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The femoral gland secretions of two xeric-adapted agamid lizards *Uromastyx aegyptia* and *U. ornata* (Squamata: Agamidae): a comparative study

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Lizards possess epidermal glands which produce secretions playing a role as semiochemicals. Classic anatomical studies do not give detailed information on the nature of the secretions. Here I used GC-MS analysis of gland secretions to focus on the molecular structure of femoral gland secretions in two xeric-adapted agamid lizards, *Uromastyx aegyptia* and *U. ornata*. Steroids, alcohols, carboxylic acids, alkanes, aldehydes, carboxylic acid esters and squalene were detected as lipidic compounds. Monoglycerides of fatty acids and glycerol monoethers of long chain alcohols previously only detected in Lacertidae and Gekkonidae were also identified. The compounds constituting femoral secretions are possibly an adaptation to hot and dry habitats, with specific chemical profiles for each species. The presented data support the hypothesis that *Uromastyx* (and lizards in general) use femoral gland secretions for chemical communication.

Key words: agamidae, chemical communication, femoral glands, pheromones, *Uromastyx*

INTRODUCTION

Vertebrates communicate chemically using a variety of sources including excretions, secretions, and material recycled from other organisms and the environment (Muller-Schwarze, 2006). Among reptiles, lizards evolved femoral or pre-anal glands which are arranged in rows on the ventral surface of the hindlegs or proximal to the cloacal shield. These glands are more active in the breeding season, and generally larger in males than in females (Khannoon, 2009). The first author to discuss the femoral glands of lizards was Otth (1833), before Schaefer (1902) and Abraham (1930) provided morphological descriptions, followed by a characterisation of the histology and ultrastructure (Cole, 1966; Chiu & Maderson, 1975; Chauhan, 1986a; Mouton et al., 2010; Khannoon et al., 2013) as well as the chemical components secreted from these glands (López & Martín, 2005a, b; Gabirot et al., 2010; Martín et al., 2011; Pellitteri-Rosa et al., 2014).

Femoral secretions are used for species recognition and the marking of home ranges, and stimulate tongue flicking to assess their chemical nature (Alberts, 1993; Khannoon et al., 2010, 2011a); they thus serve a pheromonal function (Aragon et al., 2001; Lopez et al., 2006; Martin et al., 2007). Molecular techniques such as gas chromatography-mass spectrometry (GC-MS) revealed the lipophilic compounds in the femoral gland secretions of lacertids, comprising alcohols, steroids, carboxylic acids, esters, and squalene (López & Martín, 2005a, b, 2009; Martín & López, 2006; Khannoon et al., 2011b). Across a range of different lizard families, Integumental secretions in general have been suggested to participate in chemical signalling (Alberts, 1990, 1992; Alberts & Werner 1993), and consist of chemical compounds which can widely differ across families (teiids: Martín et al., 2011; cordylids: Louw et al., 2007, 2011; tropidurids: Escobar et al., 2001, 2003; gekkonids: Khannoon, 2012). Typically, major lipophilic compounds in femoral gland secretions of lizards are steroids and carboxylic or fatty acids. High molecular weight fatty acids are believed to maximise efficacy of substrate scent marks. Being less volatile, they are favoured in areas with high temperatures and high humidity (Alberts, 1992). Steroids, and cholesterol in particular, are used to form an unreactive apolar matrix that holds and protects other lipids in the scent marks (Escobar et al., 2003), and the relative amount of cholesterol could suggest a signalling function (Martín & López, 2007; Khannoon et al., 2011a). Alcohols may form waxy esters that help femoral secretions to become more cohesive, enhancing the durability of possible pheromonal signals in xeric habitats (López & Martín, 2005a; Khannoon et al. 2011a).

Agamid lizards are good candidates for studying femoral gland secretions (e.g., Chauhan, 1986b; Martin et al., 2012; Martin et al., 2013). *Uromastyx aegyptia* and *U. ornata* are common xeric species ubiquitously distributed in Egypt (Baha El Din, 2006), and only males

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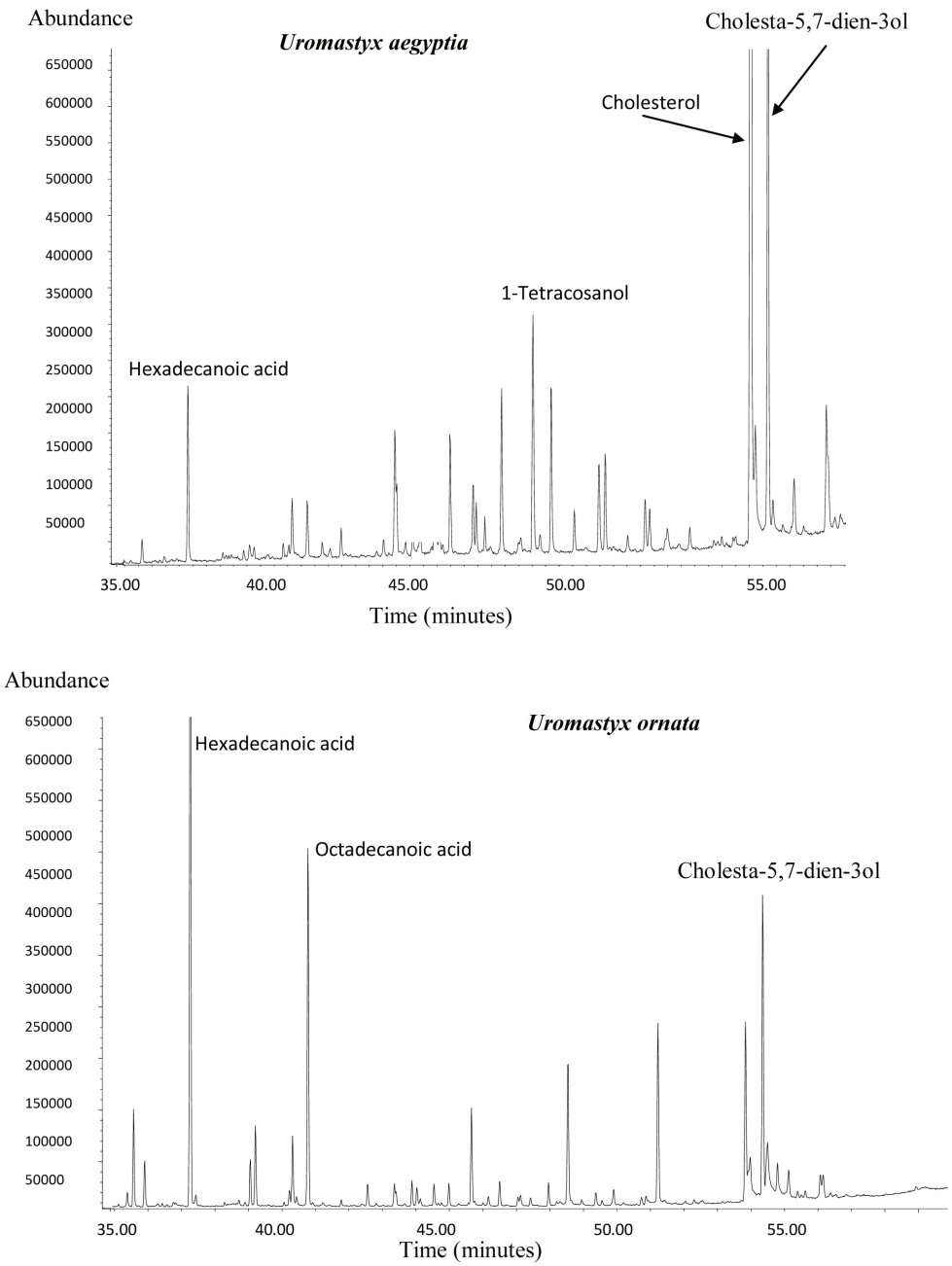

Fig. 1. GC traces (selected parts) of femoral gland secretions collected in dichloromethane from male agamid lizards, *Uromastyx aegyptia* and *U. ornata*. Compounds, detected as the respective trimethylsilylated, represented the highest relative abundance are shown.

possess well-developed femoral glands (female *U. ornata,* however, possess femoral glands in other areas of their range, Martin et al., 2012). Here I investigate the chemical composition of the epidermal glands of *U. aegyptia* and *U. ornata* to determine whether 1) the femoral secretion composition of xeric species differs from previously studied mesic species 2) the chemical fingerprint suggests the use of secretions in chemical communication, and 3) the two selected species can be discriminated based on their secretions.

MATERIALS AND METHODS

Adult *U. aegyptia* (*n*=6) and *U. ornata* (*n*=5) were collected by noosing in Sinai, Egypt during the breeding season (May–June). Only adult males of similar sizes were considered to avoid age effects (*U. aegyptia*: SVL=257±5 mm; *U. ornata*: SVL=135±5 mm). Individuals were housed in transparent plastic cages (80×45×35 cm) and released after the collection of secretions into glass vials with Teflon-lined caps by gently squeezing the plugs of the femoral pores. Secretions were then dissolved in 250 µl of dichloromethane (DCM, Aldrich, GC grade), and kept for 1–3 days at -18°C until processing. Control samples

Table 1. List of compounds identified in at least one sample of *Uromastyx aegyptia and U. ornata*. The gas chromatographic retention time (RT) is also given. Alcohols and acids were detected as the respective trimethylsilylated compounds, thus the RT shown is that of the respective derivative. The relative amount of each component was determined as the percent of the total ion current (TIC) and reported as the average ± standard error.*=Unknown alcohol.

RT	Compound	*Uromastyx aegyptia* (N = 6)	*U. ornata* (N = 5)	RT	Compound	*Uromastyx aegyptia* (N = 6)	*U. ornata* (N = 5)
14.88	2-Hydroxypropanoic acid	0.01±0.68	0.06±0.05	43.52	Glycerol 1-pentadecyl ether	0.11±0.55	-
14.98	Hexanoic acid	traces	traces	43.77	Glycerol 1-tetradecanoate	0.21±0.08	-
16.86	Oxopentanoic acid	-	0.02±0.66	44.19	Tetracosane	0.09±0.08	0.47±0.46
18.61	Nonanal	-	Traces	44.33	Acetate (alcohol unknown)	0.24±0.22	-
19.01	Decanal	-	0.01±0.33	44.41	Eicosenoic acid	0.28±0.44	-
19.58	Octanoic acid	-	0.03±0.32	44.57	Eicosanoic acid	3.81±0.94	0.68±0.34
19.95	Glycerol	0.15±0.06	0.30±0.28	44.72	Glycerolmomoether*	0.01±0.13	-
22.65	2,3-Dihydroxypropanoic acid	0.06±0.11	-	44.91	1-Heneicosanol	Traces	0.27±0.11
23.1	Nonanoic acid	traces	0.04±0.02	45.21	Glycerol 1-hexadecyl ether	4.79±2.04	0.68±0.28
24.16	Decanoic acid	traces	0.03±0.02	45.45	2-Eicosenoic acid	0.08±0.08	-
25.26	Hexanedioic acid	traces	-	45.55	Pentacosane	0.52+0.33	0.51±0.12
25.87	Methyl dodecanoate	0.05±0.01	0.05±0.04	45.71	1,3-Eicosanediol	0.07±0.07	-
25.86	Dodecanoic acid	0.06±0.02	0.17±0.01	46.03	Heneicosanoic acid	1.14±1.11	-
26.59	Alcohol (unknown)	0.01±0.01	0.07±0.11	46.19	1-Docosanol	2.53±0.98	1.65
33.01	Heptadecane	-	0.18±0.22	46.64	Glycerol 1-heptadecyl ether	0.01±0.66	0.41±0.21
33.24	Unknown	1.63±0.86	1.89±1.53	46.79	Glycerol 1-hexadecanoate	0.38±0.07	0.27±0.44
33.45	12-Methytridecanoic acid	-	0.24±0.12	46.81	Hexacosane	1.01±0.63	0.57±0.13
33.65	1-Tetradecanol	0.02±0.16	0.30±0.75	47.23	Docosenoic acid	-	0.36±0.19
33.9	Octadecane	0.02±0.65	-	47.61	Docosanoic acid	3.24±0.33	-
33.99	12-Methytridecanoic acid	0.01±0.01	0.31±0.36	47.87	1-Tricosanol	0.63±0.25	0.40±0.16
34.21	Tetradecanoic acid	0.09±0.03	0.47±0.23	48.11	Glycerol 1-octadecyl ether	1.79±0.52	0.40±0.25
34.45	13-Methyltetradecanoic acid	0.09±0.04	0.21±0.07	48.36	Glycerol 1-heptadecanoate	0.06±0.07	0.36±0.77
34.69	12-Methyltetradecanoic acid	0.04±0.15	0.31±0.21	48.48	Heptacosane	0.73±0.53	0.45±0.06
34.89	Methyl hexadecanoate	0.01±0.16	-	48.61	1,3-Docosanediol	0.12±0.14	-
35.34	Nonadecane	-	0.38±0.45	48.72	Tetracosen-1-ol	0.20±3.11	-
35.5	Pentadecanoic acid	0.04±0.19	0.51±0.18	49.05	1-Tetracosanol	10.45±2.66	2.72±0.20
36.01	1-Hexadecanol	1.12±0.65	1.42±0.05	49.43	Glycerol 1-octadecadienoate	0.24±0.85	0.52±0.34
36.4	Eicosane	-	0.41±0.55	49.57	Octacosane	0.64±0.42	0.38±13
36.74	14-Methylpentadecanoic acid	0.05±0.02	0.55±0.33	49.88	Squalene	1.03±1.33	-
37.35	Hexadecenoic acid	0.21±0.03	1.08±0.66	50.15	Tetracosenoic acid	0.16±0.64	-
37.52	Hexadecanoic acid	10.22±0.14	9.38±2.87	50.32	Tetracosanoic acid	1.61±0.55	Traces
37.77	1-Heptadecanol	0.18±0.15	0.47±0.17	50.61	1-Pentacosanol	1.39±0.07	0.19±0.18
37.96	Acid (unknown)	0.05±0.23	0.54±0.45	50.71	Nonacosane	0.46±0.14	0.27±0.11
38.32	Acid (unknown)	0.02±0.10	0.30±0.28	51.49	Cholesta-3,5-diene	0.53±0.19	0.01±0.80
38.77	Heneicosane	-	0.61±0.65	51.69	Hexacosen-1-ol	0.08±1.76	-
38.99	15-Methylhexadecanoic acid	0.07±0.001	0.26±0.23	51.81	1-Hexacosanol	0.11±0.77	3.51±0.10
39.25	14-Methylhexadecanoic acid	0.09±0.01	0.77±0.17	52.45	Glycerol 1-eicosanoate	0.070.03	0.220.0.91
39.49	Methyl octadecanoate	-	0.13±0.59	52.74	Hexacosanoic acid	Traces	traces
39.7	Heptadecanoic acid	0.72±0.65	0.99±0.23	52.82	Triacontane	0.19±0.12	0.27±0.18
39.68	1-Octadecanol	0.20±0.10	1.29±0.08	53.51	1-Heptacosanol	0.01±0.44	0.01±0.61
40.54	Docosane	-	0.90±0.44	54.03	Hentriacontane	-	0.21
40.67	Octadecadienoic acid	0.61±0.34	0.52±0.21	54.23	1-Octacosanol	Traces	trces
40.92	Octadecenoic acid	2.24±0.56	1.83±0.32	54.36	Cholesterol	19.75±6.67	3.46±0.36
41.5	Octadecanoic acid	10.06±2.92	6.12±0.05	54.55	Cholestan-3-ol	2.10±0.37	1.46±0.50
41.95	Glycerol 1-tetradecyl ether	0.13±0.07	-	54.91	Cholesta-5,7-dien-3ol	15.67±6.30	5.45±0.05
42.26	Tricosane	0.22±0.11	0.50±0.33	55.26	Steroid (unknown)	1.63±0.74	1.83±0.85
42.41	Glycerolmonoether*	0.01±0.26	-	55.42	Campesterol	1.08±0.20	0.87±0.13
42.85	2-Octadecenoic acid	0.02±0.23	-	55.75	Stigmasterol	0.11±0.22	0.21±0.01
42.94	1,3-Octanediol	Traces	-	56.23	Steroid (unknown)	-	0.21±0.001
43.15	Nonadecanoic acid	0.18±0.09	-	56.76	β-sitosterol	0.58±0.29	0.57±0.02
43.31	1-Eicosanol	0.32±0.28	0.53±0.12				

with the solvent at the same conditions of collecting the secretion were used to exclude impurities. To identify the polar compounds with poor elution properties, the extracts were also derivatised with N-methyl-N-trimethylsilyltrifluoroacetamide (MSTFA, Sigma-Aldrich) before analyses (see Khannoon et al., 2011a, Khannoon, 2012). Fifty µL of the liquid secretion was placed in a 2 ml vial, and the solvent was removed in a gentle stream of nitrogen at 50°C. The residue was taken up in 10 µL DCM, and 50 µL MSTFA was added. The mixture was heated to 50°C for 30–60 min in a vial with a closed cap. The solvent and the remaining reagent were evaporated in a gentle stream of nitrogen at 50°C and the residue was taken up in 10 µL DCM.

One µl of the residue was injected into a Hewlett–Packard model 6890 gas chromatograph connected to a Hewlett–Packard model 5973 mass-selective detector equipped with a 30 m × 0.32 mm BPX-5 column (0.25 µm film thickness, SGE). The temperature program was 50°C for 5 minutes, followed by a 5°C/min increase to 320°C and a final hold time of 30 minutes. Helium was used as carrier gas with 1 ml/min in constant flow mode. Accelerating voltage of MS was 70eV. Primarily, identification of secretion components was done by comparison of mass spectra in computerised mass spectral library (NIST02/NIH 2003). Identifications were confirmed by comparison of mass spectra and retention indices of derivatised and underivatised samples with those of reference compounds purchased from Sigma–Aldrich Chemical Company.

RESULTS

A total of 124 chemicals were identified in both species (Table 1), comprising steroids, alcohols, carboxylic acids, alkanes, amides, aldehydes, carboxylic acid esters, squalene. Analysis after derivatisation with MSTFA to form trimethylsilyl-derivatives also led to the identification of glycerolmonoethers and monoglycerides. The major compound groups present in the secretion of adult male *U. aegyptia* in percentage of the total ion current (TIC) were steroids (41.02%), carboxylic acids (17.28%), alcohols (8.86%), glycerolmonoethers (7.55%), and alkanes (3.12%). The other classes occurred only in minor amounts. The most abundant chemical detected (Fig. 1) was cholesterol (19.75%), followed by cholesta-3,5-dien-3-ol (15.66%) and 1-tetraosanol (10.45%). A different mixture of compounds was detected in the femoral secretion of *U. ornata*. The major compounds were acids (31.71%), steroids (14.43%), alcohols (11.54%), and alkanes (4.75%). The most abundant chemical detected (Fig. 1) was hexadecanoic acid (9.38%), followed by octadecanoic acid (6.12%) and cholesta-3,5-dien-3-ol (5.54%).

The following four groups were also detected. Monoglycerides carrying the carboxylic acid at C-1 were identified by their characteristic ions at m/z M-103 (M-$(CH_3)_3SiOCH_2^+$), 103 ($(CH_3)_3SiOCH_2^+$) and 205 ($(CH_3)_3SiOCH_2(CH_3)_3SiOCH^+$). Secondly, related monoethers of glycerol connected at C-1 were identified by showing a characteristic base peak at m/z 205 which is of low abundance in respective monoglycerides; an ion m/z M-147 (M-$(CH_3)_3SiO(CH_3)_2$) is characteristic together with M-205-2 H. Thirdly, 1, 3-alkanediols were identified by the ions m/z 103 ($(CH_3)_3SiOCH_2^+$), 219 ($(CH_3)_3SiOCH_2CH_2(CH_3)_3SiOCH^+$), and M-117 (M-$(CH_3)_3SiOCH_2CH_2^+$). Finally, respective glycerol ethers of the alkanediols connected terminally at both alcohols were also found, indicating the presence of three trimethylsilyl groups; a characteristic ion, e.g., m/z 313 in the mass spectra indicates the position of the silyloxy group in the long chain, and the other ions can be explained as above. These four groups were identified by comparison with synthetic reference compounds (see also Khannoon et al., 2011b).

DISCUSSION

The agamid lizards *U. aegyptia* and *U. ornata* are xeric-adapted. The presence of high molecular weight compounds in their femoral gland secretions was therefore expected to reduce the evaporation of chemical signals (Escobar et al., 2003). Steroids were the most abundant component in the femoral secretions of *U. aegyptia*, and the second-most common representative in the secretion of *U. ornata* (Table 1). High molecular weight steroids, and cholesterol in particular, were suggested to function as fixatives for semiochemicals or controlled-release carriers by constituting an unreactive, polar matrix (Escobar et al., 2003). Cholesterol and cholesta-3,5-dien-3ol (dehydrocholesterol) are indeed abundant in the secretions of both studied species. Such compounds might also reflect the physical condition of individuals in the context of dominance detection and mate choice (Martin & Lopez, 2006; Khannoon et al. 2011a, b). Carboxylic acids found in the present study ranged between C_3 and C_{26}. High molecular weight acids are likely compounds of low volatility, which could be important for the persistence of scent markings for territorial males. Tetradecanoic, hexadecanoic, octadecanoic, and octadecenoic acids are also present in internal tissue (Nicolaides, 1974), which confirms the holocrine secretion of femoral glands. Alcohols are usually found at high proportions in the femoral gland secretion of lizards, but represent the most common compounds only in lacertids (Lopez & Martin 2005a, b; Martin et al., 2007; Khannoon et al., 2011a, b). Alcohols indeed occurred at lower proportions than cholesterol and acids in the gland secretions of the agamids in the present study.

The four groups of compounds described here in detail (glycerolmonoethers, monoglycerides, 1,3 alkanediols, and glycerolethers of alkanediols) deserve further attention. These groups were initially detected in the lacertid *Acanthodactylus boskianus* (Khannoon et al., 2011b), and only monoglycerides and 1,3 alkanediol were found in geckos at rather low proportions (Khannoon, 2012). The presence of these compounds in the secretions of agamids parallels the xeric-adapted *A. boskianus*, likely acting as preservatives or carriers for other low volatile chemicals. For example glycerol alkyl monoethers were only rarely previously identified

in other taxa (starfish, Snyder et al., 1969; rats, Paltauf & Polheim, 1970; marine sponges, Quijano et al., 1994; octopus, Jahnke et al., 2001; bacteria Ring et al., 2006; clams and mussels, Hanus et al., 2009). Other compounds which were detected at low proportions could play a role as a communication signal, secured within the high molecular lipids and protein secretions and thus slowly released into the environment, similar to the volatiles of house mice *Mus domesticus* which are released at slow pace as triggered by major urinary proteins (Humphries et al., 1999).

The two agamid lizard species showed different bouquets of femoral gland chemicals. In *U. aegyptia*, steroids are approximately twice as abundant as acids, whereas acids are approximately twice more common than steroids in *U. ornata*. In addition to other differences between groups and individual compounds, this leads to both species having a specific chemical fingerprint despite characteristic features common with other members of the agamid family (e.g., Chauhan, 1986b). A more recent detailed study on the agamid *Acanthocercus atricollis* revealed the presence of ketones and steroids not detected in the present study, but failed to detect any alcohols (Martín et al., 2013). These differences could be linked to phylogenetic divergence between the studied genera as well as ecological differences between north African deserts and southern European habitats. The present study also revealed differences in comparison with a previously studied *U. aegyptia* population from the Qatar Desert (Martín et al., 2012), where steroids represented a higher proportion of femoral gland secretions (on average 58.6% compared to 41.02% in our study and also 83.2% in females, Martin et al., 2012). Some compounds such as ketones detected in the Qatar Desert population were not recorded in the present study, whereas alcohols were under-represented (0.5% in males and 0.1% in females in Qatar, compared to 8.86% in the present study). Differences in male secretion compounds could be due to differential ecological conditions, geographic separation, or a response to females also producing gland secretions. Silylation enabled the identification of compounds such as glycerolmonoethers and monoglycerides, which were not previously detected in agamid lizards including *U. aegyptia* (Chauhan, 1986b; Martín et al., 2012, 2013). This reinforces the importance of specific techniques used for characterisation of chemical compounds in chemical ecology.

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