	0	1	1	0	1	0
C_{29}	2	2	1	4	1	4	1
C_{30}	0	0	1	0	0	0	0
C_{31}	1	1	1	1	1	1	0
C_{33}	0	0	1	0	0	0	0
Monomethylalkanes							
7-Me C_{13}	0	0	1	0	0	0	0
5-Me C_{13}	0	0	1	0	0	0	0
4-Me C_{14}	0	0	1	0	0	0	0
4-Me C_{16}	0	0	1	0	0	0	0
11-Me C_{23}	0	0	1	0	0	0	1
9-Me C_{23}	0	0	1	0	0	0	1
7-Me C_{23}	0	0	1	0	0	0	0
5-Me C_{23}	1	1	1	0	0	0	0
3-Me C_{23}	0	1	1	0	0	0	0
13-Me C_{25}	1	1	1	1	1	1	2
11-Me C_{25}	1	1	1	1	1	1	2
9-Me C_{25}	1	0	1	1	0	1	1
7-Me C_{25}	1	1	1	1	1	1	1
5-Me C_{25}	2	1	1	1	1	1	0
4-Me C_{25}	0	1	0	0	0	0	0
3-Me C_{25}	0	1	1	1	1	1	2
13-Me C_{26}	1	1	0	0	0	0	1
12-Me C_{26}	1	1	0	0	0	0	0
11-Me C_{26}	1	1	1	0	0	0	1
10-Me C_{26}	1	1	0	0	0	0	0
9-Me C_{26}	1	0	1	1	0	1	0
8-Me C_{26}	0	0	0	0	0	0	1
7-Me C_{26}	0	1	1	0	0	0	0
6-Me C_{26}	1	0	0	0	0	0	0
5-Me C_{26}	1	1	1	1	0	1	0
4-Me C_{26}	1	1	1	1	0	1	0
3-Mae C_{26}	0	1	0	0	0	0	0
2-Me C_{26}	0	1	0	1	0	0	0
13-Me C_{27}	4	2	2	1	4	1	4
11-Me C_{27}	4	2	2	1	4	1	4
9-Me C_{27}	4	2	2	4	2	1	0
7-Me C_{27}	3	1	1	1	2	1	1
5-Me C_{27}	4	1	1	4	1	1	1
4-Me C_{27}	0	0	0	1	0	0	0
3-Me C_{27}	3	2	1	4	2	1	0
14-Me C_{28}	3	2	0	1	2	1	2
13-Me C_{28}	3	2	0	1	2	1	2
12-Me C_{28}	3	2	1	1	2	1	2
11-Me C_{28}	3	2	1	1	2	1	2
10-Me C_{28}	3	2	1	0	0	1	0
9-Me C_{28}	3	2	1	0	0	0	0
6-Me C_{28}	1	1	0	1	0	1	0
5-Me C_{28}	1	1	0	1	0	1	0
4-Me C_{28}	2	1	0	1	1	1	0
2-Me C_{28}	1	1	1	0	0	1	0
15-Me C_{29}	4	4	3	2	4	4	3
13-Me C_{29}	4	4	3	2	4	4	3
11-Me C_{29}	4	4	3	2	4	4	3
9-Me C_{29}	4	4	3	2	2	4	0
7-Me C_{29}	4	3	1	2	1	2	1
5-Me C_{29}	0	3	1	2	0	2	0
4-Me C_{29}	0	0	0	1	0	0	0
3-Me C_{29}	3	3	0	2	1	4	0
15-Me C_{30}	1	1	0	1	1	0	2
14-Me C_{30}	1	1	0	1	1	2	0
13-Me C_{30}	1	1	0	1	1	2	2
12-Me C_{30}	1	1	0	1	1	2	0
11-Me C_{30}	1	1	0	1	1	2	2
9-Me C_{30}	0	0	0	0	0	0	1
6-Me C_{30}	1	1	0	0	0	0	0
5-Me C_{30}	0	1	0	0	0	0	0
15-Me C_{31}	1	2	4	1	2	2	2
13-Me C_{31}	1	2	4	1	2	4	2
11-Me C_{31}	1	2	4	1	2	4	2
9-Me C_{31}	0	1	4	1	1	2	0
7-Me C_{31}	1	1	1	1	1	0	0
3-Me C_{31}	0	0	0	1	1	0	0
16-Me C_{32}	1	1	0	0	0	0	0
15-Me C_{32}	1	1	0	0	0	0	0
14-Me C_{32}	1	1	0	0	0	1	0
13-Me C_{32}	1	1	0	0	0	0	0
12-Me C_{32}	1	1	0	0	0	0	0
11-Me C_{32}	1	0	0	0	0	0	0
10-Me C_{32}	0	0	0	0	0	1	0
17-Me C_{33}	1	1	0	0	1	1	0
15-Me C_{33}	1	1	2	0	1	1	0
13-Me C_{33}	1	1	2	0	1	1	0
11-Me C_{33}	1	1	2	0	1	1	0
9-Me C_{33}	1	0	0	0	1	0	0
7-Me C_{33}	0	0	1	0	0	0	0
17-Me C_{34}	1	0	0	0	0	0	0
16-Me C_{34}	1	0	0	0	0	0	0
15-Me C_{34}	1	0	0	0	0	0	0
14-Me C_{34}	1	0	0	0	0	0	0
13-Me C_{34}	1	0	0	0	0	0	0
12-Me C_{34}	1	0	0	0	0	0	0
11-Me C_{34}	1	0	0	0	0	0	0
17-Me C_{35}	1	1	1	0	1	0	0
15-Me C_{35}	1	1	1	0	1	0	0
13-Me C_{35}	1	1	1	0	1	0	0
11-Me C_{35}	1	1	1	0	1	0	0
Dimethylalkanes							
3,7-DiMe C_{23}	0	1	0	0	0	0	0
13,15-DiMe C_{25}	0	0	0	0	0	0	2
11,15-DiMe C_{25}	1	0	0	0	0	0	0
11,13-DiMe C_{25}	0	0	0	0	0	0	2
9,11-DiMe C_{25}	0	0	0	0	0	0	1
7,17-DiMe C_{25}	0	0	0	0	0	0	1
7,15-DiMe C_{25}	0	0	0	0	0	0	1
5,9-DiMe C_{25}	2	1	0	0	0	1	0
3,7-DiMe C_{25}	2	0	0	0	0	1	0
3,5-DiMe C_{25}	2	0	0	0	0	1	0
11,15-DiMe C_{26}	0	0	0	0	0	0	1
6,16-DiMe C_{26}	0	1	0	0	0	0	0
5,11-DiMe C_{26}	1	0	0	0	0	0	0
5,9-DiMe C_{26}	1	1	1	0	0	0	0
4,14-DiMe C_{26}	0	1	0	0	0	0	0
11,15-DiMe C_{27}	0	1	0	0	1	0	2
11,13-DiMe C_{27}	2	1	0	0	0	0	0
9,17-DiMe C_{27}	0	1	0	0	0	0	0
9,15-DiMe C_{27}	0	0	0	0	1	0	0

Table 3 (continued)

Compound	RO	IB	HI	HU	VE	FL	BO
9,13-DiMe C_{27}	2	0	0	1	0	1	0
7,11-DiMe C_{27}	2	1	0	0	0	1	0
5,11-DiMe C_{27}	4	0	1	0	0	0	0
5,9-DiMe C_{27}	3	2	1	1	1	1	0
3,15-DiMe C_{27}	0	3	0	0	0	0	1
3,13-DiMe C_{27}	4	3	0	0	0	0	0
3,11-DiMe C_{27}	4	3	0	0	0	0	0
3,9-DiMe C_{27}	4	3	0	2	4	0	0
3,7-DiMe C_{27}	4	3	0	0	0	0	0
9,13-DiMe C_{28}	2	0	0	0	0	0	0
9,11-DiMe C_{28}	2	0	0	0	0	0	0
8,12-DiMe C_{28}	0	0	0	0	0	0	1
6,12-DiMe C_{28}	1	0	0	0	0	0	1
6,10-DiMe C_{28}	0	1	0	0	0	0	1
5,13-DiMe C_{28}	1	0	0	0	0	0	0
5,11-DiMe C_{28}	1	0	0	0	0	0	0
5,9-DiMe C_{28}	1	1	0	0	0	0	0
4,12-DiMe C_{28}	1	0	0	0	0	0	1
4,10-DiMe C_{28}	1	0	0	0	0	0	0
4,8-DiMe C_{28}	1	1	0	0	0	0	0
3,9-DiMe C_{28}	0	1	0	0	0	0	0
3,7-DiMe C_{28}	0	1	0	0	0	0	0
13,15-DiMe C_{29}	0	0	0	0	0	0	2
11,17-DiMe C_{29}	4	4	0	1	1	0	0
11,15-DiMe C_{29}	4	4	0	1	1	0	3
10,20-DiMe C_{29}	0	3	0	0	0	0	0
9,23-DiMe C_{29}	3	0	0	0	0	1	0
9,17-DiMe C_{29}	0	3	0	0	1	0	0
9,15-DiMe C_{29}	0	3	0	0	1	0	0
9,13-DiMe C_{29}	0	0	0	0	0	4	2
9,11-DiMe C_{29}	0	0	0	1	0	0	0
7,21-DiMe C_{29}	0	0	0	0	0	0	1
7,17-DiMe C_{29}	0	3	1	0	0	0	0
7,13-DiMe C_{29}	3	0	0	0	0	1	0
7,11-DiMe C_{29}	3	0	0	0	0	1	1
5,17-DiMe C_{29}	0	0	0	0	0	0	3
5,11-DiMe C_{29}	0	0	0	0	1	2	0
5,9-DiMe C_{29}	0	3	0	0	0	2	0
3,15-DiMe C_{29}	2	4	0	0	0	0	0
3,13-DiMe C_{29}	2	4	0	0	0	0	0
3,11-DiMe C_{29}	2	4	0	1	0	3	0
3,9-DiMe C_{29}	2	4	1	0	0	3	0
3,7-DiMe C_{29}	2	4	1	0	0	0	0
13,17-DiMe C_{30}	2	0	0	0	0	0	0
11,17-DiMe C_{30}	2	0	0	0	0	0	0
11,15-DiMe C_{30}	2	2	0	0	0	0	0
10,18-DiMe C_{30}	2	0	0	0	0	0	0
6,14-DiMe C_{30}	1	0	0	0	0	0	0
6,12-DiMe C_{30}	1	0	0	0	0	0	1
4,10-DiMe C_{30}	1	0	0	0	0	0	1
4,8-DiMe C_{30}	1	1	0	0	0	0	0
13,17-DiMe C_{31}	2	2	0	0	4	0	0
11,15-DiMe C_{31}	0	0	0	0	0	4	1
9,19-DiMe C_{31}	0	1	0	0	0	0	0
9,17-DiMe C_{31}	0	1	0	0	0	0	0
9,13-DiMe C_{31}	0	0	0	0	0	0	3
7,17-DiMe C_{31}	0	1	0	0	0	0	0
7,11-DiMe C_{31}	0	1	0	0	0	1	0
5,15-DiMe C_{31}	0	0	0	0	0	0	1
5,11-DiMe C_{31}	1	0	0	0	0	1	0
5,9-DiMe C_{31}	1	1	0	0	0	1	0
15,19-DiMe C_{32}	0	0	0	0	1	0	0
13,17-DiMe C_{32}	1	1	0	0	0	0	0
12,20-DiMe C_{32}	1	0	0	0	0	0	0
12,16-DiMe C_{32}	1	0	0	0	0	1	0
11,19-DiMe C_{32}	1	0	0	0	0	0	0
9,17-DiMe C_{32}	0	1	0	0	0	0	0
15,19-DiMe C_{33}	0	0	0	0	1	0	0
13,19-DiMe C_{33}	1	0	0	0	0	0	0

Table 3 (continued)

Compound	RO	IB	HI	HU	VE	FL	BO
13,17-DiMe C_{33}	1	1	0	0	0	0	0
13,15-DiMe C_{33}	0	1	0	0	0	0	0
11,21-DiMe C_{33}	1	0	0	0	0	0	0
15,19-DiMe C_{34}	1	0	0	0	0	0	0
14,18-DiMe C_{34}	1	0	0	0	0	0	0
13,17-DiMe C_{34}	1	0	0	0	0	0	0
15,19-DiMe C_{35}	1	0	0	0	1	0	0
Trimethylalkanes							
9,13,17-TriMe C_{27}	0	1	0	0	0	0	1
9,15,21-TriMe C_{29}	3	0	0	0	0	0	0
7,15,21-TriMe C_{29}	0	0	0	0	0	0	1
9,15,19-TriMe C_{31}	1	1	0	0	0	0	0
7,15,19-TriMe C_{31}	1	1	0	0	0	0	0
5,15,19-TriMe C_{31}	1	1	0	0	0	0	0
7,17,23-TriMe C_{32}	1	0	0	0	0	0	0
7,17,21-TriMe C_{33}	1	0	0	0	0	0	0
Alkenes							
$C_{16:1}$	1	0	0	0	0	0	0
$C_{18:1}$	1	1	0	0	0	1	0
9-$C_{23:1}$	0	1	0	0	0	0	0
$C_{25:2}$	0	0	1	0	0	0	0
9-$C_{25:1}$	0	0	1	1	0	1	0
7-$C_{25:1}$	0	0	1	1	0	0	0
9-$C_{26:1}$	0	0	0	1	0	0	0
$C_{27:2}$	1	0	0	0	0	0	0
9-$C_{27:1}$	0	0	0	2	0	1	1
7-$C_{27:1}$	1	0	1	4	0	0	0
$C_{29:2}$	0	0	0	1	0	0	0
9-$C_{29:1}$	1	0	2	1	1	1	1
7-$C_{29:1}$	1	0	1	1	0	1	0
6-$C_{29:1}$	0	0	0	0	0	1	0
9-$C_{30:1}$	0	0	1	0	0	0	0
$C_{31:3}$	0	0	0	1	0	0	0
$C_{31:2}$	0	0	1	1	0	0	0
9-$C_{31:1}$	1	0	2	1	0	2	0
7-$C_{31:1}$	0	0	1	1	0	1	0
11 Me $C_{31:1}$	0	0	0	0	0	1	0
10-$C_{32:1}$	0	1	0	0	0	0	0
12 Me $C_{32:1}$	0	1	0	0	0	0	0
$C_{33:2}$	0	0	0	1	1	0	0
9-$C_{33:1}$	0	1	0	1	1	0	0
11 Me $C_{33:1}$	0	1	0	0	0	0	0
$C_{35:2}$	0	0	0	2	1	0	0
$C_{35:1}$	0	0	0	1	2	0	0

in the dimethylalkanes is that they do not have a communicative role, and therefore were not subjected to the presumed interspecific competition pressure. This feature makes the dimethylalkanes in the postpharyngeal gland secretion good character states for *Cataglyphis* chemotaxonomy. This however may not be the case for other ant genera. For example, some of the dimethylalkanes present on the cuticular surface of *Camponotus vagus* were rather variable between colonies that exhibited high antagonistic behavior and were implied to play a role in nestmate recognition (Clément *et al.* 1990; Bonavita *et al.* 1990). In *Messor barbarus* dimethylalkanes could be used for discrimination between workers originating from monogynous colonies and workers originating from polygynous colonies (Provost *et al.* 1992, 1994). However all of the above data provide only circumstantial evidence on the role of dimethylalkanes in forming the

colony odor label. More explicit experiments using purified or synthetic compounds are needed to resolve these contradicting results. Notwithstanding, the finding that some hydrocarbons show plasticity in response to ecological conditions while others remain relatively conservative is very intriguing. It may indicate that the very complex mixtures present in the postpharyngeal gland secretion of ants, and consequently the complex blends of cuticular hydrocarbons have an additional non-communicative role.

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