

Secretion of the Dufour Glands of Two African Desert Ants, *Camponotus aegyptiacus* and *Cataglyphis savignyi* (Hymenoptera:Formicidae)

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Key Word Index—*Camponotus aegyptiacus*; *Camponotus vagus*; *Cataglyphis savignyi*; major workers; minor workers; Dufour gland; undecane; dodecyl acetate.

Abstract—Dufour glands of minor workers of *Camponotus aegyptiacus* contain a mixture of linear and methyl branched hydrocarbons and a trace of dodecyl acetate. Major workers contain a similar mixture of hydrocarbons but also large quantities of dodecyl acetate, some other long chain acetates and traces of propionates and farnesyl acetate. *Cataglyphis savignyi* has pentadecane as the most abundant compound with traces of ketones, alcohols and an aldehyde. *Camponotus vagus*, a Mediterranean species, has a more typical formicine mixture with undecane being the major compound. A summary of *Camponotus* Dufour substances demonstrates the species-specificity of this secretion.

Introduction

The Dufour glands of ants have been shown to be the source of a wide variety of aliphatic hydrocarbons, and related oxygenated compounds, the diversity being greatest in species of the Formicinae. From the evidence so far accumulated, it would appear that the composition of this secretion is species-specific. The purpose of this specificity is far from clear, though we have been able to show that in the genus *Myrmica* the secretion acts as a home-range marking pheromone for each species [1]. In some other species, the trail pheromone is found in the Dufour gland secretion [2].

Nearly all of the studies of the formicine Dufour glands have concentrated on European or North American species [3]. Few or none have dealt with tropical species, including the dry desert areas of Northern Africa. We have therefore turned our attention to the two common formicines of Egypt, *Camponotus aegyptiacus* Emery, which is found frequently inside and outside dwellings, foraging individually and mainly active at night, and *Cataglyphis*

savignyi (Dufour) which is highly adapted to the dry conditions, living near agricultural areas in the Nile valley. Workers forage individually, running across stones and soil during the heat of the day and returning to the nest before sunset. In addition, the dimorphic aspect of the worker caste in *C. aegyptiacus* offered the opportunity to investigate this dimorphism from a chemical aspect. Such a caste-related analysis of Dufour gland contents has not previously been attempted among the Formicinae, and is restricted among other subfamilies to a report on the difference in chemical content between major and minor workers of the myrmicine species *Pheidole pallidula* [4]. The only caste-related studies on Dufour glands of Formicinae deal with a comparison between females and workers of *Camponotus aethiops* [5] and of *Formica sanguinea* [6], in which only slight differences were found.

The Dufour glands of formicine ants are characterized by the presence of long chain alkanes and alkenes, together with related oxygenated compounds, chiefly acetates and alcohols. The dominant component, often representing over two thirds of the total mass, is undecane. In just a few species there may be more tridecane than undecane. The oxygenated

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compounds are normally minor components but display much greater variety of type than the hydrocarbons, and do most to provide the specificity of composition. *Camponotus* is a large genus, and the investigations of a number of species have been recorded. We have already examined one Mediterranean species, *C. aethiops* and include here another, *C. vagus* (Scopoli) for comparison with *C. aegyptiacus*.

We have found complex mixtures of compounds in both *C. aegyptiacus* and *C. savignyi* and moreover, distinctly different composition in the two forms of workers of *C. aegyptiacus*.

Results

From the size of their heads, the workers of *C. aegyptiacus* form two distinct castes (Fig. 1), therefore the two groups were examined separately. Individual glands dissected from workers, were subjected to gas chromatography, linked to mass spectrometry, as described in the Experimental.

The Dufour gland secretion of minor workers of *C. aegyptiacus*, as shown in a typical chromatogram (Fig. 2), contains mainly hydro-

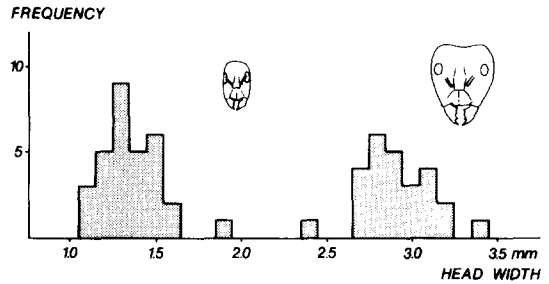


FIG. 1. DIMORPHISM IN WORKERS OF *C. AEGYPTIACUS*, DETERMINED BY HEAD WIDTH MEASUREMENTS ON 57 INDIVIDUALS (CF. [7]).

carbons in addition to one acetate, dodecyl acetate. The hydrocarbons range from C_{10} to C_{17} with undecane as the major component (78%) followed by tridecane (9%) and decane (3%). Only two branched hydrocarbons were identified represented by 5-methylundecane and 3-methylundecane (1.5 and 4.2%, respectively). The mean values and percentages of the compounds are listed in Table 1.

The Dufour gland secretion of major workers of *C. aegyptiacus* consists mainly of hydrocarbons and acetates in addition to trace compounds of two alcohols, two propionates and

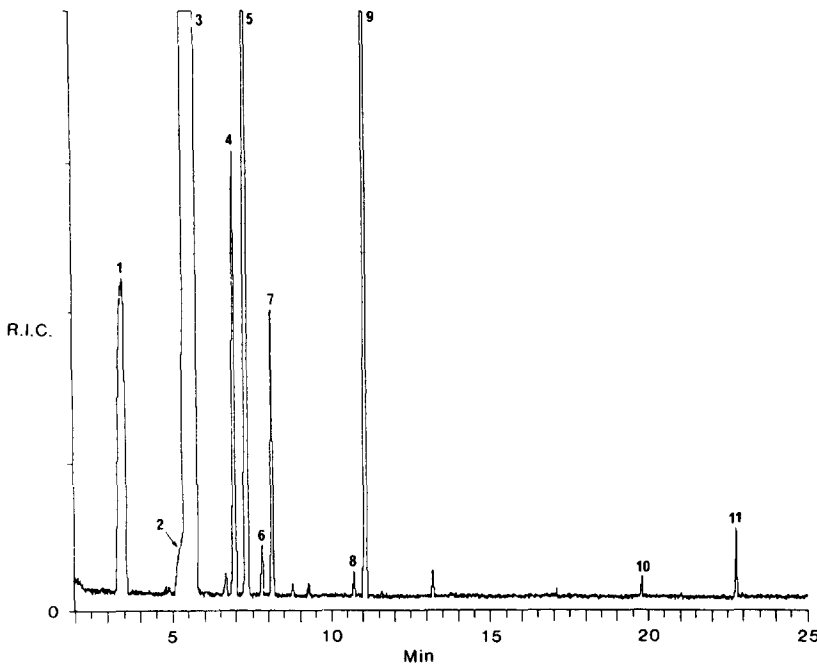


FIG. 2. A REPRESENTATIVE GAS CHROMATOGRAM OF THE DUFOUR GLAND OF A SINGLE MINOR WORKER OF *C. AEGYPTIACUS* ANALYSED ON AN OV-1 CAPILLARY COLUMN. The peak numbers refer to Table 1.

TABLE 1. MEAN VALUES AND PERCENTAGE COMPOSITION, TOGETHER WITH SAMPLE STANDARD DEVIATIONS FOR THE COMPOSITION OF THE CONTENTS OF THE DUFOUR GLAND OF *CAMPONOTUS AEGYPTIACUS* MINOR WORKERS DETERMINED BY GC AND MS ON INDIVIDUAL SAMPLES

Peak	Compound	%	SD	Mean quantity	
				(μg)	(SD)
1	<i>n</i> -Decane	2.8	0.9	0.21	0.09
2	Undecene	0.2	0.3	0.01	0.02
3	<i>n</i> -Undecane	78.4	9.1	6.16	2.36
4	5-Methylundecane	1.5	1.0	0.12	0.11
5	3-Methylundecane	4.2	2.2	0.34	0.26
6	Dodecene	0.3	0.3	0.02	0.04
7	<i>n</i> -Dodecane	1.6	0.7	0.12	0.07
8	Tridecene	0.3	0.3	0.02	0.03
9	<i>n</i> -Tridecane	8.7	3.7	0.63	0.54
10	Dodecyl acetate	0.2	0.2	0.01	0.01
11	<i>n</i> -Heptadecane	0.5	0.4	0.04	0.04
Total amount in μg				7.77	2.98

one terpenoid compound, farnesyl acetate. The gas chromatographic profile of the secretion is shown in Fig. 3. The hydrocarbons comprise branched and unbranched, saturated and unsaturated compounds ranging from C_{10} to C_{19} with undecane (52%) as the major compound followed by tridecane (14%). The branched chain hydrocarbons were present only in traces with 5-methyltridecane the most abundant (0.3%). The acetates (C_{10} – C_{20}) were the second most abundant compounds, with dodecyl acetate the major compound (28%), followed by undecyl acetate (6.8%). One branched acetate, an incompletely identified methyl dodecyl acetate, was present in a trace amount. Dodecanol and tetradecanol, and the two propionates were present in traces. The mean values and percentages of the compounds are listed in Table 2.

The Dufour gland of *Cataglyphis savignyi* workers is filled with branched, and saturated and unsaturated hydrocarbons in addition to four ketones, three alcohols and one aldehyde as minor components (Fig. 4). The straight chain hydrocarbons range from C_{11} to C_{23} with pentadecane as the major compound (58%) followed by tridecane (14%) and heptadecane (8%). The branched chains contain methyl groups in the 3-, 5- or 7-position. All the branched compounds were present in small or trace amounts with 3-methylpentadecane and 5-methylpentadecane the most abundant. The

TABLE 2. MEAN VALUES FOR THE COMPOSITION OF THE CONTENTS OF THE DUFOUR GLAND OF *CAMPONOTUS AEGYPTIACUS* MAJOR WORKERS DETERMINED BY GC AND MS.

Peak	Compound	%	SD	Mean quantity	
				(μg)	(SD)
1	<i>n</i> -Decane	0.5	0.3	0.12	0.10
2	<i>n</i> -Undecane	52.2	16.1	12.3	11.2
3	5-Methylundecane	t		t	
4	3-Methylundecane	t		t	
5	<i>n</i> -Dodecane	0.5	0.9	0.1	0.15
6	Tridecene	t		t	
7	<i>n</i> -Tridecane	3.9	1.3	0.93	0.94
8	Terpenoid	t		t	
9	5-Methyltridecane	0.3	0.4	0.06	0.08
10	3-Methyltridecane	t		t	
11	Decyl acetate	t		t	
12	Dodecanol	t		t	
13	Undecyl acetate	6.8	9.5	1.36	1.66
14	<i>n</i> -Pentadecane	1.1	0.6	0.18	0.17
15	Dodecyl acetate	t		t	
16	Dodecyl acetate	28.2	10.5	4.8	1.99
17	Branched tridecyl acetate	t		t	
18	Tetradecanol	t		t	
19	Heptadecene	t		t	
20	Dodecyl propionate	t		t	
21	Tridecyl acetate	t		t	
22	<i>n</i> -Heptadecane	1.5	1.4	0.31	0.28
23	Tetradecyl acetate	1.2	0.4	0.22	0.12
24	<i>n</i> -Octadecane	t		t	
25	Farnesyl acetate	0.2	0.2	0.04	0.04
26	<i>n</i> -Nonadecane	t		t	
27	Hexadecyl acetate	0.2	0.2	0.04	0.07
28	Octadecyl acetate	2.4	1.3	0.04	0.24
29	Octadecyl propionate	t		t	
30	Nonadecyl acetate	t		t	
31	Eicosyl acetate	t		t	
Total amount in μg				21.15	14.15

Average of five samples. t=trace.

mean values and percentages of the compound are listed in Table 3.

The Dufour gland secretion of *C. vagus* consists mainly of hydrocarbons in addition to small quantities of alkyl acetates (C_{12} – C_{16}) and one alcohol (Fig. 5). Approximately 99% of the glandular contents is a narrow range of alkanes (C_9 – C_{15}) and alkenes (C_{11} – C_{19}) with undecane as the major compound (70%), followed by tridecane (22%) (Table 4). The major alkene, tridecene was resolved into a double peak indicating two compounds, differing in double bond position. Insufficient material was available to determine the double bond position. Three methyl-branched alkanes, four acetates and dodecanol were all present in small quantities.

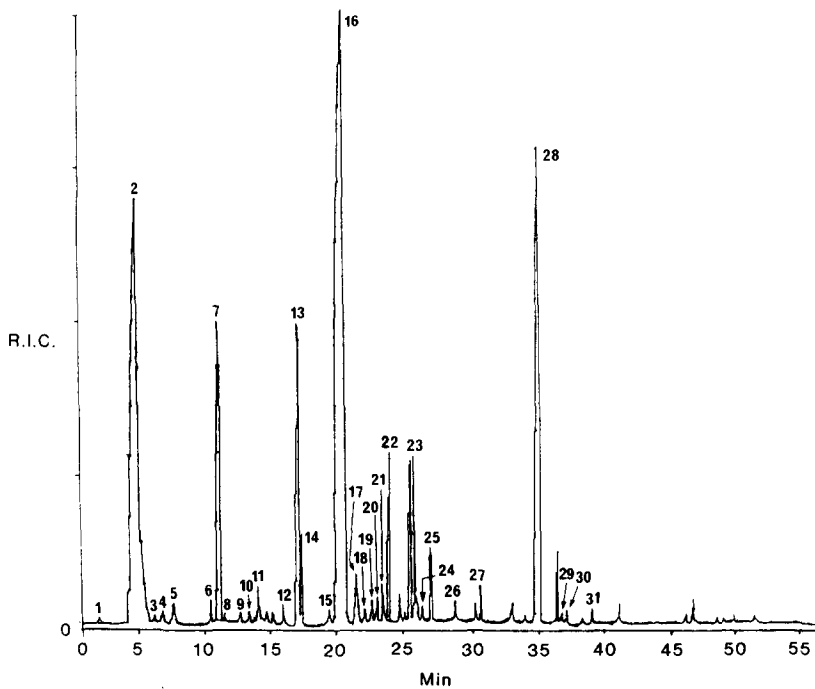


FIG. 3. GAS CHROMATOGRAM OF THE DUFOUR GLAND OF A SINGLE MAJOR WORKER OF *C. AEGYPTIACUS*. Conditions as in Fig. 2. Numbers refer to identification in Table 2.

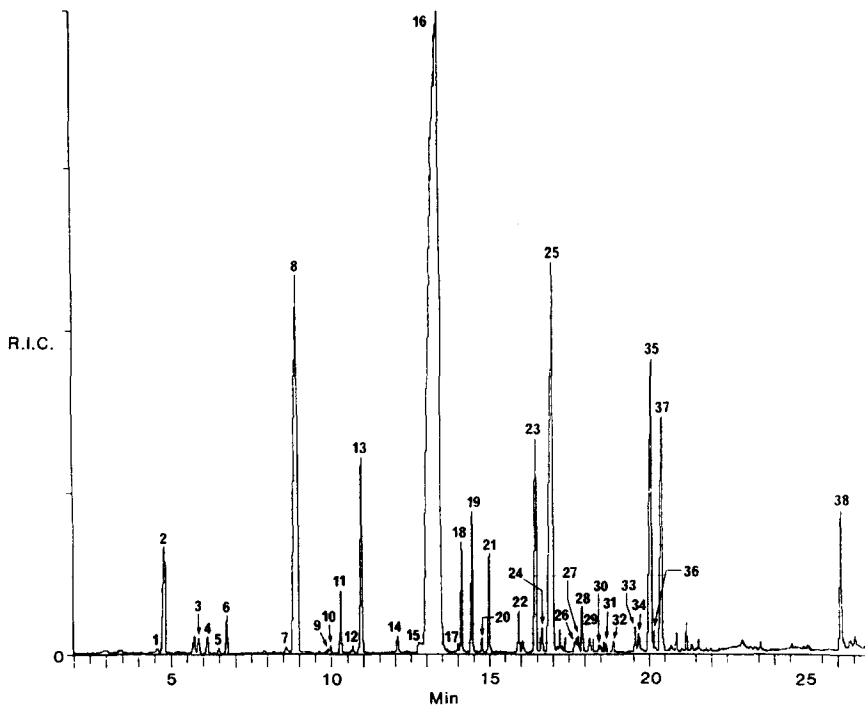


FIG. 4. GAS CHROMATOGRAM OF A SINGLE WORKER DUFOUR GLAND OF *C. SAVIGNYI*. Numbers refer to identification in Table 3.

TABLE 3. MEAN VALUES FOR THE COMPOSITION OF THE CONTENTS OF THE DUFOUR GLAND OF *CATAGLYPHIS SAVIGNYI* WORKERS DETERMINED BY GC AND MS

Peak	Compound	%	SD	Mean quantity	
				(μg)	(SD)
1	Undecane	t		t	
2	<i>n</i> -Undecane	2.0	0.7	0.51	0.97
3	5-Methylundecane	0.2	0.1	0.03	0.02
4	3-Methylundecane	0.2	0.1	0.03	0.02
5	Dodecene	t		t	
6	<i>n</i> -Dodecane	0.4	0.1	0.05	0.03
7	Tridecene	t		t	
8	<i>n</i> -Tridecane	14.2	2.0	1.55	0.7
9	7-Methyltridecane	t		t	
10	5-Methyltridecane	t		t	
11	3-Methyltridecane	0.8	0.5	0.09	0.10
12	Tetradecene	t		t	
13	<i>n</i> -Tetradecane	4.2	0.8	0.48	0.29
14	Dodecan-1-ol	0.5	0.5	0.05	0.05
15	Pentadecene	0.3	0.2	0.06	0.12
16	<i>n</i> -Pentadecane	58.2	5.9	6.02	1.78
17	7-Methylpentadecane	t		t	
18	5-Methylpentadecane	1.4	0.8	0.17	0.17
19	3-Methylpentadecane	1.7	1.0	0.20	0.20
20	Hexadecene	t		t	
21	<i>n</i> -Hexadecane	1.2	0.3	0.14	0.10
22	2-Methyltetradecanal	0.5	0.3	0.06	0.06
23	2-Pentadecanone	1.7	0.5	0.20	0.15
24	Heptadecene	0.2	0.1	0.02	0.01
25	<i>n</i> -Heptadecane	7.9	1.8	0.89	0.54
26	7-Methylheptadecane	t		t	
27	5-Methylheptadecane	t		t	
28	Pentadecan-1-ol	0.5	0.2	0.05	0.04
29	3-Methylheptadecane	t		t	
30	2-Hexadecanone	t		t	
31	Octadecene	t		t	
32	<i>n</i> -Octadecane	0.1	0.1	0.02	0.02
33	2-Methylhexadecanal	0.3	0.1	0.03	0.03
34	Hexadecan-1-ol	t		t	
35	2-Heptadecanone	1.6	0.4	0.18	0.10
36	Nonadecene	t		t	
37	<i>n</i> -Nonadecane	1.1	0.3	0.12	0.09
38	Tricosene	0.3	0.5	0.03	0.06
Total amount in μg				10.8	4.4

t=trace.

In each case the amounts of each of the substances in a single gland were calculated and the percentage composition for that individual determined. The means and sample deviations were then calculated from the individual values. This was done because we have found (e.g. [8]) that while the total amount in an individual worker's gland may vary considerably, as indicated by the standard deviations, the percentage composition does remain relatively constant for the sample.

TABLE 4. MEAN VALUES FOR THE COMPOSITION OF THE CONTENTS OF THE DUFOUR GLAND OF *CAMPONOTUS VAGUS* WORKERS DETERMINED BY GC AND MS

Peak	Compound	%	SD	Mean quantity	
				(μg)	(SD)
1	<i>n</i> -Nonane	t		t	
2	<i>n</i> -Decane	1.8	0.7	0.06	0.05
3	Undecene	0.6	0.5	0.02	0.03
4	<i>n</i> -Undecane	69.6	5.2	2.02	1.27
5	5-Methylundecane	0.1	0.1	0.005	0.004
6	3-Methylundecane	0.9	0.6	0.03	0.03
7	Dodecene	0.1	0.1	0.02	0.03
8	<i>n</i> -Dodecane	0.8	0.2	0.02	0.02
9	Tridecene	{ 0.4	0.2	{ 0.01	0.008
		{ 0.7	0.3	{ 0.02	0.02
10	<i>n</i> -Tridecane	21.8	6.2	0.65	0.52
11	Terpenoid	0.1	0.04	0.002	0.002
12	5-Methyltridecane	0.1	0.05	0.003	0.002
13	<i>n</i> -Tetradecane	0.04	0.3	0.002	0.002
14	Dodecanol	t		t	
15	<i>n</i> -Pentadecane	1.8	1.1	0.05	0.06
16	Dodecyl acetate	0.4	0.2	0.01	0.01
17	Heptadecene	0.04	0.05	0.009	0.03
18	Tridecyl acetate	t		t	
19	Tetradecyl acetate	0.04	0.04	0.002	0.002
20	Nonadecene	0.2	0.2	0.005	0.009
21	Unknown	0.1	0.1	0.003	0.006
22	Hexadecyl acetate	0.1	0.1	0.003	0.006
Total amount in μg				2.94	1.9

t=trace.

Discussion

The first important discovery is that the two castes of workers in *C. aegyptiacus* have distinctly different compositions in their Dufour glands. This parallels the only other study available ([4] and our own unpublished observations) on *Pheidole pallidula*, where the heavily armoured major workers have a distinctly different composition in their Dufour glands from that of minor workers. The richer blend of substances in *C. aegyptiacus* major workers and the presence of unusually large quantities of long chain acetates must provide a starting point for an interesting study of the function of this secretion and the division of labour between minor and major castes.

The second interesting discovery is that pentadecane is the most abundant substance in the glands of *C. savignyi*. Since this ant forages at daytime in a very hot environment (Delye has shown that *Cataglyphis* may survive temperatures of 50° for at least 1 h [9]), we presumed that it required a less volatile substance for

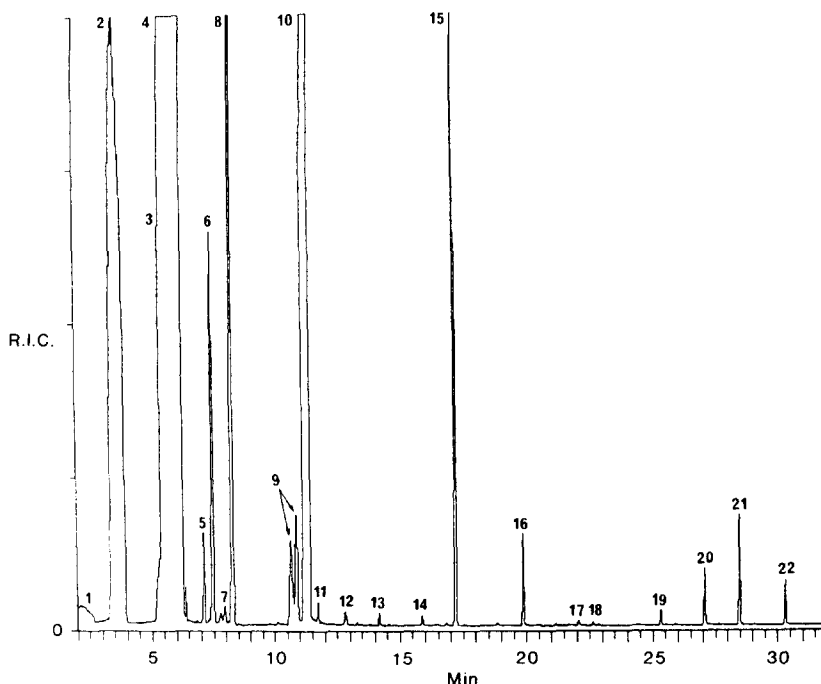


FIG. 5. GAS CHROMATOGRAM OF A DUFOUR GLAND FROM A WORKER OF *C. VAGUS*. Numbers refer to identification in Table 4.

whatever function it serves in these conditions. However, Hefetz and Orion, in examining the Dufour gland secretion of six species of *Cataglyphis* from Israel, found one, *C. bombycina*, that also produced pentadecane as its major component (70% [10]). This species was collected at Mount Hermon at a height of 2000 m, a very different habitat from the Nile valley. We also found a branched chain aldehyde, 2-methylhexadecanal (0.3%) in *C. savignyi*, not previously detected in Dufour glands, though other long chain aldehydes are known in *Nothomyrmecia* [8] and *Myrmecia* [11] from Australia. Although the workers varied in size in *C. savignyi*, there was no evidence of dimorphism in the sample of workers collected. It is noteworthy that Hefetz and Orion report that hexadecane is the major component in *Cataglyphis isis* and is 20% of the total in *C. viaticoides* [10]. This is surprising since we know of no other example in Dufour glands or elsewhere in insects where an even-numbered alkane is present in quantities greater than similar odd numbered alkanes, let alone as a major substance.

There are no records of volatiles in the mandibular glands of *Camponotus* species other than in males [3] and an early report of massoi-

lactone (δ -dec-2-enolactone) [12] in two unnamed Australian species. We found no volatiles in *C. aegyptiacus* or *C. vagus*. Hefetz and Lloyd reported that the mandibular glands of *Cataglyphis bombycina* contained citronellol and geraniol, and *C. nigra* contained only geraniol in smaller quantities [13]. They did not report on the other four *Cataglyphis* species they collected. We found no volatile substances in the heads of *C. savignyi*, but negative results from worker ants collected in this way must be treated cautiously, since the glandular contents could be discharged in alarm. Our techniques would detect as little as 1 ng of material and it seems unlikely that discharge would be so complete that not 1 or 0.1% secretion would remain.

The Dufour gland contents of a sufficiently large number of species of *Camponotus* from different parts of the world have now been recorded, to make it useful to review them here. We also had the opportunity to examine *C. vagus* from the Mediterranean littoral and include it here. Its Dufour gland composition was typical of many formicines, with undecane the most abundant compound but with minor oxygenated compounds also present.

In the very first study by Ayre and Blum [14],

undecane was the major substance in three species. In *C. americanus*, four alkanes and two alkenes were found with no oxygenated compounds, in *C. pennsylvanicus* a different mixture of alkanes and alkenes but again no oxygenated derivatives, and similarly in *C. americanus*, which had pentadecene, not present in the other two [14]. *Camponotus ligniperda* was shown to contain 37 identified and six unidentified compounds, including alkanes, alkenes, methyl-branched alkanes, 1-alcohols and 2-alkanones, alkyl and alkenyl acetates, farnesene and farnesyl acetate [15]. *Camponotus herculeanus* contains a similar mixture with 29 identified substances and five unidentified, but with only two alkanols, one alkanone and no farnesyl acetate [15]. In both these species, tridecane was the major substance, though in the sample of *C. herculeanus* from North America, examined by Ayre and Blum [14], undecane was the major component. The Australian species *C. intrepidus* showed tridecane as the major substance (30%) with undecane second (25%) [16]. It contained 11 *n*-alkanes and alkenes and 10 methyl-branched alkanes. In *C. japonicus* and *C. obscuripes* Hayashi and Komae found only four alkanes and one branched alkane; undecane was the major component [17]. Hefetz and Orion examined five species from Israel, of which two, *C. thoracicus fellah* and *C. thoracicus sanctoides* had undecane as the major substance, 92 and 75%, respectively [10]. *Camponotus lateralis rebecca* had 93% tridecane and little else, *C. sericeus* had 70% tridecane but a more complex mixture and *C. gestroi* had 5-methylpentadecane as the major substance (30%) with tridecane second (21%). This is the only species from any subfamily in which a branched alkane is the major, or anywhere near being the major Dufour substance [10]. No oxygenated substances were found in any of the five Israeli species. We similarly found a simple mixture of linear alkanes with undecane dominant in *C. aethiops* from Corsica [5]. With *C. vagus* also collected in Corsica, undecane is most abundant, but a more complex mixture with oxygenated compounds (Table 4) has been found. In *C. aegyptiacus*, the Dufour gland secretion of major workers is quite different from that in minor workers, in that the major workers contain acetates in high

quantities, alcohols, propionates and farnesyl acetate, which were not found in minors. *Camponotus aegyptiacus* major workers show a similarity in their secretion to those of both *C. ligniperda* and *C. herculeanus* which contain branched, saturated and unsaturated hydrocarbons, acetates, aliphatic alcohols, one terpenoid compound and farnesyl acetate, but *C. ligniperda* and *C. herculeanus* contain ketones not found in *C. aegyptiacus*. *Camponotus aegyptiacus* majors contain propionates, which have only been previously identified in *Myrmecia pilosula* [11] and *Lasius niger* [18]. The results of this comparison are summarized in Table 5. It is clear that the pattern of Dufour gland substances in this widely dispersed and diverse genus varies considerably, and is species-specific. What is not clear is its function. Hefetz and Orion were the only ones to attempt behavioural experiments with the secretion, and they concluded "the role of the Dufour gland in this behaviour (the alarm-defence system) is ambiguous" [10]. Ayre and Blum found from experiments with undecane and formic acid that undecane was a mild attractant, but then a mixture of the two produced a greater, but short-lived response [14].

Experimental

Camponotus aegyptiacus Emery and *C. savignyi* were collected at Minia, Egypt in August 1986 and brought live to Keele and maintained in artificial nests in the laboratory. The identification was made by C. A. Collingwood. *Camponotus vagus* (Scopoli) were collected in Corsica and identified by J. P. J. Billen. *Camponotus aegyptiacus* and *C. savignyi* were kept at 28° and photoperiod 16:8 (light-dark). All colonies were fed with water and sugar solution continually and at least once a week were given mealworm or dipteran larvae.

Preparation of glands for analysis. The samples for injection were prepared by anaesthetizing worker ants by momentarily immersing them in the cold vapour above liquid nitrogen, and then dissecting out the gland in distilled water under a binocular microscope with sharp tweezers. The Dufour gland was removed by gently pulling off the sternite from the abdominal tip, and then removing the gland and cleaning off other tissues. Excess water was removed by touching the gland with tissue paper after placing the gland on a fragment of glass. This was placed in a glass capillary (20 mm×1.8 mm) sealed at one end, and the other end was then immediately sealed in a flame.

Gas chromatography was carried out on a Carlo Erba Fractovap 4160 series instrument with a flame ionization detector and a Shimadzu Chromatopac C-R3A data processor. A fused silica capillary column (25 m×0.32 mm) coated with OV1 stationary phase of 0.4 µm film thickness was used for

TABLE 5. SUMMARY OF THE DISTINGUISHING FEATURES OF THE DUFOUR GLAND SECRETIONS OF *CAMPONOTUS* SPECIES

Species	Origin	Major compound	Amount (%)	Acetates*	Others†	Reference
<i>C. aethiops</i>	Corsica	C ₁₁	72	—	—	5
<i>C. americanus</i>	USA	C ₁₁	> 90	—	E	14
<i>C. japonicus</i>	Japan	C ₁₁	97	—	M	15
<i>C. obscuripes</i>	Japan	C ₁₁	96	—	M	15
<i>C. pennsylvanicus</i>	USA	C ₁₁	‡	—	E	14
<i>C. thoracicus fellah</i>	Israel	C ₁₁	92	—	E	10
<i>C. thoracicus sanctoides</i>	Israel	C ₁₁	75	—	E	10
<i>C. intrepidus</i>	Australia	C ₁₃	30	—	E,M	16
<i>C. lateralis rebecca</i>	Israel	C ₁₃	93	—	E	10
<i>C. sericeus</i>	Israel	C ₁₃	70	—	E,M	10
<i>C. gestroi</i>	Israel	5MeC ₁₅	30	—	M	10
<i>C. aegyptiacus</i> minors	Egypt	C ₁₁	78	±	E,M	§
<i>C. aegyptiacus</i> majors	Egypt	C ₁₁	52	+	E,M,A,F	§
<i>C. vagus</i>	Corsica	C ₁₁	70	+	E,M,A	§
<i>C. herculeanus</i>	Sweden	C ₁₃	—	+	E,M,A,K	15
<i>C. ligniperda</i>	Sweden	C ₁₃	—	+	E,M,F,A,K	15

*—, Acetates not present; +, acetates present.

†Presence of other compounds denoted by E=alkenes, M=methyl-branched compounds, F=farnesene or derivatives of it, A=alcohols, K=ketones.

‡Percentage not given.

§Data from this paper.

the analysis. Helium was used as the carrier gas at a flow rate of 1.0 ml min⁻¹.

The capillary tubes containing the samples were kept in the solid injector [19] in the injection port at 220° for 2 min before crushing. The split vent was kept closed during the injection and opened after 1 min. The oven temperature was initially 100° and increased at a rate of 6° min⁻¹ to 270°.

At least 10 individual glands (except *C. aegyptiacus* majors, where insufficient material was available) were analysed for each group. The absolute quantity of each component was determined by comparing with the peak area given by a solution of pentadecane in hexane of known concentration and giving comparable peak areas.

Representative samples were analysed by GC-MS, on a Hewlett Packard 5890 Gas Chromatograph and 5970B Mass Selective Detector with HP59970C ChemStation. A fused silica capillary column (12 m×0.2 mm) coated with HP-1 (cross linked methylsilicone gum ≡ OV-1) of 0.33 µm film thickness was used. The carrier gas was helium at 10 psi column head pressure (≡ 1 ml min⁻¹ flow rate). The samples were introduced by the solid injection method [19] described above. The oven temperature was initially 60° and increased at a rate of 4° min⁻¹ to 250°. The mass selective detector was set to monitor *m/z* 35–350 in the scan mode (≡ 1.5 scan s⁻¹) under "Autotune" conditions using 70 eV ionization.

Acknowledgements—We thank the Egyptian government for a research fellowship, and the University of Minia for leave of absence to M.F.A. We also thank the British Council for support to J.P.J.B. and E.D.M., the SERC for a studentship to B.D.J., and the Royal Society and SERC for grants for equipment to E.D.M. We thank C.A. Collingwood for help in identification of the species. This work was carried out under MAFF licence number PHF 244/27,28 issued under the Import and Export (Plant Health) (Great Britain) Order 1980 and the Plant Pests (Great Britain) Order 1980 by the Ministry of Agriculture, Fisheries and Food.

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