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Alkaloids from scent glands of Travunioidea (Opiliones, Laniatores): insights from *Peltonychia*

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Abstract. The scent gland secretion of a cladonychiid harvestman from Europe, *Peltonychia clavigera* (Simon, 1879) (Opiliones, Laniatores, Travunioidea), was investigated by gas chromatography–mass spectrometry. The exudates contained *N,N*-dimethyl-2-phenylethan-1-amine and various alkylpyrazines, being clearly different from the tobacco alkaloid-type that is known from other European Travunioidea. The *N,N*-dimethyl-2-phenylethan-1-amine-type has so far been regarded as characteristic for western North American species only. Regarding the wide taxonomic distribution of *N,N*-dimethyl-2-phenylethan-1-amine and tobacco alkaloids across representatives of Travunioidea, we consider both groups of compounds phylogenetically old chemical characters of Travunioidea, having evolved before the separation of North America and Europe in the Eocene.

Keywords: *N,N*-dimethyl-2-phenylethylamine, tobacco alkaloids, nicotine, anabaseine, Insidiatores, Cladonychiidae
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The Travunioidea comprise small-sized north temperate laniatorean harvestmen that show a circumpolar distribution from western and eastern North America to Europe and East Asia. Currently, about 75 species have been described (Kury et al. 2023), and the latest taxonomic revision by Derkarabetian et al. (2018) recognizes four families, Travuniidae, Cladonychiidae, Cryptomastridae, and Paranonychidae. While Travuniidae are exclusively European, Paranonychidae occur in western North America and East Asia, Cryptomastridae exclusively in western North America, and Cladonychiidae in western and eastern North America, Europe, and one species has recently been recorded for China (Zhang & Derkarabetian 2021).

Like all harvestmen, and particularly the Laniatores, travunioids possess large prosomal scent glands, which are considered to represent means of chemical protection and predator defense. While scent gland secretions of various taxa are well known to consist of quinones, phenols, ketones and alcohols (e.g., Gnaspini & Hara 2007; Raspotnig 2012), travunioid exudates are unique among harvestmen and appear to be rich in nitrogen-containing alkaloid compounds. Though knowledge of the secretions of Travunioidea is based on three publications only (Ekpa et al. 1984; Raspotnig et al. 2011; Shear et al. 2014), the chemistry of 15 species from 10 (out of 24) genera and three (out of four) families is therein described.

These chemically investigated species include western American Paranonychidae (genera *Sclerobunus* Banks, 1893, *Metanonychus* Briggs, 1971, *Paranonychus* Briggs, 1971), western American Cryptomastridae (*Cryptomaster* Briggs, 1969, *Speleomaster* Briggs, 1969) as well as western and eastern American and European Cladonychiidae (*Briggsus* Özdikmen & Demir, 2008, *Speleonychia* Briggs, 1974, *Erebomaster* Briggs, 1969, *Theromaster* Briggs, 1969, *Holoscotolemon* Roewer, 1915). No data are available for the fourth family, Travuniidae.

According to the three publications mentioned above, mainly alkaloids, terpenes, thiazoles and phenolics are distributed across travunioid taxa (Shear et al. 2014). Among these, the alkaloids are of particular interest: they appear to be lacking in other Insidiatores, such as Triaenonychoidea, neither they are found in any other group of Opiliones, suggesting an apomorphic chemical trait of Travunioidea. Travunioid alkaloids comprise rare natural products such as *N,N*-dimethyl-2-phenylethan-1-amine but also tobacco alkaloids such as nicotine and anabaseine, related pyridines, and possibly also alkylpyrazines (Ekpa et al. 1984; Raspotnig et al. 2011).

To gain deeper insights into the alkaloid chemistry of travunioids and to establish a sound basis to evaluate the taxonomic distribution and a possible phyletic signal of these chemical characters, we investigated a representative of the European genus *Peltonychia* Roewer, 1935. This genus, previously placed within Travuniidae (Kury et al. 2014), was recently transferred to Cladonychiidae by novel molecular data (Derkarabetian et al. 2018).

METHODS

Twenty-one adult individuals of *Peltonychia clavigera* (Simon, 1879) were collected under stones at Col de Spandelles, near Ferrieres, southern France (43°0′34.33″N, 0°13′54.10″W; 1177m above sea level), on 20th May 2011 (leg. Karaman & Raspotnig). Scent gland exudates were sampled either directly from ozopores (on filter paper) or extracted from whole bodies in hexane. Crude extracts, i.e., without further processing, were used for gas chromatographic–mass spectrometric analyses on a Trace GC-DSQ I system from Thermo, Vienna.

Chromatographic conditions were: ZB-5 column (30 m × 0.25 mm × 25 μm); splitless injection (1.5 μl crude extract); injector temperature at 240°C; helium as carrier gas at a flow rate of 1.2 ml/min; temperature program: 50°C (1 min), ramping to 300° C by 10° C/min, then 5 min isotherm at 300° C; transfer line at 310° C.

Mass spectrometric conditions were: EI at 70eV; ion source at 200° C; scan from *m/z* 40–550.

We used an alkane standard (C7 – C30) to calculate retention indices (Van den Dool & Kratz 1963). Reference compounds such as *N,N*-dimethyl-2-phenylethan-1-amine were purchased from Sigma (Vienna, Austria). For the identification of further compounds, we used reference spectra and indices previously published for alkylpyrazines (Wagner et al. 1999; Showalter et al. 2010; Xu et al. 2018, 2019).

To visualize position and morphology of scent gland orifices, scanning electron micrographs (SEM) were prepared: one male and one female specimen of *P. clavigera* were fixed and dehydrated in 100% ethanol, air-dried overnight, then mounted onto aluminium pin stubs (Agar Scientific, Biedermannsdorf, Austria), sputtercoated with gold (Agar Sputter Coater; Christine Gröpl, Tulln, Austria), and investigated with a Hitachi FlexSEM1000

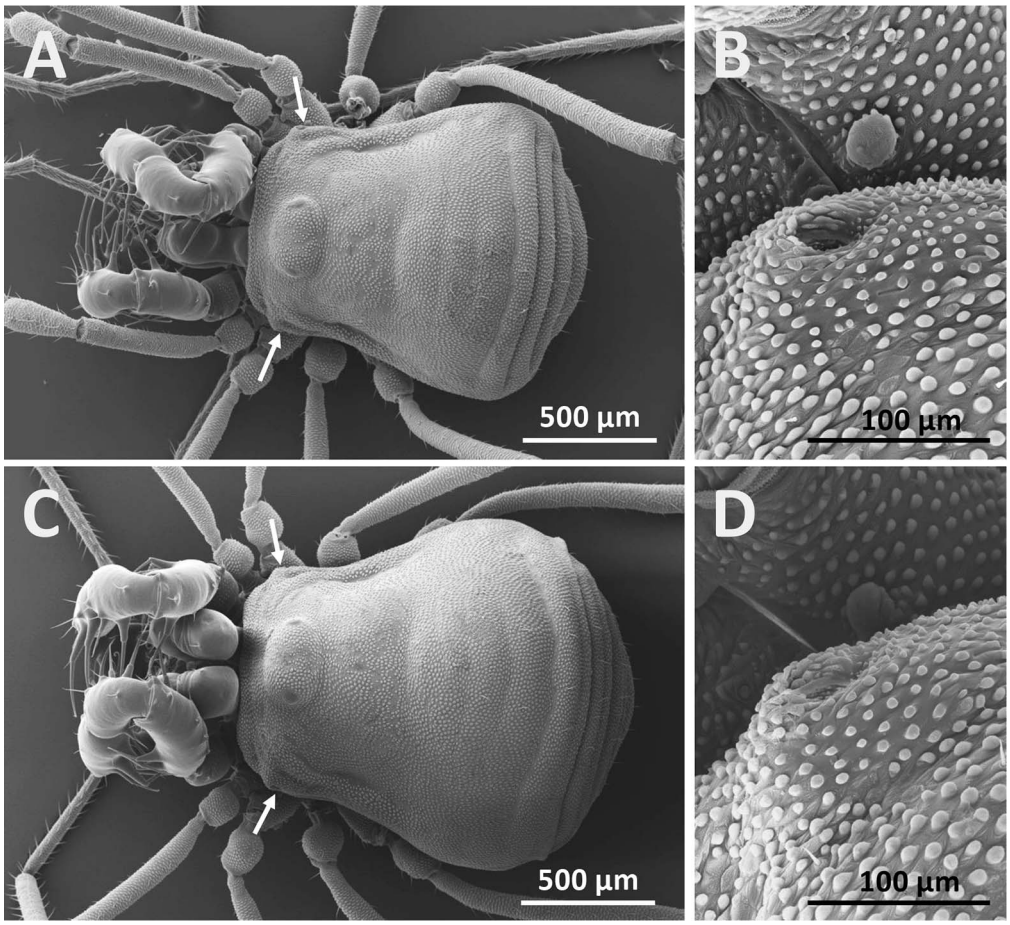


Figure 1.—Position of scent gland openings dorsal to coxae II (white arrows) and details of pore openings in *Peltonychia clavigera*. (A) male individual; (B) detail of scent gland pore in a male. (C) female individual; (D) detail of scent gland pore in a female.

(Tokyo, Japan) using 20 kV acceleration voltage in the high vacuum mode.

RESULTS

From 21 individual extracts (11♂, 10♀) of *P. clavigera* (Fig. 1), 19 extracts contained scent gland secretion (peaks ***A***, ***B*** and ***I – IV*** in Fig. 2). The remaining two extracts appeared to be "empty", showing no components.

In secretion-loaded extracts, two major peaks were consistently present, corresponding to *N,N*-dimethyl-2-phenylethan-1-amine (= *N,N*-dimethyl-2-phenylethylamine or *N,N*-DMPEA: peak ***A***, M^+ at *m/z* 149; about 80% of the whole secretion profile) and 3,5-dimethyl-2-(1-methylpropyl)pyrazine (= 2,6-dimethyl-3-(2-methypropyl)pyrazine: peak ***B***, M^+ at *m/z* 164; about 10%). Both compounds were identified by GC-MS data and their comparison to authentic standards and literature, respectively (Table 1).

In addition, four minor peaks, all of which in amounts below 5% of the total secretion profile, co-occurred in the extracts but could not be retrieved in each of the samples. The minor peaks were tentatively identified as benzylhydrazine (peak ***I***), 2,5-dimethyl-3-(2-methylbutyl)pyrazine (peak ***II***), 2,5-dimethyl-3-(3-methylbutyl)pyrazine (= 3-isopentyl-2,5-dimethylpyrazine) (peak ***III***) and *N*-methyl-1,2,3,4-tetrahydroquinoline (peak ***IV***). The identification of these compounds was based on the comparison of GC–MS data to mass spectra and retention indices as published in literature (Table 1).

Neither qualitative nor quantitative differences between male and female extracts were observed.

DISCUSSION

Alkaloid distribution in Travunioidea.—All compounds detected in secretion-loaded extracts of *P. clavigera* are alkaloids (Fig. 3). This is in good accordance with the current picture of travunioid scent gland chemistry (Ekpa et al. 1984; Raspotnig et al. 2011; Shear et al. 2014). Though other component classes have also been described from this group, alkaloids appear to represent the predominant chemical class in travunioid exudates. Previously published data on the secretions of Travunioidea not only suggested a widespread, if not general alkaloidal chemistry but also at least two chemical lineages: a taxonomically diverse, but chemically homogenous western American lineage relying on *N,N*-dimethyl-2-phenylethan-1-amine and a taxonomically restricted eastern North American/European lineage producing tobacco alkaloids (Shear et al. 2014). This situation implied a geographical dependence of secretion chemistry which was neither reflected by current taxonomy nor phylogeny. According to Shear et al. (2014), the *N,N*-dimethyl-2-phenylethan-1-amine-type of western North American species is realized in different families, namely Paranonychidae, Cryptomastridae and

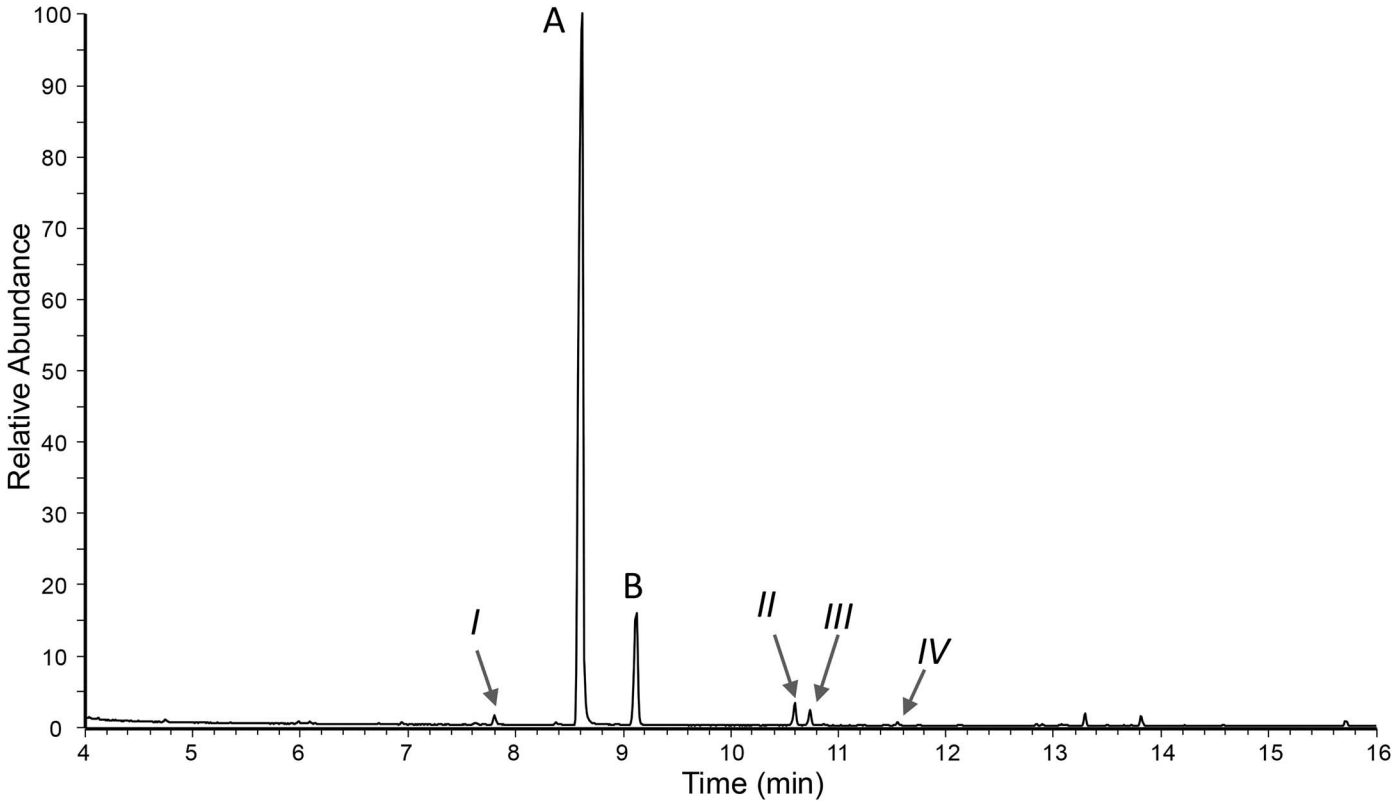


Figure 2.—Characteristic gas chromatographic profiles of secretion-loaded extracts of *Peltonychia clavigera*: Major compounds: Peak A (*N,N*-dimethyl-2-phenylethan-1-amine), peak B (3,5-dimethyl-2-(1-methylpropyl)pyrazine (= 2,6-dimethyl-3-(2-methylpropyl)pyrazine)). Minor compounds: peak *I* (benzylhydrazine), peak *II* (2,5-dimethyl-3-(2-methylbutyl)pyrazine), peak *III* (2,5-dimethyl-3-(3-methylbutyl)pyrazine (= 3-isopentyl-2,5-dimethylpyrazine)), peak *IV* (*N*-methyl-1,2,3,4-tetrahydroquinoline).

Cladonychiidae. On the other hand, a part of the Cladonychiidae, namely Eastern American and European species, appear to form a tobacco-alkaloid lineage. However, this chemical dichotomy appears to be not too strict, since mixed types also exist – some Paranochychidae from western North America show both *N,N*-dimethyl-2-phenylethan-1-amine as well as tobacoo alkaloids. An overview on the secretion types of the 15 species so far investigated is given in Table 2.

Table 1.—Gas chromatographic – mass spectrometric data to extract components of *Peltonychia clavigera*.

Peak no.	RI*	RI^{ref}	EI-fragmentation pattern [*m/z* (rel. Int.)]	Rel. abundance**	Identified as
Major peaks					
A	1168	1168	149(0.7), 148(0.5), 146(1), 133(0.7), 132(0.7), 105(2.5), 103(1.8), 91(2.8), 77(3.5), 58(100), 42(4)	86	*N,N*-dimethyl-2-phenylethan-1-amine
B	1201	1205	164(4), 163(3), 149(9), 122(100), 121(17), 107(3), 80(3), 53(5), 42(5)	10	3,5-dimethyl-2-(1-methylpropyl)pyrazine (= 2,6-dimethyl-3-(2-methylpropyl) pyrazine)
Minor peaks (tentatively identified)					
I	1112	1118	122(33), 92(56), 91(100), 77(8), 65(26), 57(18), 56(13), 51(6)	<1	benzylhydrazine
II	1305	1309	177(<1), 163(6), 149(4), 122(100), 121(14)	2	2,5-dimethyl-3-(2-methylbutyl)pyrazine
III	1316	1319	163(6), 135(12), 122(100), 121(14)	1	2,5-dimethyl-3-(3-methylbutyl)pyrazine (= 3-isopentyl-2,5-dimethylpyrazine)
IV	1377	1377	148(19), 147(100), 146(64), 144(29), 132(16), 131(15), 130(23), 117(16), 105(18), 104(16), 102(11), 91(35), 77(9), 56(29)	<1	*N*-methyl-1,2,3,4-tetrahydroquinoline

*Normal alkane index (Van den Dool and Kratz 1963) as measured; reference indices (RI^{ref}): for *N,N*-dimethyl-2-phenylethan-1-amine, an authentic standard was used; for the remaining alkylpyrazines, RI^{ref} were found in Xu et al. (2018), for benzylhydrazine in Miyazawa et al. (2011), for *N*-methyl-1,2,3,4-tetrahydroquinoline, we found a corresponding note in the NIST Webbook (https://webbook.nist.gov/cgi/inchi?ID=U380567&Mask=2000).
**%Peak area of total extract components.

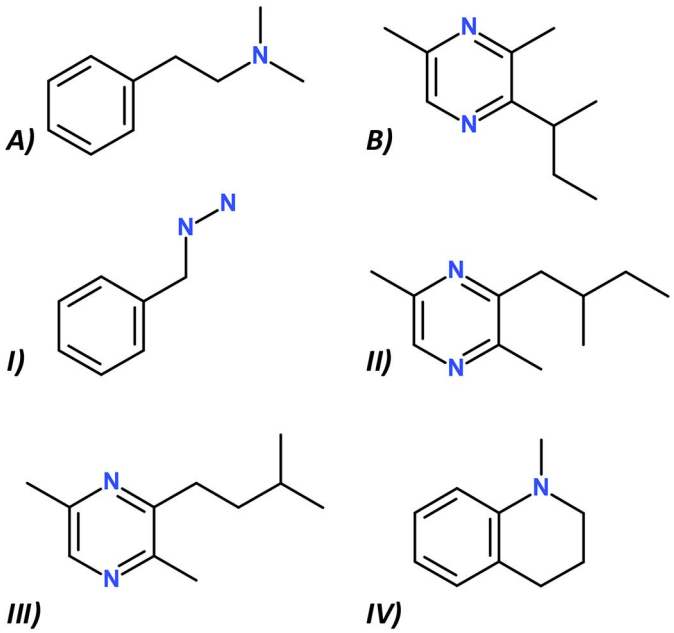


Figure 3.—Compounds identified from secretion-loaded extracts of *Peltonychia clavigera*. Major compounds: (A) *N,N*-dimethyl-2-phenylethan-1-amine; (B) 3,5-dimethyl-2-(1-methylpropyl)pyrazine (= 2,6-dimethyl-3-(2-methylpropyl)pyrazine). Minor compounds: (I) benzylhydrazine; (II) 2,5-dimethyl-3-(2-methylbutyl)pyrazine; (III) 2,5-dimethyl-3-(3-methylbutyl)pyrazine (= 3-isopentyl-2,5-dimethylpyrazine); (IV) *N*-methyl-1,2,3,4-tetrahydroquinoline.

Our present study on *Peltonychia* contradicts the idea of geographic chemical lineages: *Peltonychia clavigera*, a European species, does not show any sign of tobacco alkaloids such as nicotine and/or anabaseine, thus clearly diverging from an assumed European tobacco alkaloid-lineage. By contrast, *P. clavigera* produces *N,N*-dimethyl-2-phenylethan-1-amine, just like travunioids from western North America. To the best of our knowledge, *N,N*-dimethyl-2-phenylethan-1-amine is a unique exocrine compound, highly specific for travunioids, and not found in any other animal group. It is thus reasonable to assume a single evolutionary origin of this compound over its multiple convergent evolution, particularly within a rather small taxonomic entity such as Travunioidea.

On this ground, we here propose a phylogenetic, rather than a geographic hypothesis on the taxonomic distribution of alkaloids in the scent gland secretions of travunioids. We argue: the presence of *N,N*-dimethyl-2-phenylethan-1-amine has been established for representatives of three (of the four) families of Travunioidea, namely for Cladonychiidae, Cryptomastridae and Paranonychidae. The fourth family, the basally-branching Travuniidae, has remained unstudied in this respect. Thus, *N,N*-dimethyl-2-phenylethan-1-amine appears to represent a synapomorphy of three, if not all four families of Travunioidea. Its absence in several species of Cladonychiidae such as *Holoscotolemon* ssp., *Erebomaster* and *Theromaster* may be interpreted as convergent loss. In this respect, it should be noted that the loss of a compound is much more easily achieved than its repeated evolution (see Raspotnig et al. 2015). In travunioids, such as Cryptomastridae and Paranonychidae, *N,N*-dimethyl-2-phenylethan-1-amine is even present in all species so far investigated.

On the other hand, the phyletic status of tobacco alkaloids is less clear: these compounds have been found in a part of Cladonychiidae (such as *Holoscotolemon*, *Theromaster*, *Erebomaster*) but also in some Paranonychidae. Tobacco alkaloid-containing Cladonychiidae conspicuously lack *N,N*-dimethyl-2-phenylethan-1-amine, implying that tobacco alkaloids and *N,N*-dimethyl-2-phenylethan-1-amine may be interchangeable or at least biochemically related. This, however, has not been demonstrated, and with respect to the quite differing chemical structures of these components, easy interchangeability is not to be expected. Moreover, the existence of mixed secretion types which contain both groups of alkaloids, as in the paranonychids *Sclerobunus* and *Metanonychus*, is not consistent with interchangeability: in these cases, however, *N,N*-dimethyl-2-phenylethan-1-amine has been reported to be the predominating compound with tobacco alkaloids being minor or trace components (Shear et al. 2014). For representatives of the two remaining travunioid families, Cryptomastridae and Travuniidae, the occurrence of tobacco alkaloids has not been established: In hitherto analysed species of Cryptomastridae tobacco alkaloids have not yet been detected; for Travuniidae, chemical data is

Table 2.—Chemical types of secretion in Travunioidea based on alkaloid composition.

Travunioid family	Species chemically investigated	Distribution	Secretion-type*	References
Paranonychidae	*Sclerobunus robustus*	Western USA	Mixed type	Ekpa et al. 1984
	Sclerobunus nondimorphicus	Western USA	Mixed type	Shear et al. 2014
	Paranonychus brunneus	Western USA	DMPEA-type	Shear et al. 2014
	Metanonychus idahoensis	Western USA	Mixed type	Shear et al. 2014
Cryptomastridae	*Cryptomaster leviathan*	Western USA	DMPEA-type	Shear et al. 2014
	Speleomaster lexi	Western USA	DMPEA-type	Shear et al. 2014
	Speleomaster pecki	Western USA	DMPEA-type	Shear et al. 2014
Cladonychiidae	*Briggsus flavescens*	Western USA	DMPEA-type	Shear et al. 2014
	Speleonychia sengeri	Western USA	DMPEA-type	Shear et al. 2014
	Erebomaster flavescens	Eastern USA	TA-type	Shear et al. 2014
	Theromaster brunneus	Eastern USA	TA-type	Shear et al. 2014
	Holoscotolemon lessiniense	Europe	TA-type	Raspotnig et al. 2011
	Holoscotolemon jaqueti	Europe	TA-type	Raspotnig et al. 2011
	Holoscotolemon oreophilum	Europe	TA-type	Raspotnig et al. 2011
	Holoscotolemon unicolor	Europe	Alkylpyrazines?	Raspotnig et al. 2011

*DMPEA-type = *N,N*-dimethyl-2-phenylethan-1-amine-type. TA-type = tobacco alkaloid-type, based on nicotine or anabaseine. Mixed type = containing both, DMPEA and TAs.

generally missing. Thus, considering the distribution of tobacco alkaloids in representatives of (at least) two families of Travunioidea as well as in representatives of travunioids on two continents, also these compounds appear to represent old chemical signals. We thus conclude that both *N,N*-dimethyl-2-phenylethan-1-amine and tobacco alkaloids evolved early in scent gland secretions of travunioids, namely before the separation of North America and Europe in the Eocene, i.e., at least 50 million years ago.

Alternatively, alkylpyrazines as in *Peltonychia* may represent an apomorphic trait in a distinct lineage of European Cladonychidae: so far, alkylpyrazines have not been found in North American species, but may be present in the secretions of some *Holoscotolemon* from Europe, though this needs confirmation (Raspotnig et al. 2011). Contrasting the occurrence of rare compounds such as *N,N*-dimethyl-2-phenylethan-1-amine and anabaseine, alkylpyrazines are quite widespread exocrine products in the animal kingdom, obviously having evolved several times independently. They occur in the secretions of many ants where they function as various pheromones (e.g., Morgan 2009; Showalter et al. 2010; Silva-Junior et al. 2018; Xu et al. 2018). Alkylpyrazines similar to those in *Peltonychia* have also been found in some bacteria (Silva-Junior et al. 2018), and alkylpyrazines have even been detected in the urine of mammals where they exhibit a kairomonal function (Osada et al. 2013).

In *Peltonychia*, the biological significance of alkylpyrazines is still unclear but, in analogy to other harvestmen exudates, a generally protective, probably allomonal role is to be expected. Tobacco alkaloids of cladonychiids such as *Holoscotolemon* spp. are likely to affect the nervous system of predators by interacting with nicotinic acetylcholine receptors, as known to be expressed in the central nervous system of Arthropoda. For *N,N*-dimethyl-2-phenylethan-1-amine, which is a structural analog to the neurotoxic central nervous stimulant methamphetamine, target receptors in the nervous system of predators may be assumed.

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