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The Dufour Gland Contents of Three Species of Euro-African *Messor* Ants and a Comparison with those of North American *Pogonomyrmex* (Hymenoptera:Formicidae)

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Key Word Index—*Messor minor*; *Messor capitatus*; *Messor bouvieri*; workers; queens; Dufour gland; harvester ants; caste differences.

Abstract—The Dufour gland secretions of *Messor minor, Messor capitatus* and *Messor bouvieri* differ from those of other myrmicine ants so far studied in having no sesquiterpenoids present. *M. minor resembles the North American harvester ants, Pogonomyrmex,* in containing branched chain hydrocarbons. *Messor* and *Pogonomyrmex* appear anomalous among myrmicines and more closely resemble some formicines in this respect. *M. minor* queens contain chiefly pentadecene (57%), a substance absent from workers (major substance, tridecane, 33%), but are otherwise similar. *M. capitatus* workers contain tridecane (28%) and nonadecane (26%) and no branched hydrocarbons. *M. bouvieri* workers contain linear hydrocarbons, with heptadecadiene (50%) as the major substance, but also small quantities of citronellyl decanoate, a new natural product.

Introduction

Harvester ants (belonging to the subfamily Myrmicinae) occur in the warmer regions of the Northern Hemisphere [1, 2]. The Old and New World species occupy very similar or even identical ecological habitats and display the same behavioural characteristics of harvesting and storing seeds, but they differ considerably in their stinging abilities. The European and North African *Messor* have a very much reduced and probably non-functional sting, whereas the North American *Pogonomyrmex* species possess an extremely effective and powerful sting apparatus.

The two main exocrine glands that discharge through the formicid sting are the venom gland and the Dufour gland. The former generally produces the toxic and mostly proteinaceous venom, while the Dufour gland contents can perform a variety of pheromonal functions [3], and moreover has a species-specific composition [4]. This character therefore has recently been used as a reliable chemotaxonomic tool. From an earlier and preliminary study of the Dufour gland substances of two *Messor* species, we formed the view that they bore considerable resemblance to at least one species of *Pogonomyrmex* [5].

When this present work was done, the only published investigations of Dufour gland substances of harvester ants were two studies on *Pogonomyrmex* species [6, 7]. In the few species examined, there appeared to be a divergence from the normal pattern of substances found in myrmicine ants, in that they include methyl-branched hydrocarbons in addition to straight chains.

We therefore wished to examine again, with the more powerful techniques now available (capillary gas chromatography and linked mass spectrometry), some *Messor* species and to compare them with the results available on *Pogonomyrmex* and other myrmicine species. We describe here our examination of *Messor minor* (André), *Messor capitatus* (Latr.) and *Messor bouvieri* Bondroit. By chance, in collecting *M. minor* workers, a number of deallated queens were collected also. We have therefore included data on both queens and workers in order to build up a picture of specificity between

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these castes in our efforts to understand the function of this secretion.

Results

In each case, single glands dissected from freshly anaesthetized insects were analysed, without the intervention of solvents, by the method of Morgan and Wadhams [8]. The results from at least ten determinations were used to calculate the mean and sample standard deviation of amount and percentage composition. As in previous studies, although the total amount per individual varied widely, the percentage composition remained rather constant, as indicated by the sample standard deviations given in Tables 1–4.

The composition of the secretion in the glands of *M. minor* queens and workers has one distinct difference. The major substance in the queens is pentadecene, while this was not detected at all in workers (Figs 1 and 2). Otherwise, the glands of both castes are filled with similar mixtures of straight chain and branched alkanes and straight chain alkenes with traces of dienes, with the substances in roughly the same proportions in both. The glands of queens contain about three times as much as those of workers, roughly reflecting their difference in body size. No oxygenated compounds nor terpenoids were detected. If present, these latter substances must be in quantities of less than 10 ng or representing less than 0.1% of the total.

M. capitatus workers had a relatively simple mixture of straight chain alkanes and alkenes (Fig. 3) with no branched chains, terpenes or oxygenated compounds. Tridecane (28%) and nonadecane (26%) are by far the major compounds (Table 3).

M. bouvieri workers had relatively small Dufour glands. Only three worker glands were successfully dissected, and for these, a mean value of 365 ng of secretion was obtained. The

TABLE 1. MEAN AMOUNTS AND PERCENTAGES OF THE DUFOUR GLAND COMPOUNDS OF *MESSOR MINOR* WORKERS DETERMINED BY GAS CHROMATOGRAPHY AND MASS SPECTROMETRY

Number	Compound	%±SD		Mean quantity* (µg±SD)	
1	*n*-Undecane	4.0	1.2	0.09	0.04
2	5-Methylundecane	1.2	1.6	0.02	0.01
3	3-Methylundecane	1.5	0.5	0.03	0.01
4	*n*-Dodecane	1.7	0.2	0.04	0.02
5	Tridecene	t		t	
6	*n*-Tridecane	33.4	3.6	0.85	0.33
7	7-Methyltridecane	3.8	0.7	0.09	0.08
8	5-Methyltridecane	4.6	0.4	0.11	0.05
9	3-Methyltridecane	5.2	0.4	0.12	0.06
10	Tetradecene	0.8	0.2	0.02	0.01
11	*n*-Tetradecane	2.3	0.4	0.06	0.03
12	*n*-Pentadecane	16.7	1.5	0.40	0.19
13	7-Methylpentadecane	0.3	0.2	0.08	0.05
14	5-Methylpentadecane	0.9	0.2	0.02	0.01
15	3-Methylpentadecane	1.9	0.4	0.05	0.03
16	Hexadecene	0.6	0.1	0.02	0.01
17	*n*-Hexadecane	1.3	0.2	0.03	0.02
18	Heptadecadiene	1.2	0.3	0.03	0.01
19	Heptadecene	0.5	0.3	0.02	0.01
20	*n*-Heptadecane	4.9	0.4	0.12	0.05
21	Octadecene	0.7	0.1	0.02	0.007
22	Nonadecadiene	0.9	0.5	0.02	0.01
23	Nonadecene	9.9	2.4	0.23	0.11
24	*n*-Nonadecane	0.2	0.4	0.003	0.004
Total amount in µg				2.34±1.0	

t=Trace.
*Computed as previously described [4].

TABLE 2. MEAN AMOUNTS AND PERCENTAGES OF THE DUFOUR GLAND COMPOUNDS OF *MESSOR MINOR* QUEENS DETERMINED BY GAS CHROMATOGRAPHY AND MASS SPECTROMETRY

Number	Compound	%±SD		Mean quantity* (µg±SD)	
1	*n*-Undecane	1.2	0.7	0.09	0.05
2	5-Methylundecane	0.1	0.1	0.006	0.005
3	3-Methylundecane	0.1	0.1	0.001	0.01
4	*n*-Dodecane	0.3	0.1	0.02	0.01
5	Tridecene	1.0	0.3	0.08	0.04
6	*n*-Tridecane	14.4	2.4	1.05	0.36
7	7-Methyltridecane	0.7	0.3	0.05	0.03
8	3-Methyltridecane	0.8	0.4	0.06	0.03
9	Tetradecene	2.5	0.4	0.18	0.07
10	*n*-Tetradecane	1.2	0.3	0.09	0.03
11	Pentadecadiene	0.4	0.1	0.03	0.007
12	Pentadecene	56.5	7.2	4.02	0.89
13	*n*-Pentadecane	13.5	2.5	0.97	0.25
14	7-Methylpentadecane	t		t	
15	5-Methylpentadecane	0.4	0.2	0.03	0.02
16	3-Methylpentadecane	1.4	0.3	0.10	0.03
17	Hexadecene	0.3	0.1	0.02	0.009
18	*n*-Hexadecane	0.7	0.2	0.05	0.02
19	Heptadecene	0.6	0.1	0.04	0.01
20	*n*-Heptadecane	2.3	0.7	0.16	0.06
Total amount in µg				7.16±1.54	

t=Trace.

TABLE 3. MEAN AMOUNTS AND PERCENTAGES OF THE DUFOUR GLAND COMPOUNDS OF *MESSOR CAPITATUS* WORKERS DETERMINED BY GAS CHROMATOGRAPHY AND MASS SPECTROMETRY

Number	Compound	%±SD		Mean quantity* (µg±SD)	
1	*n*-Undecane	0.4	0.3	0.009	0.009
2	*n*-Dodecane	0.4	0.3	0.009	0.009
3	Tridecene	1.9	0.4	0.04	0.04
4	*n*-Tridecane	27.6	5.9	0.58	0.47
5	Pentadecene	6.5	1.3	0.14	0.12
6	*n*-Pentadecane	3.3	0.9	0.07	0.06
7	*n*-Hexadecane	t		t	
8	Heptadecene	3.6	1.0	0.08	0.10
9	*n*-Heptadecane	3.7	1.4	0.08	0.11
10	Octadecene	0.3	0.2	0.006	0.008
11	*n*-Octadecane	1.4	0.3	0.03	0.03
12	Nonadecene	8.8	2.9	0.21	0.22
13	*n*-Nonadecane	25.8	6.5	0.53	0.44
14	Eicosene	0.5	0.3	0.01	0.01
15	*n*-Eisocane	0.5	0.2	0.01	0.01
16	Heneicosene	9.6	4.6	0.20	0.18
17	*n*-Heneicosane	4.1	1.2	0.10	0.10
Total amount in µg				2.15±1.93	

t=Trace.

secretion consisted almost entirely of linear alkanes, alkenes, dienes and trienes (Table 4). A small amount of two esters were found, citronellyl decanoate (1.5% of total) and decyl decanoate, but no sesquiterpenes of the farnesene type (Fig. 4).

TABLE 4. MEAN AMOUNTS AND PERCENTAGES OF THE DUFOUR GLAND COMPOUNDS OF *MESSOR BOUVIERI* WORKERS DETERMINED BY GAS CHROMATOGRAPHY AND MASS SPECTROMETRY. The values are based on only three samples

Number	Compound	%±SD		Mean quantity* (µg±SD)	
1	*n*-Undecane	3.2	1.9	15.1	13.4
2	Dodecane	0.1	0.1	0.5	0.5
3	Tridecadiene	0.1	0.1	0.7	0.6
4	Tridecene	0.3	0.1	1.3	1.3
5	Tridecane	5.3	0.4	19.8	14.8
6	Tetradecene	t		t	
7	Tetradecane	0.3	0.2	1.3	1.4
8	Pentadecadiene	2.7	1.8	8.1	6.7
9	Pentadecene	4.9	1.4	19.3	14.3
10	Pentadecane	6.9	1.7	23.5	17.7
11	Hexadecatriene	0.3	0.1	1.0	0.8
12	Hexadecadiene	0.9	0.2	3.5	3.2
13	Hexadecene	0.2	0.1	0.6	0.7
14	Hexadecane	0.5	0.1	1.8	1.5
15	Heptadecatriene	10.3	3.8	41.5	31.5
16	Heptadecadiene	50.1	2.5	179	123
17	Heptadecene	2.5	0.5	8.5	6.1
18	Heptadecane	4.7	1.7	12.3	10.1
19	Octadecane	0.2	0.1	0.8	0.7
20	Nonadecadiene	2.0	1.1	8.7	7.4
21	Nonadecene	1.4	0.4	5.5	4.9
22	Nonadecane	0.1	0.1	0.6	0.5
23	Unknown	0.4	0.1	1.1	1.3
24	Eicosane	t		t	
25	Unknown	0.2	0.1	0.6	0.8
26	Heneicosane	t		t	
27	Citronellyl decanoate	1.5	0.5	5.9	5.5
28	Unknown	0.2	0.1	0.6	0.6
29	Decyl decanoate	1.5	0.8	4.2	2.0
30	Docosane	t		t	
Total amount in ng				365.3	

t—Trace.

Discussion

We carried out a study on *Messor minor* workers' Dufour glands some years ago, using packed chromatography columns. The data from that work is not widely available [5]. The major substance found in the earlier work was tridecane (36%) followed by pentadecane (22%), methyltridecanes (together 17%), undecane (5%) and heptadecane (5%) (mean values from 13 determinations). Given the greater accuracy obtainable now, this is remarkably close to the results in Table 1 and supports our belief that the composition is constant for a species. Both the *Messor minor* samples were collected in Corsica, 4 years apart, but in an examination of *Tetramorium caespitum* over a wide area of western Europe we found a variation in only one district [9].

The second point to note is that none of the species of *Messor* showed any evidence of farnesene or its related sesquiterpenes. The Dufour glands of at least 29 species of Myrmicinae have now been examined. In 19 of them farnesene (or homofarnesene or bishomofarnesene, for structures see [10]) have been recorded, namely *Aphaenogaster longiceps* [11], *Harpagoxenus sublaevis* [12], 13 species of *Myrmica* [9, 13, 14], *Manica rubida* [15], *Pheidole pallidula* [16], *Pogonomyrmex occidentalis* [7, 17] *Solenopsis geminata* [Morgan *et al.* unpublished data], *S. invicata* [18]. In four others, related sesquiterpene compounds called tetramorenes have been identified, in *Leptothorax acervorum* [19], *L. nylanderi* [19], *Tetramorium caespitum* [20], *T. impurum* [20] and *T. semilaeve* [Morgan *et al.*, unpublished data]. For six other species we

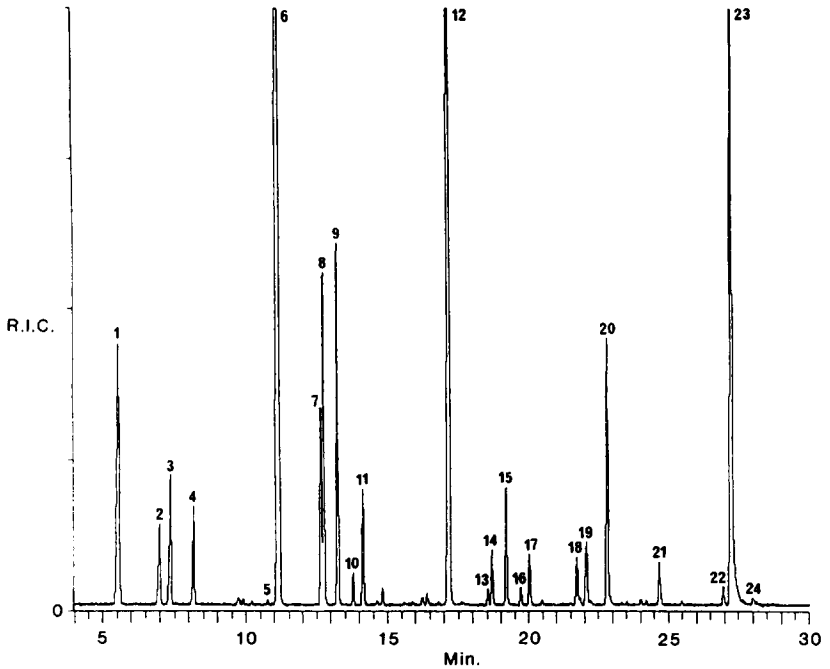

FIG. 1. GAS CHROMATOGRAM OF THE DUFOUR GLAND FROM A SINGLE WORKER OF *MESSOR MINOR*. The substances corresponding to the numbered peaks are identified in Table 1.

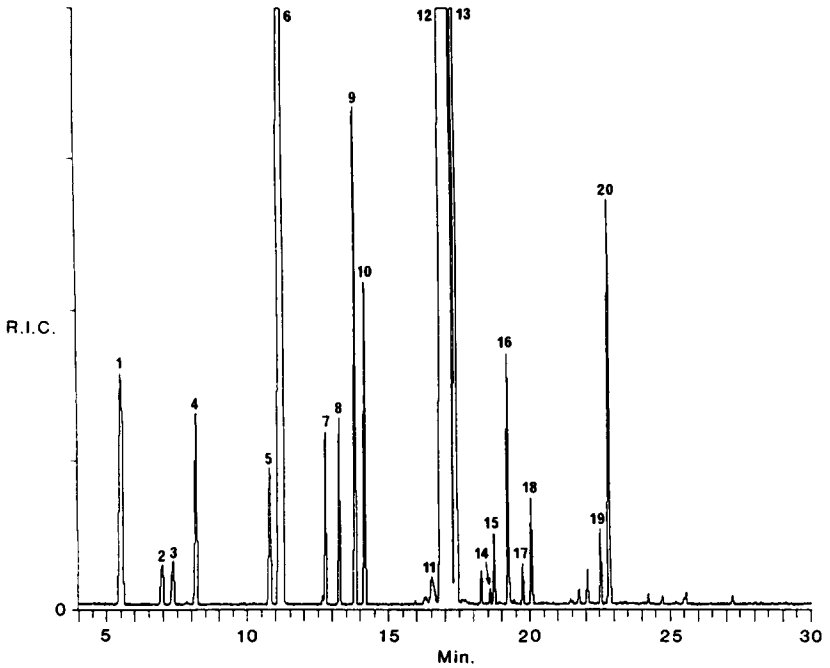

FIG. 2. GAS CHROMATOGRAM OF THE DUFOUR GLAND OF A SINGLE QUEEN OF *M. MINOR*. For identification of peaks, see Table 2. No. 12 is pentadecene.

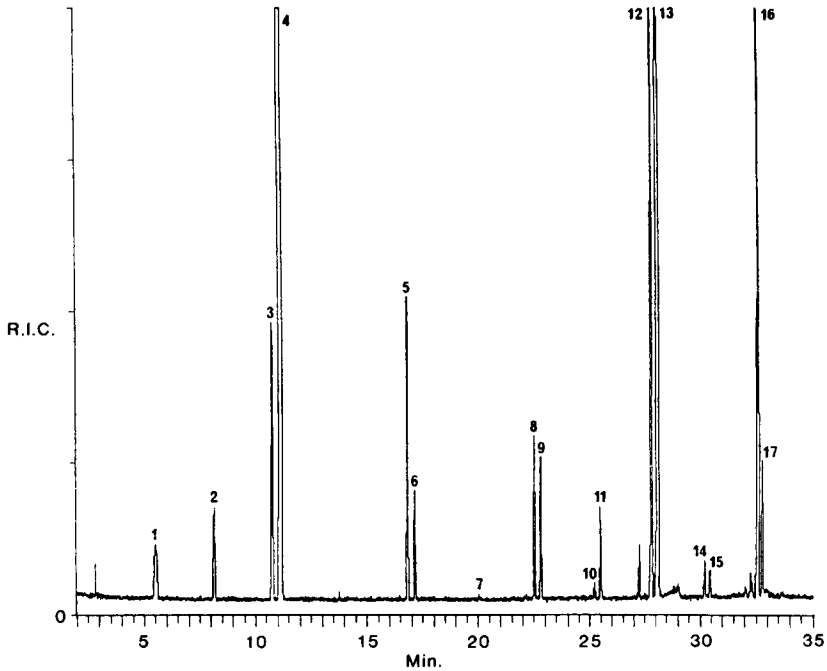

FIG. 3. GAS CHROMATOGRAM OF A DUFOUR GLAND FROM A SINGLE WORKER OF *MESSOR* CAPITATUS. The numbers correspond to those in Table 3.

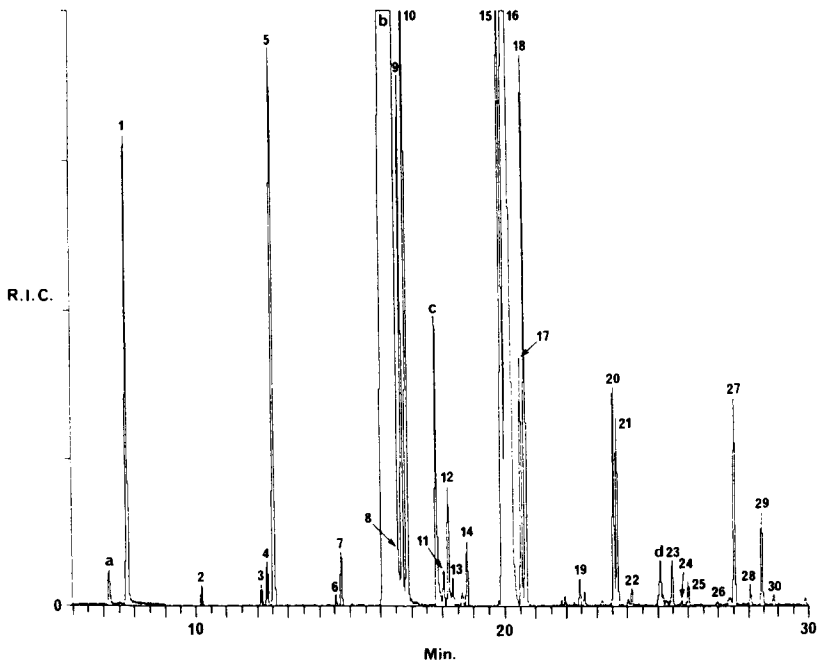

FIG. 4. GAS CHROMATOGRAM OF A SINGLE POISON APPARATUS FROM A WORKER OF *MESSOR BOUVIERI*. The numbers correspond to those compounds listed in Table 4. The other compounds, (a) ethyldimethylpyrazine, (b) anabasine and (c) anabaseine, all come from the poison reservoir (see [31]). Phthalate esters (d) from plastics are ubiquitous contaminants.

must reserve decision until they have been re-examined. The published gas chromatograms of *Novomessor cockerelli* [21], *Pogonomyrmex barbatus* [6], *P. rugosus* [6], *Solenopsis richteri* [22] and *S. xyloni* [22] show the presence of unidentified compounds which could be farnesene or homofarnesene, judging from their retention times. Since we carried out this work, there have been two papers on *Messor* species that mention Dufour gland contents. Hefetz *et al.* [23] have looked at the poison apparatus (described as the adnexal glands) of *Messor ebeninus* Forel from Israel and report that the Dufour gland contained a series of *n*-alkanes and alkenes from C_{13} to C_{17} with pentadecane the major component. Another report on *Messor galla* (Mayr) from Nigeria reports the Dufour gland to contain C_{13} to C_{21} *n*-alkanes and alkenes with pentadecane the major substance (23%) [24]. This paper reports benzyl alcohol (2%) and 4-phenyl-3-buten-2-one (2%) as being present also in the Dufour gland. If this is correct, it represents a most unusual appearance of these compounds in Dufour glands and would deserve further, particularly behavioural, investigation. No mention of sesquiterpenes or branched hydrocarbons was made in either paper. From recent, still incomplete, studies, on *Pogonomyrmex* it appears that while branched chain hydrocarbons are always present, sesquiterpenes may or may not be found. *Messor* species are the first myrmicines clearly shown to lack farnesenes or related sesquiterpenes in their Dufour glands.

Messor Dufour glands contents therefore do not fit the typical pattern of myrmicine Dufour glands, but resemble *Pogonomyrmex* species more closely than any other myrmicines. This anomalous position, shared by *Messor* and *Pogonomyrmex* within the Myrmicinae is the more interesting, since it brings closer together two ecologically similar genera, even though they occcur in two different continents, and possess a considerably different sting capacity. Not only do *Messor* not contain farnesene or related sesquiterpenes, one at least *M. minor*, contains branched hydrocarbons, much more characteristic of many formicine species, a characteristic it shares with *Pogonomyrmex. M. bouvieri* also bears a resemblance to many formicines in having significant quantities of undecane and tridecane and it is the first myrmicine found to contain aliphatic esters in its Dufour gland. Decyl decanoate has already been identified in the Dufour gland of the formicine *Lasius niger* [25]; citronellyl decanoate is a new substance, not previously described. *M. capitatus* and *M. galla* are noteworthy for being the first species, of any subfamily, in which nonadecane has appeared in anything more than trace quantities, 26% in *M. capitatus* and 18% in *M. galla.*

Hölldobler has extensively studied the behaviour of harvester ants and shown that they display territorality [26] and home range orientation [27]. Although he was unable to come to any clear conclusion about the purpose of the Dufour gland secretion, he concluded that it had some part in recruitment and foraging in *Pogonomyrmex badius* [28]. Hefetz *et al.* [23] found that Dufour substances of *Messor* did not induce aggression or excitement in workers but the mixture induced recruitment and the ants tended to remain on the marked area for a long time. Both Hölldobler and Wilson [28] and Hefetz *et al.* [28] note that the Dufour secretion has a longer lasting effect than other glandular secretions. Hefetz and Orion [29] found similar mild behavioural responses to the Dufour secretion with *Camponotus, Cataglyphis* and *Polyrhachis* species from the formicine subfamily. We have shown that in a number of species of *Myrmica*, the Dufour gland secretion provides a home-range marking pheromone [30]. Perhaps this function of the secretion is more widely shared with other genera and subfamilies. We have recently shown that for *M. bouvieri,* while 3-ethyl-2,5-dimethylpyrazine from the poison gland induces trail following, the contents of the Dufour gland can also induce workers of this species to follow trails [31].

The opportunity of collecting sufficient samples of both queens and workers of *M. minor* enabled us to add to the few comparisons that have been made of the substances in the Dufour glands of the two castes. Bergström and Löfqvist found no differences between the Dufour gland secretions of workers and females of the formicine ant *Formica sanguinea* except that nonyl acetate was present in females but absent from workers [32]. When comparing virgin and egg-laying females of *Formica polyctena* they

found the virgin females had much larger glands with undecane (74%) the major substance. The old queens had smaller glands with tridecane (50%) the chief component, and undecane less than 1% [33]. We found very little difference between workers and virgin females of the formicine *Camponotus aethiops* [3] or the myrmicine *Leptothorax acervorum* [19]. The presence of pentadecane as the major substance in *M. minor* queens and its absence from workers makes a distinct difference between the castes and contrasts with the general similarity of their secretions. In the two examined cases, where there is dimorphism in workers the difference between major and minor workers is clear cut [4, 16] and invites behaviour investigation. The significance of a difference between queens and workers remains obscure.

Experimental

Collection and maintenance of colonies. Workers and queens of *Messor minor* and workers of *M. capitatus* from Calvi and Solenzara, Corsica and *M. bouvieri* from Hammamet, Tunisia were reared in artificial nests made from plastic bottles, partially filled with moistened plaster of Paris. Some torn tissue paper was placed in the bottle. The nest was placed in a plastic bowl to serve as a foraging area. The inner vertical walls of the bowl were covered with Fluon paste to prevent the ants from escaping. The ants were kept in the laboratory on a diet of sugar solution and grass seeds.

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, 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 a fragment of tissue paper after placing the gland on a fragment of glass. This was placed in a glass capillary (2 cm × 1.8 mm) sealed at one end, and the other end was then immediately sealed in a flame.

Gas chromatography. Gas chromatography was carried out on a Carlo Erba Fractovap 4160 series intrument 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 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 [8] in the injection port at 220°C 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°C and increased at a rate of 6° min^{-1} to 270°C.

At least 10 individual glands were analysed for each group except *M. bouvieri*. 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.

Mass spectrometry. 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 [8] described above. The oven temperature was initially 60°C and increased at a rate of 4°C min^{-1} to 250°C. The mass selective detector was set to monitor *m/z* 35–350 in the scan mode (≈ 1.5 scan sec^{-1}) under "Autotune" conditions using 70 eV ionization.

Citronellyl decanoate and decyl decanoate were synthesized from the appropriate alcohol and decanoic acid by the method used for a mixture of esters in [25].

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