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Cite this article: Wong JWY, Meunier J, Lucas C, Kölliker M. 2014 Paternal signature in kin recognition cues of a social insect: concealed in juveniles, revealed in adults. *Proc. R. Soc. B* **281**: 20141236.
<http://dx.doi.org/10.1098/rspb.2014.1236>

Received: 21 May 2014

Accepted: 22 July 2014

Subject Areas:

evolution, behaviour

Keywords:

cuticular hydrocarbons, maternal care, family life, patriline, insects, kin recognition

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.1236> or via <http://rspb.royalsocietypublishing.org>.

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Paternal signature in kin recognition cues of a social insect: concealed in juveniles, revealed in adults

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Kin recognition is a key mechanism to direct social behaviours towards related individuals or avoid inbreeding depression. In insects, recognition is generally mediated by cuticular hydrocarbon (CHC) compounds, which are partly inherited from parents. However, in social insects, potential nepotistic conflicts between group members from different patrilines are predicted to select against the expression of patriline-specific signatures in CHC profiles. Whereas this key prediction in the evolution of insect signalling received empirical support in eusocial insects, it remains unclear whether it can be generalized beyond eusociality to less-derived forms of social life. Here, we addressed this issue by manipulating the number of fathers siring clutches tended by females of the European earwig, *Forficula auricularia*, analysing the CHC profiles of the resulting juvenile and adult offspring, and using discriminant analysis to estimate the information content of CHC with respect to the maternal and paternal origin of individuals. As predicted, if paternally inherited cues are concealed during family life, increases in mating number had no effect on information content of CHC profiles among earwig juveniles, but significantly decreased the one among adult offspring. We suggest that age-dependent expression of patriline-specific cues evolved to limit the risks of nepotism as family-living juveniles and favour sibling-mating avoidance as group-living adults. These results highlight the role of parental care and social life in the evolution of chemical communication and recognition cues.

1. Introduction

The evolution of group living selects for recognition mechanisms ensuring that cooperative and aggressive behaviours are directed towards the appropriate individuals, but also that adult group members avoid the costs of sibling-mating. In insects, information about encountered individuals is typically displayed by the chemical cues present on the waxy layer covering their cuticle: the cuticular hydrocarbons (CHCs) [1–3]. CHC profiles have been shown to reflect information about different aspects of an individual's identity, such as the species [4] or the sex [5]. Inter-individual variation in CHC profiles is common in nature and typically due to various not mutually exclusive sources. For instance, CHC profiles have been shown to change over the course of an individual's life cycle, e.g. owing to aging [6] or to changes in individual tasks within colonies of eusocial insects [7], they can be influenced by the environment, such as the nesting substrate [8,9], nutritional condition [10,11] or social interactions with conspecifics, which mediates the active or passive transfer of chemical compounds between individuals [12–14]. Finally, CHC profiles can also vary owing to genetic differences between individuals (e.g. [15,16]). A heritable component to variation in CHCs is important for long-term similarities of CHC profiles among individuals originating from the same family or colony and thus, for CHCs to represent informative and sufficiently stable cues for individual identity and kin recognition (e.g. [3,17]).

Figure 1. Experimental design used to extract the CHC profiles from nymph and adult earwigs.

The importance of social conflicts on the expression of parent-of-origin specific cues in offspring has been a central and often controversial point in the research on the evolution of insect communication and social life (e.g. [18,19]). In particular, it has been suggested that polyandrous colonies of eusocial insects (ants, some bees and wasps) select against the expression of patriline-specific signals in their offspring (e.g. eggs, larvae and workers), because the expression of such signals could enhance the risks of paternally driven nepotistic conflicts between colony members and thus ultimately reduce colony efficiency and the fitness of group members [18,20]. Whereas this prediction received empirical support in several Hymenoptera species (e.g. reviewed in [21]; but see [22–24]), it remains unclear whether this process is specific to the derived eusocial systems or a more widespread phenomenon involved in the early evolution of social life. Disentangling these issues therefore requires investigating the occurrence of such a mechanism in insect species expressing non-derived forms of social life, such as the ones with temporary family life and maternal care. In families with uniparental female care and where multiple paternity occurs within a female's clutch, paternally inherited genes are predicted to select for the expression of patriline-specific signals in their offspring, which would favour cooperation between their own descendants and competition against the paternally unrelated half-siblings. Conversely, sibling competition generally reduces the number and/or quality of a mother's offspring [25], so that tending females (and/or the maternally inherited genes) could benefit from limiting the expression of patriline-specific cues in the offspring. Importantly under this hypothesis, the maternal concealment of information about the paternal origin of offspring should be limited to juveniles. When offspring become reproductive adults, they could otherwise suffer from the concealment of cues that are possibly used to limit the risks of inbreeding depression. Although this age-specific expression of patriline-specific cues in offspring is of key importance to better understand the joint evolution of insect communication and social life, its occurrence remained surprisingly unexplored so far.

In this study, we investigated whether variation in CHC profiles contains information allowing kin recognition in the European earwig *Forficula auricularia* L. (Dermaptera: Forficulidae), and whether the profiles are associated with an age-specific expression of paternally inherited cues in offspring. In this species, clutches are often sired by multiple males [26,27]. The offspring (nymphs) live in family groups for several weeks, during which females provide multiple

forms of care, such as egg and offspring attendance and food provisioning [27,28]. Previous work has shown that sibling competition and cannibalism are common in this species [29] and occurs significantly earlier and more often between unrelated nymphs from different clutches [29]. Thus, kin recognition cues seem to be present and used, and cannibalism is a potential form of nepotistic interactions among young nymphs. Once adult, *F. auricularia* individuals live in mixed-sex groups [27]. Inbreeding (sibling-mating) was shown to entail substantial fitness costs in this species [30], which could have thus selected for the expression of maternally and/or paternally inherited recognition cues to allow individuals avoiding mating with close relatives and thus limiting inbreeding depression.

We addressed the four following questions to test the predictions on the information content of CHC profiles in *F. auricularia*. (i) Is variation in CHC profiles smaller among individuals from the same than from different families, as expected if chemical signatures are family specific? (ii) Is within family variation larger in broods sired by multiple males compared with broods sired by a single male, as expected if the cues are heritable and display a signature of paternal origin? (iii) Is the expression of a paternal signature, i.e. higher variation in CHC profiles among offspring in multiply sired clutches, absent in offspring, but present in adults, as predicted under age-dependent concealment of paternally inherited cues? Finally, (iv) does the environment shared by adults also contribute to variation in their chemical profiles and thus possibly hamper family recognition after family disruption?

2. Material and methods

(a) Experimental design

The chemical signatures of 112 nymphs and 329 adults of *F. auricularia* were extracted from 16 experimental clutches (figure 1). These clutches were second clutches of either nine females mated to a single male ('singly mated females' = 1 M-treatment) or seven females mated to four successive unrelated males (each male was used only once across all the mating trials; 'multiply mated females' = 4 M-treatment). The 16 mothers (and their mates) were from a second laboratory-born generation of individuals sampled in May 2009 in Dolcedo (Italy). They were reared under standardized laboratory conditions until each female produced her first clutch (see details in [31]). Sixteen days after their first clutch hatched, all 16 females were isolated individually in a small Petri dish (10 cm diameter) for a second clutch production. The Petri dishes were kept in a

climate chamber at 15°C, 60% humidity and complete darkness until egg laying and hatching.

One day after hatching of their second clutch (day 1), each mother and 37.6 ± 1.28 nymphs (mean $\pm$ s.e.) of her second clutch were transferred into new Petri dishes and subsequently reared at 20°C, 60% humidity and 14 L:10 D cycle. On day seven, eight nymphs per clutch (from seven 1 M and seven 4 M clutches) were randomly sampled, singly isolated in glass-vials (300 μ l) and immediately frozen at -20°C for later chemical extractions. The remaining nymphs were kept with their mothers until day 14. Then mothers were removed and all nymphs were transferred to large Petri dishes (14 cm diameter) until their adulthood [31]. Just after moulting into adults, males and females of each family were separated in two new large Petri dishes to prevent sibling-mating. Once all individuals became adults, eight males and eight females were randomly sampled in each family and set up in new large Petri dishes (called family groups) with seven 1 M groups and seven 4 M groups per sex. We used the same seven 4 M families to sample nymphs and adults. But owing to small clutch sizes, we used five 1 M families to sample both nymphs and adults, two 1 M families to sample only nymphs and two different 1 M families to sample only adults.

To test the influence of shared environment (i.e. the Petri dish) on variations in adult chemical profiles, we mixed adults from 12 experimental clutches (both 1 M and 4 M) to form seven groups of eight unrelated females and seven groups of eight unrelated males (called unrelated groups, figure 1). One month later, all adults were frozen during 2 h at -20°C, then individually transferred to a 2 ml glass vial and kept at -20°C until chemical extractions. Except when mentioned, all Petri dishes contained humid sand as a substrate, one plastic tube as shelter and received ad libitum food changed twice a week [31].

(b) Chemical extraction

CHCs from nymph, female and male were extracted individually for 10 min using 60 μ l (nymphs) or 800 μ l (adults) of *n*-Heptane (Carl-Roth AG, Arlesheim, Switzerland) as solvent, and *n*-Octadecane as internal standard (concentration of 2.5 ng μ l⁻¹, Fluka Analytical, Sigma-Aldrich, Buchs, Switzerland). The extracts were subsequently analysed by gas chromatography-mass spectrometry. Full description of chemical analyses are provided in the electronic supplementary material.

(c) Statistical analyses

Chemical extraction resulted in a total of 19 peaks of CHCs in nymphs and 19 in adults. Peaks 18 (nymphs) and 25 (adults) were excluded from the analyses because peak 18 was collinear to peak 19 in nymphs (table 1; Pearson correlation, $t_{110} = 29.55$, $r = 0.94$, $p < 0.0001$) and peak 24 to peak 25 in adults (table 1; Pearson correlation; $t_{327} = 54.53$, $r = 0.95$, $p < 0.0001$), resulting in 18 peaks in adults and nymphs. The results remained unchanged when peaks 19 and 25 were excluded instead. We subsequently conducted a series of linear discriminant analyses (DA) to investigate the degree to which the chemical signature of nymphs and adults reflected their family of origin, and how this information content varied with the number of fathers that sired the clutch (table 1). The significance of each DA was evaluated both using Wilks' λ tests and prediction success (by estimating the percentage of correct assignment of individuals to their family of origin) through cross validation (leave-one-out method). The cross validation allowed us to control for potential overfitting of the data by the statistical models. We used 18 peaks for adults and 18 for nymphs, which corresponded to the recommendation in multivariate statistics like DA, that sample size should be at least three times the number of variables used [11]. To avoid limitations inherent to analyses of compositional data (as is the case for the CHC profiles), the area of each peak

was transformed according to Aitchison formula [32] prior to DA (for details, see [13]). Comparable results were found when the DA were done on an estimation of the absolute quantity of each peak using a known internal standard.

We first tested the degree to which the chemical signature of nymphs and adults generally reflected their family of origin using two DA based on the chemical signatures of either all nymphs or all adults reared in family groups. We then analysed whether these DA remained significant when taking into account the mating treatment and the age (and the adult sex) of the tested individuals by conducting a series of six DA based on each combination of nymphs, males and females sampled in 1 M and 4 M groups (table 1). Finally, we tested whether the chemical signature of adults at least partly reflected their shared environment (i.e. the shared Petri dish) using two DA based on the chemical signatures of either males or females from unrelated groups.

The prediction successes obtained from the cross-validation method were compared using general linear models (GLMs) with binomial error distribution. To this end, the prediction success obtained from the cross-validation method on each DA was converted into a binomial vector (1 or 0 values) of a length equal to the number of individuals involved in the DA and wherein the proportion of 1 was equal to the prediction success obtained from the cross-validation method. The prediction successes of nymphs from 1 M and 4 M families was compared using a GLM wherein 1 M/4 M was entered as fixed factor, and the two binomial vectors reflecting the respective prediction success concatenated to form the response variable (we used the same process to generate the response variables in all the following GLMs). The prediction successes of adults from 1 M and 4 M families were then compared using a GLM wherein mating treatment, sex and their interaction were entered as fixed factors. Adult sex was included in the model to control for potential sex-specific CHC profiles in earwig adults. Finally, whether the chemical signature of adults at least partly reflects their shared environment was tested by comparing the prediction successes of adults between 1 M families and unrelated groups and the ones of adults between 4 M families and unrelated groups using two GLMs, in which the type of group (family versus unrelated), the sex of the adults and their interactions were entered as fixed factors. Adults from 1 M and 4 M groups were analysed separately because mating treatment influenced the prediction success of adults (see Results). All statistical analyses were conducted using the software R. 3.0.2 (<http://www.r-project.org/>).

3. Results

The 19 CHCs present on the cuticular extracts of individual earwigs did not only exhibit quantitative differences between life-stages (table 1), but also qualitative ones with eight CHCs specific to nymphs and eight to adults. Overall, the chemical signatures of nymphs and adults significantly predicted their family of origin (nymphs: Wilk's $\lambda < 0.0001$, approx. $f = 11.06$, $p < 0.0001$; adults: Wilk's $\lambda = 0.0001$, approx. $f = 4.70$, $p < 0.0001$). The prediction successes were 92.0% and 64.1% using cross validation for nymphs and adults, respectively. Interestingly, these predictions remained significant when taking into account the sex of the tested adults and/or the mating treatment (table 2 and figure 2, all $p < 0.0001$), with the corresponding successes ranging from 52.7 to 81.8% (figure 2).

As predicted under the age-dependent concealment of paternally inherited cues in offspring, the mating treatments did not affect variation in the nymph chemical profiles, but affected the ones in adult chemical profiles. The prediction success of nymphs was not significantly different between the mating treatments (figure 2; GLM, Likelihood ratio (LR) $\chi^2_1 = 0.44$, $p = 0.506$), but the one of adults was significantly higher in the 1

Table 1. Mean relative peak area (%) of the CHCs extracted from 112 nymphs, 163 females and 166 males of the European earwig. (KI, mean Kovats retention index; IS, internal standard.)

	CHC	KI	males	females	nymphs
(1)	nC13	1300	—	—	7.24
(2)	nC15	1500	—	—	1.18
IS	nC18	1801	—	—	—
(3)	nC21	2100	—	—	4.77
(4)	X,X'-nC23 : 2 + X''-nC23 : 1	2275	—	—	10.68
(5)	X'''-nC23 : 1	2281	—	—	2.86
(6)	nC23	2300	0.14	0.15	9.33
(7)	11-, 9-MeC23	2334	—	—	1.15
(8)	5-MeC23	2348	—	—	0.68
(9)	3-MeC23 + (X-nC24 : 1)	2370	—	—	1.45
(10)	X,X'-nC25 : 2 + X''-nC25 : 1	2474	0.08	0.22	38.51
(11)	nC25	2501	1.37	2.20	3.84
(12)	13-, 11-, 9-MeC25	2533	1.03	2.60	2.77
(13)	3-MeC25 + (X-nC26 : 1)	2570	0.20	0.88	1.19
(14)	13-, 11-, 9-MeC26	2633	0.10	0.29	—
(15)	X,X'-nC27 : 2 + X''-nC27 : 1	2675	0.44	0.63	3.36
(16)	nC27	2701	1.62	1.58	0.37
(17)	13-, 11-, 9-, 7-MeC27	2743	25.91	35.94	2.99
(18)	7,15-; 7,19-; 11,15-; 11,17-; 11,19-diMeC27 ^a	2769	6.87	14.33	0.58
(19)	2,17-; 2,19-; 2,21-; 2,23-diMeC27	2776	4.25	8.30	0.70
(20)	13-, 11-, 9-, 7-MeC28	2836	0.94	1.15	—
(21)	9,15-diMeC28	2865	1.30	1.76	—
(22)	13-, 11-, 9-, 7-MeC29	2943	24.46	11.38	0.47
(23)	7,19-; 9,19-; 11,17-; 11,19-diMeC29	2966	22.94	13.22	—
(24)	15-, 13-, 11-, 9-MeC30	3037	3.69	2.00	—
(25)	15-, 13-, 11-, 9-MeC31 ^b	3138	1.58	0.39	—
(26)	7,19-; 9,19-; 9,21-diMeC31	3167	1.49	0.36	—
(27)	13-, 11-MeC33	3335	0.17	0.09	—

^aExcluded from the DA on nymphs owing to collinearity.^bExcluded from the DA on adults owing to collinearity.**Table 2.** Results of discrimination analyses of earwig individuals according to their life stage, their sex (only for adults), the type of rearing group (family or unrelated) and the mating treatment (1 M or 4 M). (The table indicates the number of families used (*N* fam) and the total number of individuals (*N* ind) per type of experimental group.)

life stage	rearing group	mating treatment	<i>N</i> fam	<i>N</i> ind	λ	approx. <i>f</i> -value	<i>p</i> -value
nymphs	family	1 M	7	56	<0.0001	11.05	<0.0001
	family	4 M	7	56	<0.0001	15.2	<0.0001
males	family	1 M	7	55	0.0002	5.69	<0.0001
	family	4 M	7	56	0.0003	4.87	<0.0001
	unrelated	—	7	55	0.0095	1.97	<0.0001
females	family	1 M	7	54	0.0009	3.67	<0.0001
	family	4 M	7	55	0.0033	2.67	<0.0001
	unrelated	—	7	54	0.0083	1.98	<0.0001

M compared with the 4 M groups (figure 2; GLM, LR $\chi^2_1 = 5.55$, $p = 0.018$). The prediction success of adults was also significantly higher among males than females (figure 2; GLM, LR

$\chi^2_1 = 5.13$, $p = 0.024$), but not significantly influenced by an interaction between the mating treatments and the sexes of the adult individuals (GLM, LR $\chi^2_1 = 0.49$, $p = 0.485$).

Figure 2. Prediction success by jack-knife cross validation of earwig individuals according to their life stage, their sexes (only for adults), the type of rearing groups (family or unrelated) and the mating treatments (1 M or 4 M). The corresponding values are given at the top of each bar.

Independently from the mating treatments, our results also showed that the chemical signature of adults partly reflected the environment in which they had been reared. The DA performed on the groups of unrelated adults significantly separated each sex according to their experimental groups (table 2 and figure 2), with 36.4% of males and 35.2% of females correctly assigned to their experimental groups by cross-validation method. Nevertheless, adult chemical profiles reflected more their clutch of origin than their groups/environments, as the prediction successes were lower among unrelated groups than 1 M family groups (GLM, group type: LR $\chi^2_1 = 18.19$, $p < 0.0001$; sex: LR $\chi^2_1 = 2.16$, $p = 0.142$; interaction: LR $\chi^2_1 = 1.34$, $p = 0.247$) or 4 M family groups (GLM, group type: LR $\chi^2_1 = 18.54$, $p < 0.0001$; sex: LR $\chi^2_1 = 1.77$, $p = 0.183$; interaction: LR $\chi^2_1 = 0.91$, $p = 0.341$).

4. Discussion

In social insect systems where progeny are sired by different males, potential conflicts between patriline emerge and may select against the expression of patriline-specific signatures in the CHC profiles of offspring. These conflicts are thought to constrain information content in the cues displayed by each group member and to limit the scope for nepotism between progeny of the same sire [18,19]. While previous research focused on eusocial systems (e.g. reviewed in [21]; but see [22–24]), we showed here that such constraints can also be found in an insect species with simpler forms of social life (maternal care and family life). In particular, our results demonstrated that mate number did not influence the inter-individual diversity of CHC profiles expressed among young earwig offspring, whereas it increased such diversity in the resulting groups of adult offspring. In other words, there was no significant information content on mate number among young nymphs, but this information was expressed among adult males and females. Our study also demonstrated that even if the CHC profiles of nymphs, adult males and adult females contained a heritable

component that could mediate the recognition patterns formerly reported in this species in terms of cannibalism and food sharing [29,33], they also reflect to a lower extent the environment and social group experienced by the individuals.

Our results supported the prediction that family life and multiple mating should favour the concealment of paternally inherited cues only in the young offspring (i.e. during family life). We did not find evidence for a paternal signature in the form of increased variability in the CHC profiles of nymphs from multiply sired clutches but found such an increase among adult offspring. Because earwig males in our experiment never encountered the eggs or the offspring they sired [27], any paternal signature in offspring CHC profiles would reflect paternally inherited variation at least partly, irrespective of the proximate mechanisms underlying the expression of heritable variation in CHC profiles. Proximally, the inherited variation can be expressed due to, for example, genetic variation in the fat metabolism, the preference for certain micro-environments or food intake behaviour, which in turn may affect CHC profiles. Different potential expression pathways may affect the temporal stability of the expressed heritable variation, but it does not change the ultimate effect that heritable information about maternal and/or paternal origin is displayed.

One hypothesis to explain the observed lack of paternally inherited cues in the chemical profiles of the nymphs is that their expression is developmentally constrained at this stage. For instance, nymphs might only be able to express immature profiles, because the paternal-cue-coding part of their genotype can only be fully expressed after a certain maturation time. In line with this hypothesis, it was shown in several dipterous insects (*Cucilidae*, *Muscidae* and *Drosophilidae*) that the CHC profile does not remain constant throughout their life [3]. In the ant *Cataglyphis niger*, the amounts of hydrocarbons in the postpharyngeal gland increased with maturation, especially in the first 7 days after emergence [34]. An alternative hypothesis is that mothers conceal information about their offspring's paternal origin by transferring CHCs to the eggs during oogenesis, as reported in the German cockroach *Blattella germanica* [35], or continuously to the nymphs during the period of maternal care. In the European earwig, the continuous transfer of CHCs to the eggs [36] and the frequent maternal grooming of nymphs [37] could allow females to progressively shape nymph CHCs by applying hydrocarbons. Ultimately, maternal concealment of paternal signatures in the nymph CHC profiles may either reflect a side effect of maternal behaviour (e.g. body contact, grooming and food provisioning), or an evolved maternal strategy to limit nepotistic/antagonistic sibling interactions among the different patrilines inside her brood. Further research on the mechanism and adaptive function of the found patterns is needed. But consistent with the hypothesis that selection on mothers favoured concealment of paternally inherited signatures on her offspring, previous experiments showed discrimination in cannibalism among nymphs from different clutches (i.e. with different mothers) [29], but lack of effect of multiple mating on cannibalism rate within clutches [38].

Our results further demonstrated that the CHC profiles of *F. auricularia* adults not only have a heritable component, but also partly reflected the shared environment and social group. In particular, experimental groups of unrelated adults were successfully assigned to their new group (although at a significantly lower success rate compared with the family

groups). It was shown before that multiple abiotic factors can influence the chemical profiles of individuals, such as temperature [39], nesting substrate [8,40] or diet [10]. As we kept abiotic factors constant between our groups, we consider them an unlikely influence on group-specific profiles. Hence, the most likely explanation for the reported result is that social interactions passively (e.g. body contacts) and/or actively (e.g. allogrooming) mediated the transfer of chemical compounds between adults and thus contributed to the partial homogenization of odours within groups, a common process in colonies of eusocial insects [41,42]. In *F. auricularia*, old nymphs and adults are known to aggregate densely for foraging, resting and mating [43,44], as well as to express allogrooming [45], which both offer scope for social transfer of chemical compounds. Social transfer of recognition cues within groups may be beneficial for instance because it can facilitate the expression of group-directed forms of social behaviour [46].

A somewhat surprising result from our analyses was that the family-specificity of CHC profiles was higher among male than female adult family groups, suggesting a sex-difference in the expressed heritable variation in CHCs or an enhanced CHC exchange between males as compared with females, e.g. owing to higher levels of allogrooming and close physical contacts [12,41,47]. Because we found no difference in the group-specificity of CHC of unrelated males versus unrelated females (figure 2), the sex difference in the expressed CHC variation is more likely owing to

intrinsic differences between the sexes, that is, a difference in the expression of heritable variation as was found in *Drosophila simulans* [48].

The discovered patterns of expressed CHC variation in *F. auricularia* are consistent with a scenario where mothers conceal any paternal signature in their offspring's chemical profiles to minimize antagonistic interactions among patriline inside her brood, and where later in life information about both maternal and paternal origin are expressed potentially to avoid costs of sibling-mating in adults. However, the mechanisms of how paternal signatures in kin recognition cues of juveniles are concealed, and their adaptive function, require further investigation. Overall, our results provide insight into the role of parental care and social life in the evolution of chemical communication and recognition cues.

Acknowledgements. We thank Hope Klug and two anonymous reviewers for their insightful comments on this manuscript. We also thank Anne-Geneviève Bagnères and Michel Vancassel for offering access to unpublished results on the CHCs of *F. auricularia*, which were helpful for their identification in this study. We are grateful to Alain Lenoir for his advice on chemical identifications.

Data accessibility. Data are deposited in the Dryad repository (doi:10.5061/dryad.73180).

Funding statement. This study was supported financially by the Swiss National Science Foundation (grant no. PP00A-119190 to M.K.), the Fonds zur Förderung von Lehre und Forschung, the Freiwillige Akademische Gesellschaft (scholarship to J.W.Y.W.), the German Science Foundation (DFG; ME4179/1-1 to J.M.) and the PRES Centre Val de Loire Université (APR-IA 2012 to C.L.; GDR3658).

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