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Chemotaxonomy of some *Cataglyphis* ants from Morocco and Burkina Faso

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ABSTRACT

The taxonomy of *Cataglyphis* ants has many unsolved problems and chemotaxonomy can provide additional insight for their resolution. We describe here the chemical content of the postpharyngeal and Dufour glands of three *Cataglyphis* ant species: *C. viaticus*, *C. mauritanicus* from Morocco and for the first time a Sub-Saharan *Cataglyphis*, *C. sp.* (*BF*) from Burkina Faso. These three species are very distinct chemically with respect to both the postpharyngeal and Dufour glands. Methyl-alkenes, rare in ants, are characteristic of *C. sp.* (*BF*) postpharyngeal glands. A comparison with *C. bicolor* from Tunisia indicated that *C. sp.* (*BF*) can be included into the *bicolor* group with *C. viaticus*. We suggest that the content of the Dufour gland is a better phylogenetic indicator than the content of the postpharyngeal gland.

1. Introduction

Ants of the genus *Cataglyphis* Förster 1850 are thermophilic species distributed in Mediterranean ecosystems of the Palaearctic region from Mauritania to Gobi; with a small number known from sub-Saharan Africa. The genus includes over one hundred taxa and recently was revised by Agosti, but there are still many unsolved problems (Agosti, 1990). Ant chemotaxonomy is based mainly on the contents of glandular secretions as well as cuticular hydrocarbons. The postpharyngeal gland (PPG) serves as a storage organ for the hydrocarbons that are identical to those found on the cuticle. It constitutes a "Gestalt organ" of the colonial odour which is achieved by constant exchanges of secretions through trophallaxis and mutual grooming (Soroker et al., 1994; and see review by Lenoir et al., 1999) and was used successfully in a chemotaxonomy study of Spanish *Cataglyphis* ants (Dahbi et al., 1996).

In *Cataglyphis*, these studies concern species from Spain, South France, Israel, Tunisia, Syria and Egypt; they are based on Dufour gland, PPG and cuticular hydrocarbons contents (Hefetz and Orion, 1982; Ali et al., 1988; Hefetz and Lenoir, 1992; Keegans et al., 1992; Agosti et al., 1996; Dahbi et al., 1996; Oldham et al., 1999; Gökcen et al., 2002). Unfortunately, too little is known about PPG composition of African *Cataglyphis*. Recently, complementary genetic studies were also reported (Hasegawa et al., 2002; Knaden et al., 2005). A few *Cataglyphis* species are also found in the sub-Saharan regions (Taylor, 2006), and we recently had the opportunity to collect one such species in Sahelian Burkina Faso. This is probably a new *Cataglyphis* species that belongs to the group *bicolor* (B. Taylor, pers. commun.), which is among the more complicated groups in

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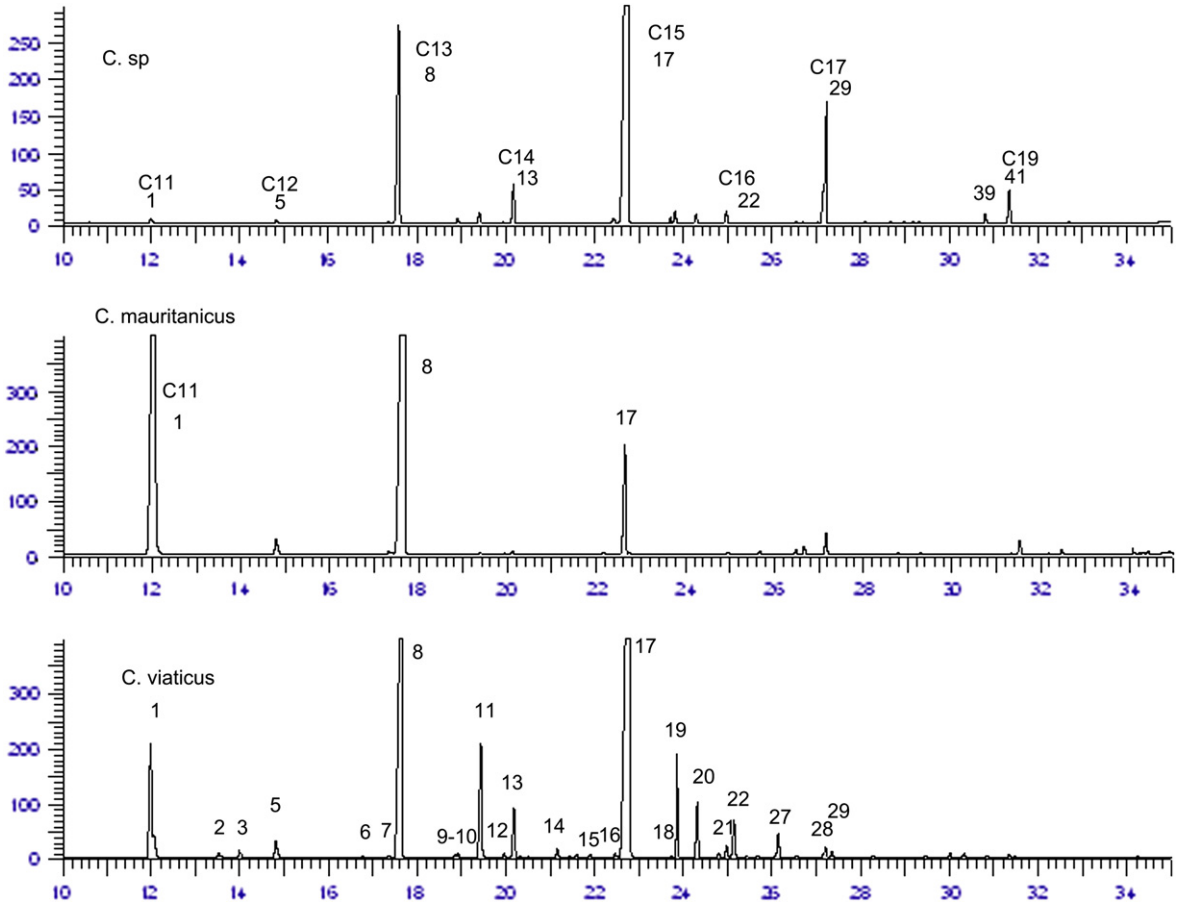

Fig. 1. Gas chromatograms of Dufour gland secretions of *C. sp.*, *C. mauritanicus* and *C. viaticus*. Only major peaks are numbered; see Table 1 for peak identification.

the genus (Wehner et al., 1994). The aim of this study was to obtain new chemical data on the *bicolor* group by comparing a species from the Sahel with another species of the *bicolor* group, *C. viaticus* from Morocco. We include data from *C. mauritanicus* (*altisquamis* group) as well from Morocco as an out-group. We discuss the evolution of the *bicolor* group after the species were separated by the formation of the Sahara desert.

2. Material and methods

Two colonies of *Cataglyphis viaticus* from Azemmour (Morocco, 33°17.60 N, 8°20.60 W, 5 m asl, voucher specimens in B. Taylor collection (Taylor and Sharaf, 2007)[1] and one from Mechra Ben-Ksiri (Morocco, 5–6 km South, 34°50.58 N, 5°93.77 W, 28 m asl), located 255 km apart, were collected in 2005. Species identification was based on the key published by R. Wehner (Wehner et al., 1994) and the website on ants from Egypt (Taylor and Sharaf, 2007). One colony of *C. mauritanicus* was collected 12 km South of Ksar el Kebir (Morocco, 34°85.65 N, 5°94.93 W, 78 m asl). Two colonies of *C. sp.* (called hereafter *C. sp. BF*) from Burkina Faso were collected in 2006 and 2007 in Burkina Faso near Bobo Dioulasso (11°07.015 N, 4°23.286 W, 460 m asl; specimens in B. Taylor collection[2]). In Sahelian Africa, only a few *Cataglyphis* species are known (Taylor, 2006) and these ants are rare in this region (A. Lenoir, personal observations).

For chemical analyses, we used the postpharyngeal (PPG) and the Dufour gland (DG) contents. The ants were frozen at −18 °C for 1 h and the glands were dissected under a stereomicroscope, immersed in 100 μl of pentane, and stored at −18 °C until analysis. Glandular content was identified by combined gas chromatography/mass spectrometry (Turbomass system, Perkin–Elmer, Norwalk, CT, USA, operating at 70 eV) using a non-polar DB-5 fused silica capillary column. PPG samples were run using a temperature program from 150 °C (2 min initial hold) to 300 °C at 5 °C min^{-1} with 10 min of final hold. Dufour gland extracts were run at a temperature program that started at 60 °C (2 min initial hold) and then raised by two

[1] http://www.nottingham.ac.uk/~plzfg/ants/ants_of_egypt_2007/cataglyphis_viaticus/cataglyphis_viaticus.htm.
[2] http://antbase.org/ants/africa/cataglyphis/cataglyphis_sp_lenoir/cataglyphis_sp_lenoir.htm.

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Table 1
Dufour gland composition (mean% ± SD) of the four species (for *C. bicolor* the numbers are the mean of two measures)

Peak no.	Name	*C. viaticus* ($n = 17$)		*C. sp.* (*BF*) ($n = 18$)		*C. mauritanicus* ($n = 6$)		*C. bicolor* ($n = 2$)
		%	SD	%	SD	%	SD	Tunisia
1	**nC11**	3.31	2.09	3.18	2.31	**40.38**	10.05	9.47
2	5-meC11	0.14	0.10	0.09	0.10			
3	3-meC11	0.20	0.16	0.34	0.29			
4	Decanal	0.08	0.09	0.67	0.98	0.10	0.09	
5	nC12	0.54	0.24	0.77	0.43	0.97	0.23	0.70
6	3-meC12	0.05	0.03	0.10	0.23			
7	x-C13:1	0.14	0.06	0.22	0.34	0.26	0.05	0.00
8	**nC13**	**20.17**	3.95	**18.64**	7.53	**47.01**	5.94	**21.08**
9	7-meC13	0.12	0.07			0.04	0.06	
10	5-meC13	0.17	0.09	0.31	0.18	0.01	0.01	
11	3-meC13	3.59	1.24	0.81	0.27	0.04	0.04	0.68
12	x-C14:1	0.21	0.14	0.54	0.83	0.11	0.09	0.10
13	nC14	2.37	0.38	2.16	0.39	0.23	0.04	1.62
14	3-meC14	0.18	0.14					
15	x-C15:1			0.10	0.22	0.10	0.07	0.94
16	x-C15:1	0.30	0.05	0.33	0.12	0.05	0.01	0.40
17	**nC15**	**57.65**	5.72	**51.51**	7.78	7.37	3.82	**60.96**
18	7-meC15	0.04	0.07	0.28	0.17			
19	5-meC15	3.58	0.85	1.24	1.79	0.01	0.01	1.52
20	3-meC15	1.80	0.57	0.42	0.22	0.01	0.01	
21	Tridecyl acetate	0.18	0.11	0.26	0.47	0.07	0.06	
22	nC16	0.44	0.13	0.82	0.38	0.16	0.04	
23	Tetradecanol	1.65	2.09	0.05	0.11	0.07	0.10	
24	2-Tetradecanone	0.12	0.06	0.14	0.20	0.14	0.07	
25	x-C17:2	0.76	0.74	0.05	0.10	0.23	0.06	
26	x-C17:1	0.12	0.07	0.18	0.16	0.15	0.34	
27	2-Pentadecanone	0.04	0.02	0.90	1.26	0.35	0.17	
28	x-C17:1	0.42	0.37	0.07	0.08	0.01	0.01	
29	nC17	0.54	0.43	**10.75**	3.99	1.23	0.68	2.55
30	Alcohol			0.03	0.07			
31	Ketone			0.02	0.06			
32	7-meC17			0.01	0.03			
33	Ketone			0.06	0.07			
34	3-meC17	0.06	0.07	0.25	0.53	0.02	0.04	
35	2-Hexadecanone	0.04	0.02	0.05	0.08	0.08	0.01	
36	nC18	0.10	0.12	0.39	0.42	0.08	0.07	
37	Hexadecanol	0.07	0.09	0.20	0.33	0.05	0.04	
38	Ketone	0.36	0.25	0.09	0.19	0.04	0.01	
39	x-C19:1	0.02	0.03	0.48	0.75	0.06	0.05	
40	2-Heptadecanone	0.18	0.14	0.95	0.98			
41	nC19	0.21	0.16	2.28	1.77	0.13	0.19	
	Alkanes	85.36	3.93	90.70	4.11	97.80	0.58	96.37
	Methyl alkanes	9.88	2.45	3.75	1.77	0.12	0.08	2.20
	Alkenes	1.62	0.83	3.69	2.55	1.66	0.13	1.43
	Ketones	0.74	0.42	0.16	0.16	0.07	0.07	
	Aldehydes	0.08	0.09	0.02	0.03	0.04	0.03	
	Alcohols	1.72	2.11	0.39	0.47	0.24	0.23	

Empty cells when the substance was not detectable. In bold: major peaks accounting more than 10%.

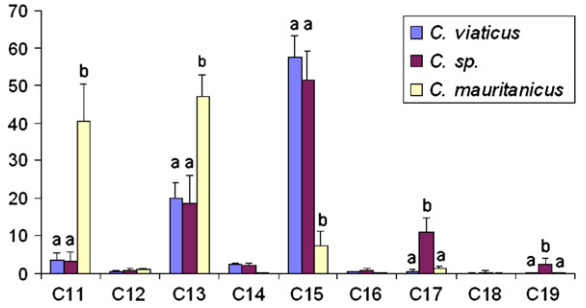

Fig. 2. Proportions of n-alkanes in the Dufour gland secretions of *C. viaticus*, *C. sp.* and *C. mauritanicus* (mean% ± SD). Different letters indicate significant differences for odd alkanes.

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gradients, at 5 °C min^{-1} to 210 °C followed by 15 °C min^{-1} to 300 °C. We used a pool of 10 glands. Quantification was achieved by gas chromatography using the same FID-GC with the above chromatographic conditions. At least five extracts were used for each colony.

Statistical analyses of the chemical profiles were done using all peaks that were identified in all the samples. Differences in profiles were explored using principal component analysis (PCA) for peaks weighing at least 1% of the total for one group. We also obtained two samples of typical *C. bicolor* from Mahares, Tunisia (37 km South of Sfax, Coll. Wehner, Senckenberg Forschunginstitut und Naturmusem, sample nos. 1597, 2 and 3). As these samples were not dissected, we analysed the cuticular profile of the whole ants and the Dufour gland profile from the same extracts but it was not possible to include them in the PCA analysis. We performed a cluster analysis only to place them comparatively to our samples. We also compared the two populations of *C. viaticus* with the Nei index, frequently used to measure the genetic or chemical distances between samples (see e.g. Akino and Yamaoka, 2002).

Data are presented as the mean ± SD. To compare the percentage values of categories of substances, we made an Arcsine (square root) transformation of the data before ANOVA and post-hoc LSD analysis (Sokal and Rohlf, 1995). All statistics were calculated using Statistica 6.1 (2003; Statsoft, Maison-Alfort, France).

3. Results

3.1. Dufour gland

The Dufour gland secretion was composed mainly of n-alkanes ranging from undecane to heneicosane (Fig. 1 and Table 1), representing more than 80% of the total composition (84.95 ± 4.02, $n = 17$; 90.14 ± 4.75, $n = 18$; 97.30 ± 0.61, $n = 6$ for *C. viaticus*, *C. sp.*(*BF*) and *C. mauritanicus*, respectively). This total relative abundance of the *n*-alkanes, however, was different across species ($ANOVA_{2,38}$, $p < 0.0001$) and the differences between these species were highly significant (LSD, $p < 0.0001$). The n-alkanes were accompanied by methyl alkanes, alkenes, decanal, dodecyl acetate, tetradecanol and several 2-alkanones all of which were present only in minor amounts or as traces (Table 1). Fig. 2 presents the relative proportions of each alkane in the various species. As can be seen the secretion is dominated by undecane, tridecane, pentadecane and to a lesser extent heptadecane and nonadecane. Pentadecane was the most abundant in *C. viaticus* and *C. sp.* (*BF*) (more than 50%) while in *C. mauritanicus* undecane and tridecane were dominant (more than 40% each). There was a significant difference between the species for the above five alkanes ($ANOVA_{2,38}$; $p < 0.0001$). LSD post-hoc tests showed that for each particular compound all species were significantly different, except between *C. viaticus* and *C. sp.* (*BF*) for the relative amounts of undecane (LSD, $p = 0.97$), tridecane (LSD, $p = 0.34$) and nonadecane (LSD, $p = 0.56$). *C. sp.* (*BF*) was had significantly greater proportion of heptadecane compared to the two other species (LSD *C. viaticus* vs. *C. mauritanicus*, $p = 0.08$). These data indicate a clear difference between *C. mauritanicus* and the two other species.

The PCA based on Dufour gland contents indicated that the species constitute three completely separated groups (Fig. 3). The first axis separates *C. mauritanicus* from the two other species of the *bicolor* group, suggesting the taxonomic classification of *C. sp.* (*BF*) within the *bicolor* group. This was confirmed by the content of *C. bicolor* gland: pentadecane is the most important peak in the *bicolor* group (Table 1). Moreover, the cluster analysis indicated that *C. mauritanicus* is completely separated from the three other species (Fig. 4).

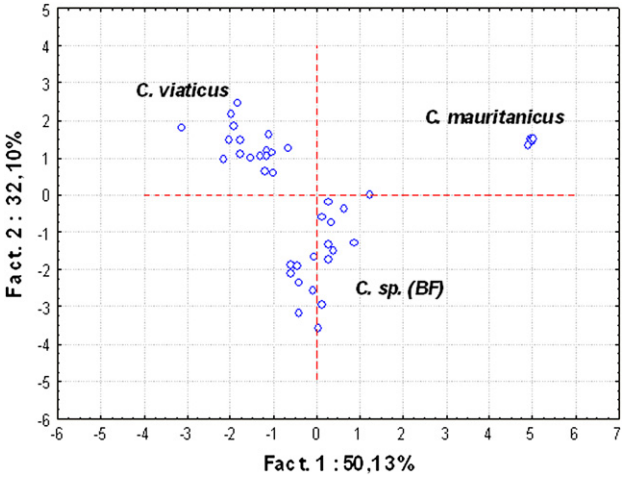

Fig. 3. PCA of Dufour gland contents of *C. viaticus*, *C. sp.* and *C. mauritanicus* based on substances representing more than 1% of the total secretion.

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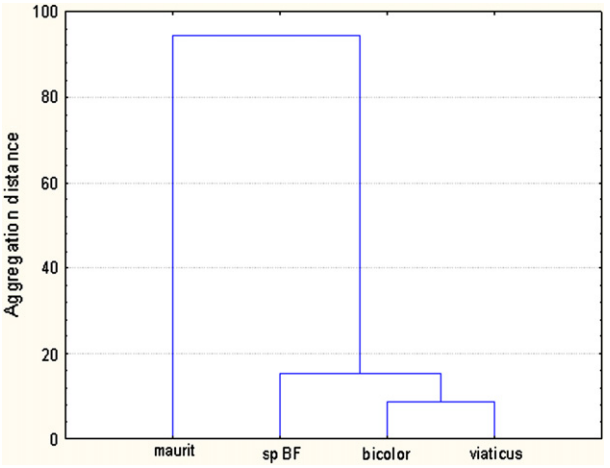

Fig. 4. Cluster analysis (Single link, Ward method) on the Dufour gland content of *C. viaticus*, *C. sp.*, *C. mauritanicus* and *C. bicolor* from Tunisia.

The intracolonial, intercolonial and interpopulation variations of *C. viaticus* were very low and not significantly different (Nei index respectively 0.987 ± 0.011, $n = 30$; 0.982 ± 0.018, $n = 30$; 0.991 ± 0.007, $n = 48$; Kruskal–Wallis $p = 0.15$, not significant).

3.2. PPG

The PPG contained only hydrocarbons ranging from pentacosane to pentatriacontane (Table 2 and Fig. 5). The differences between the species were significant for the three compound categories: n-alkanes, methyl alkanes and alkenes ($ANOVA_{2,34}$, $p < 0.0001$, Fig. 6). Methyl alkanes were the most abundant group comprising at least 50% of the total. The secretion of *C. mauritanicus* was characterized by greater proportions of heavy hydrocarbons (C33 and C35) as well as of alkenes ($34.8 \pm 8.4\%$). That of *C. sp.* (*BF*) had fewer n-alkanes ($6.84 \pm 3.8\%$) and was also characterized by higher quantities of C31 and C33 methyl alkanes. In this species, we found specific methyl alkenes.

A PCA analysis revealed the formation of three completely distinct groups according the three species (Fig. 7).

C. bicolor PPG content is different as the two major peaks are dimeC25 and 5-meC27, which are traces in other species (Table 2).

The intracolonial and intercolonial variations of *C. viaticus* were very low and not significantly different (Nei index respectively 0.987 ± 0.050, $n = 25$; 0.891 ± 0.094, $n = 20$, Kruskal–Wallis $p = 1$, not significant) while they differed between the two populations (Nei 0.574 ± 0.074, $n = 50$, Kruskal–Wallis $p < 0.001$).

4. Discussion

It appears that both PPG and Dufour gland provide a clear test for discriminating the three species and confirms their usefulness in ant chemosystematics.

4.1. Dufour gland

The Dufour gland contains mainly n-alkanes and small quantities of methyl alkanes and alkenes, as previously described in other species. At least for our four species, they appear to be reliable characters. Gökcen et al., (2002) observed that allopatric populations of the same species (from Tunisia and Egypt) were chemically differentiated and these differences were of an extent comparable to that observed between species. In Morocco, the two studied populations of *C. viaticus* separated by 255 km were not differentiated. It will be interesting to compare more distant populations. All non-hydrocarbon substances are present only as traces and not in all samples, as already signalled by Gökcen et al. (2002) and therefore cannot be used for taxonomy. We tried also to reconstruct a phylogeny based on published data, but it does not recover the taxonomic groups (results not presented). It can be hypothesized that the content of Dufour gland has evolved independently of the morphological and anatomical characteristics. It is also noticeable that the data for the Dufour gland content are very variable; for example the content changes with age (Ali et al., 1988), the gland is fragile and a part of the content may escape during dissection. It was previously suggested that Formicine ants from temperate climates usually have undecane as the major component of the Dufour gland, and as one moves to hotter climates, the major components move to tridecane and pentadecane (Keegans et al., 1992). This was not supported by our results, as *C. mauritanicus* have large quantities of undecane. The role of Dufour gland secretion is also not well known in formicines. Undecane generally acts as an alarm pheromone or wetting agent

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Table 2
PPG content (mean% ± SD) of the four species (for *C. bicolor* the numbers are the mean of two measures)

Peak no.	Name	*C. viaticus* ($n = 14$)		*C. sp.* (*BF*) ($n = 13$)		*C. mauritanicus* ($n = 5$)		*C. bicolor* ($n = 2$)
		%	SD	%	SD	%	SD	Tunisia
1	x-C25:1	0.14	0.11	0.25	0.48	1.28	0.41	4.33
2	nC25	2.48	1.97	0.39	0.40	3.88	1.52	6.35
3	9-,11-,13-meC25	3.34	2.04	1.29	1.33	2.27	0.73	9.20
4	7-meC25	0.15	0.20			1.51	0.50	0.99
5	5-meC25	0.60	0.20			0.21	0.05	2.78
6	3-meC25	5.72	3.19	0.33	0.44	1.80	0.43	0.00
7	5,9-; 7,x-dimeC25	0.21	0.34	0.07	0.26			**12.51**
8	nC26	5.79	2.94	0.27	0.50	0.45	0.33	0.66
9	8-,10-,11-,12-,13meC26	2.26	1.41	0.01	0.02	0.45	0.16	1.19
10	4-meC26	0.76	0.25	0.12	0.41	0.08	0.04	3.98
11	3-meC26	0.62	0.32					2.34
12	x-C27:1	0.96	0.63			6.63	1.92	
13	nC27	2.54	1.32	0.64	0.44	3.48	1.73	5.13
14	Octadecenamide	0.34	0.30	0.00	0.00	0.00	0.00	7.97
15	9-,11-,13meC27	**14.77**	2.86	0.57	0.45	3.44	2.10	0.00
16	5-meC27	0.93	0.23	0.22	0.19	0.89	0.26	21.53
17	11,15-; 13,15-dimeC27	4.45	3.94	0.45	0.54	1.15	0.44	0.96
18	3-meC27	9.65	7.77	6.93	6.26	**11.18**	5.93	0.00
19	nC28	9.59	7.29	0.93	1.06	1.68	1.39	**10.49**
20	8-,10-meC28	1.70	3.14	1.13	1.69			
21	12-meC28; 11,13,15-trimeC27	4.29	1.60	0.92	0.40	0.49	0.17	0.97
22	4-meC28	1.45	0.35	0.42	0.33	0.00	0.00	1.51
23	x-C29:1	0.60	0.91			1.12	0.14	
24	x-C29:1	0.86	0.76	0.07	0.14	2.39	0.56	
25	3-MeC28:1	0.69	0.69	0.16	0.16	0.00	0.00	0.40
26	nC29	0.47	0.59	3.65	2.78	0.81	0.82	
27	x-meC29:1	0.29	0.29	0.01	0.04	0.70	0.39	0.59
28	11-,13-,15-meC29	8.20	3.03	**16.61**	3.84	4.74	2.65	
29	7-meC29	0.32	0.25	0.67	0.57	0.11	0.17	3.06
30	5-meC29	1.30	1.03	1.29	0.54	0.79	0.53	0.74
31	9,15-;11,15-;13,15-dimeC29	3.68	4.27	0.75	0.62			
32	3-meC29	0.70	0.60	5.50	3.06	1.04	0.48	1.83
33	5,9-dimeC29	0.06	0.18			0.97	0.82	
34	nC30	1.14	0.86	0.14	0.20	1.45	1.42	
35	8- (12-)meC30	0.60	0.10	**10.11**	2.72	0.60	0.22	
36	11,13,15-; 13,15,17-trimeC29	0.15	0.18	3.26	0.56			
37	4-meC30	0.26	0.33	0.78	0.24			
38	x-C31:1			1.54	1.08			
39	x-C31:1			1.05	0.73			
40	x-C31:1	0.14	0.18	0.83	0.39	7.36	2.35	
41	nC31	0.74	0.78	0.82	0.54	2.80	1.01	
42	15-meC31:1	0.41	0.86	3.54	0.60			
43	9-,11-,13-,15meC31	1.84	1.16	**17.46**	3.43	4.01	1.11	
44	11,13-;11,15-;13,15-;13,17-dimeC31	2.50	1.32	1.54	0.86	3.29	2.14	0.50
45	3-meC31			0.69	0.69			
46	8-meC32			1.35	1.20			
47	12,14-;12,16-dimeC32			1.38	0.47			
48	x-C33:1			0.40	0.33			
49	x-C33:1	0.08	0.17	0.67	0.84	**12.31**	6.94	
50	15-,17-meC33:1			1.53	0.82			
51	11-,13-,15-,17-meC33	0.22	0.32	4.68	2.76			
52	11,15-; 13,15-dimeC33	0.07	0.16	2.05	1.36	4.31	1.35	
53	11,15,17-; 13,15,17-trimeC33	0.19	0.23	0.28	0.28	1.19	0.72	
54	13,x-, 15,x-meC33	0.75	0.54			0.87	0.67	
55	x-C35:1					2.72	1.27	
56	15-meC35:1			0.17	0.19	0.00	0.00	
57	11-,13-,15-meC35			1.41	1.25	3.49	1.29	
58	11,15-; 13,15-dimeC35			0.68	1.15			
	n-Alkanes	22.75	9.75	6.84	3.84	14.55	3.56	16.10
	Methyl alkanes	71.70	10.93	83.11	2.70	48.01	9.47	74.04
	Alkenes	3.48	2.14	9.88	1.92	34.51	8.56	9.86

Empty cells when the substance was not detectable. In bold: major peaks accounting more than 10%.

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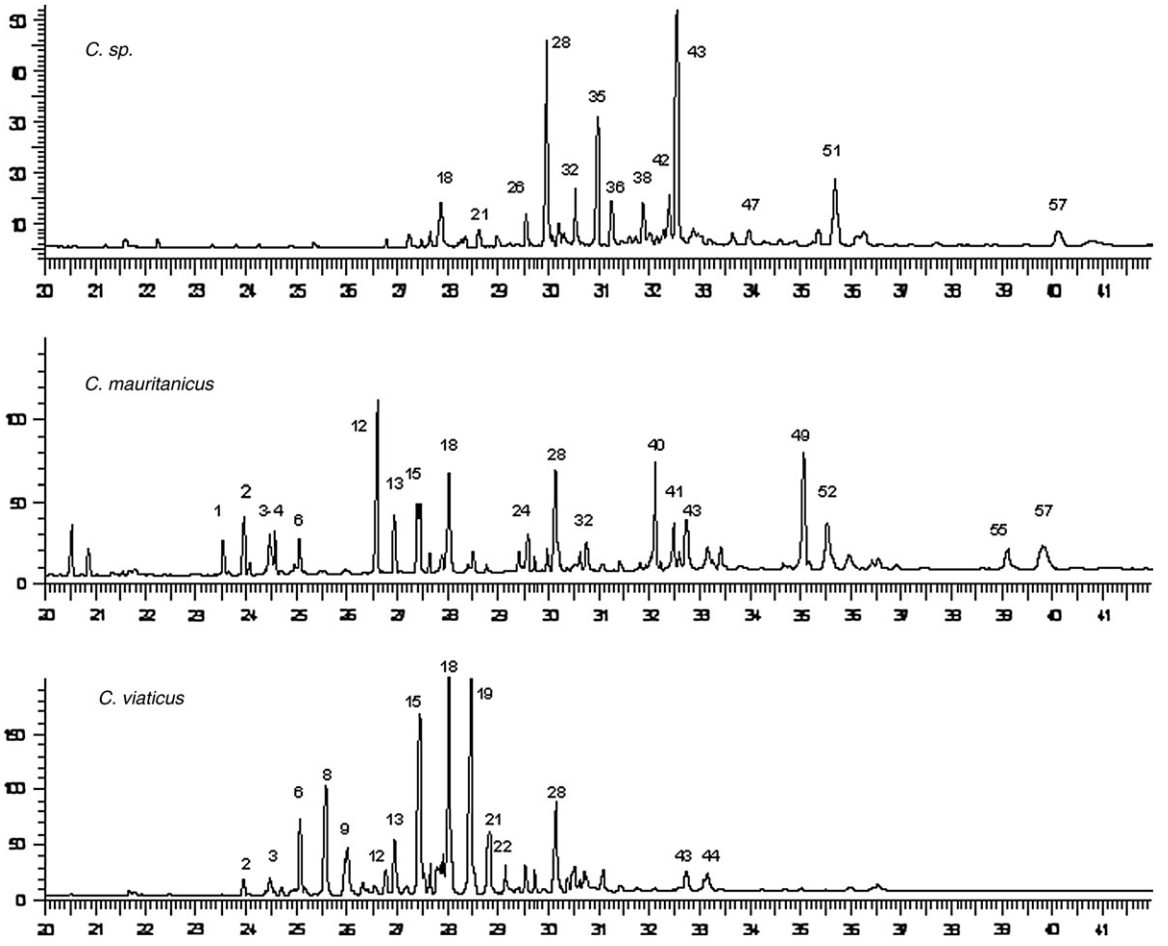

Fig. 5. Gas chromatograms of PPG of *C. sp.*, *C. mauritanicus* and *C. bicolor*. Only major peaks are numbered; see Table 2 for peak identification.

for the formic acid released from the poison gland (Blum, 1973; Hefetz and Lenoir, 1992; Mayade et al., 1993; Billen and Morgan, 1998). It has been proposed that in solitary foraging species like *Cataglyphis* it acts as general marker of home range of the colony but, at least in *C. niger*, that this function is fulfilled by the cloacal gland secretion (Wenseleers et al., 2002).

4.2. PPG content

The PPG content is classical for ants with series of saturated and unsaturated alkanes from C25 to C35. We also found methyl alkenes that are not frequent in ants. They have been found on the cuticle of some *Leptothorax* (Tentschert et al., 2002), *Pachycondyla inversa* (D'Ettorre et al., 2004; Dreier et al., 2007), *Pachychondyla villosa* (Lucas et al., 2004) and *Atta*

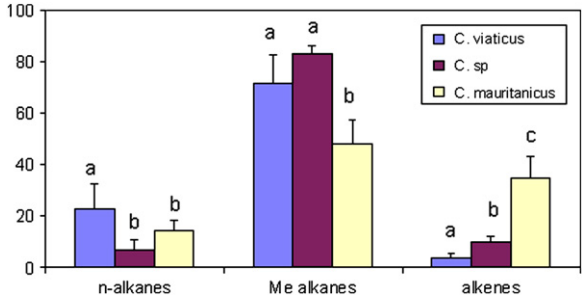

Fig. 6. PPG content of the main hydrocarbon classes for three *Cataglyphis* species (mean% ± SD). Different letters indicate significant differences.

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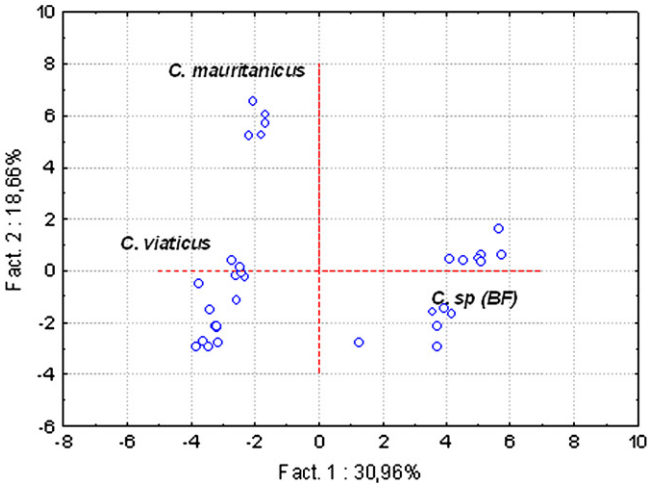

Fig. 7. PCA of PPG content based on substances present at more than 1% for at least one species.

colombica (Richard et al., 2007). The PPG content appeared to be a good indicator for phylogeny of Iberian *Cataglyphis* (Dahbi et al., 1996) but we failed to obtain a logical grouping in cluster analysis with all published data and also when we integrated *C. bicolor* (results not presented). These may be due to the differences in the analytical methods used, solid or liquid injection for example, and the extent of compound identification. More data using comparable analytical conditions are needed. It can also be due to the fact that selective pressures operating on the nestmate recognition require heritable recognition cues but are also counterbalanced to avoid nepotism (D'Ettorre and Moore, in press), and therefore cuticular hydrocarbons evolution does not reflect the phylogeny of the ants, which is constructed on morphological and anatomical characteristics. These PPG substances may be more susceptible to local environmental pressures since we observed that in *C. viaticus* they can change considerably over 255 km and the content of Dufour gland may be a better phylogenetic indicator.

In brief, we suggest that the content of the Dufour gland is a better phylogenetic indicator than the content of the postpharyngeal gland. We also conclude that the *Cataglyphis bicolor* group has evolved in different species north and south of the Sahara.

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