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Characterisation of monophyletic oribatid groups by oil gland chemistry – a novel systematic approach in Oribatida (Acari)

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Abstract

Oil glands (also called opisthonotal or latero-opisthosomatic glands) represent the largest and most striking exocrine system in both Oribatida and Astigmata: according to current knowledge, oil glands evolved only once in ancient Oribatida, and thus, all extant oil gland-bearing taxa are thought to represent a part of the large monophyletic unit of »glandulate« oribatids (including Astigmata!). Recently, an important set of taxonomic characters in glandulate groups has arisen by investigations into chemical profiles of oil gland secretions: these chemical profiles represent stable and species-specific characters, and clearly characterise monophyletic oribatid groups on any taxonomic level.

Hitherto available chemical data can be summarised as follows: hydrocarbons have been found in secretions of all species so far investigated and are regarded to be plesiomorphic. On the other hand, only Parhyposomata show naphthols and phenols, and an apomorphic set of aromatics and terpenes, the so-called »astigmatid compounds«, characterises middle-derivative Mixonomata and possibly also all groups above (i.e. Desmonomata, Brachypylida, Astigmata). Within this monophylum of »astigmatid compounds«-bearing Oribatida, certain sub-groups are characterised by e.g. the occurrence of distinctly different compositions of secretions in juvenile and adult individuals (»chemical dimorphism«), the reduction of astigmatid compounds (in a lineage from higher Desmonomata to Brachypylida) and by novel, partly unusual components (e.g. iridoid monoterpenes and diterpenes in oribotritiid Eupthiracaroidea, rhizoglyphinyl formate and farnesals in certain Desmonomata; alkaloids in Brachypylida).

Thus, besides traditional sets of morphological characters and newly arising molecular data, oil gland secretion profiles represent a third, independent pool of characters for phylogenetic studies in glandulate Oribatida. By now, secretion profiles of about 20 oribatid (and more than 50 astigmatid) species have been elucidated.

Keywords: opisthonotal glands, astigmatid compounds, chemotaxonomy, oribatid phylogeny

Zusammenfassung

Charakterisierung monophyletischer Oribatidengruppen anhand ihrer Öldrüsensekretchemie – Öldrüsen (syn. opisthonotal glands oder latero-opisthosomatische Drüsen) stellen das größte und auffälligste exokrine System der Oribatiden und der astigmaten Milben dar. Nach einer derzeit gängigen Vorstellung sind Öldrüsen nur einmal in der Evolution, und zwar innerhalb einer Ur-Hornmilbengruppe entstanden; damit gehören alle rezenten öldrüsentragenden Taxa zu einer großen monophyletischen Einheit, den sogenannten »glandulaten« Oribatiden (die auch die Astigmata mit einschließen!). Eine bedeutsame Quelle taxonomischer Daten innerhalb glandulater Gruppen wird seit kurzem über die chemische Zusammensetzung von Öldrüsensekreten erschlossen. Diese chemischen Profile repräsentieren stabile und artspezifische Merkmale und kennzeichnen monophyletische Einheiten der Oribatiden auf allen taxonomischen Ebenen.

Bisher verfügbare chemische Daten lassen sich wie folgt zusammenfassen: Kohlenwasserstoffe wurden in den Sekreten aller bisher untersuchten Arten gefunden und werden als plesiomorphe Sekretbestandteile betrachtet. Dagegen zeigen die Parhyposomata nur ihnen eigene Naphthole und Phenole, und ein weiteres Set aus Aromaten und Terpenen, die sogenannten »astigmatid compounds«, kennzeichnet mixonomate Hornmilben (außer deren primitivsten Vertretern) und wahrscheinlich alle evolutiv höherstehenden Gruppen (also Desmonomata, Brachypylida, Astigmata). Innerhalb des Monophylums der »astigmatid compounds«-tragenden Oribatiden werden bestimmte Sub-Gruppen durch das Auftreten von deutlichen Unterschieden in der Zusammensetzung von Sekreten juveniler und adulter Tiere (»chemischer Dimorphismus«), der Reduktion bestimmter »astigmatid compounds« (in einer Verwandtschaftslinie von höheren Desmonomaten zu den Brachypyliden) sowie durch neue, zum Teil recht ungewöhnliche Komponenten gekennzeichnet (z.B. iriodoide Monoterpene und Diterpene bei oribotritiiden Euphthiracaroidea; Rhizoglyphinylformiat bzw. Farnesale bei bestimmten Desmonomata; Alkaloide bei Brachypylida).

Öldrüsensekrete stellen damit neben traditionellen, morphologischen Merkmalen und neu aufkommenden molekularen Daten einen dritten, unabhängigen Pool von Merkmalen zur phylogenetischen Analyse der glandulaten Oribatiden dar. Bis jetzt sind Sekretprofile von etwa 20 Oribatidenarten (und mehr als 50 Arten astigmater Milben) chemisch aufgeklärt worden.

1. Introduction

Even though the field of chemotaxonomy is better known from plant systematics (e.g. HARBORNE & TURNER 1984), chemical characters have successfully been applied to the taxonomy of diverse animal groups as well (e.g. JACOB 1984). In arthropods, for instance, chemosystematic investigations have been performed for diverse insect groups such as beetles (DETTNER 1987) and hymenopterans (CANE 1983, BELLES et al. 1987, COX et al. 1989, HEFETZ 1993), but also for arachnids such as harvestmen (RASPOTNIG et al. 2005b). In mites, the largest arachnid order, a chemosystematic survey on ticks was published recently (ESTRADA-PENA et al. 1992a, b, 1994, 1996, ESTRADA-PENA & DUSBABEK 1993).

However, the most important demand for a chemosystematic study on a phylogenetically-

founded basis concerns the unification of chemical profiles: i.e. it is not sufficient to compare profiles of cuticular extracts (as frequently performed), but, on the contrary, chemical compounds must be derived from homologous sources. These requirements are fulfilled when 1) dealing with exocrine products of a well-defined glandular system that is homologously present throughout the taxon in consideration, and 2) when glandular contents can be accessed purely, i.e. without contaminations from other sources. Further requirements include 3) intraspecific stability of chemical profiles of glandular secretions on the one hand but 4) sufficient interspecific variability on the other hand. In oribatids (Acari: Oribatida), these prerequisites for a model chemosystematic study are ideally given.

The majority of oribatids possesses a well-defined glandular system, the so-called oil glands (synonyms are »opisthonotal« or »latero-opisthosomatic glands«) that represent very large and biologically important exocrine glands in their basic morphology (Fig. 1). The potential taxonomic value of the character »oil glands present« was already recognised by early acarologists such as GRANDJEAN (1950) and STRENZKE (1963), but not until recently, oil glands have emerged as central paradigms in oribatid phylogenetic research. In detail, oil glands are primitively absent from near-basal oribatids such as Palaeosomata and Enarthronota, but occur in all other Oribatida, i.e. these are present in Parhyposomata, Mixonomata (with a few exceptions), Desmonomata and Brachypylida. In homologous form, oil glands also are known from Astigmata (e.g. HAMMEN 1980, NORTON 1998). According to a hypothesis by NORTON (1994, 1998), oil glands evolved only once in ancient Oribatida, and thus represent homologous organs in sarcoptiform (= oribatid + astigmatid) mites. Their homology is supported by consistent data concerning their location, their morphological organisation, but also by corroborative data from their chemistry. As a consequence, all extant oil gland-bearing taxa are considered descendents of an ancestral oil gland-bearing oribatid group, all together representing a large monophyletic unit – the so-called »glandulate Oridatida« – that also includes the Astigmata (Fig. 2). However, the character »oil glands present – absent« is devalued to a plesiomorphic feature among glandulate groups, but a new dimension of oil gland characters is opened up by investigations into the chemistry of oil gland secretions.

2. Materials and Methods

Oil gland secretion analysis: an overview

Chemical investigations into oil gland secretions mainly rely on whole-body extractions of living individuals that discharge their secretions directly into the solvent. Crude extracts, containing a mixture of oil gland secretion components (but potentially also components from other parts of the body), are separated by capillary gas chromatography. Mass spectrometric fragmentation patterns of single compounds (mainly electron impact spectra) are used for structure determination, leading to propositions for the identity of extract components. For a final identification of extract components, gas chromatographic retention times (and mass spectrometric fragmentation) of synthetic reference compounds have to be compared to those of extract components. Only compounds with matching spectra and matching retention times are positively identified. (The discrimination between oil gland components of extracts and components of other body parts is outlined in the next chapter.)

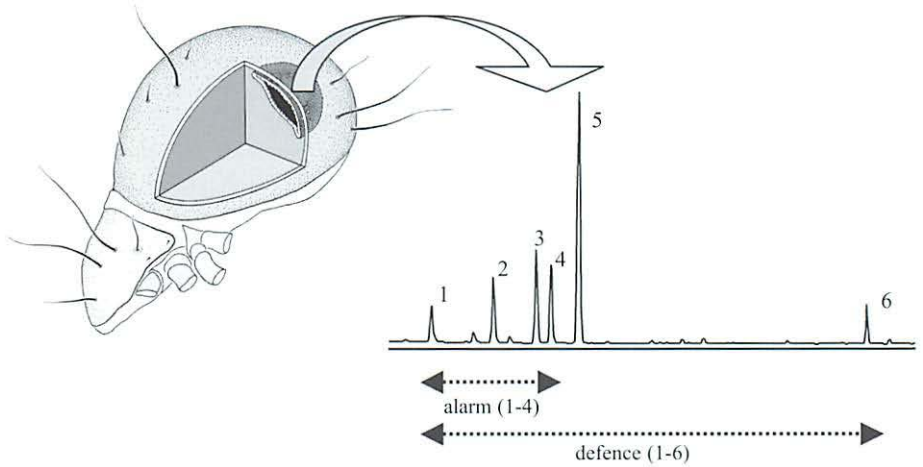

Fig. 1 The oil gland system of *Collohmannia gigantea*: an example for chemical alarm and defence. The chromatographic oil gland secretion pattern shows (1) 2-hydroxy-methyl benzaldehyde, (2) neral, (3) geranial, (4) neryl formate, (5) tridecane, (6) pentadecane. While components 1 – 4 are powerful releasers of alarm behaviour, all components exhibit repellent properties against mite predators such as scydmaenid beetles.

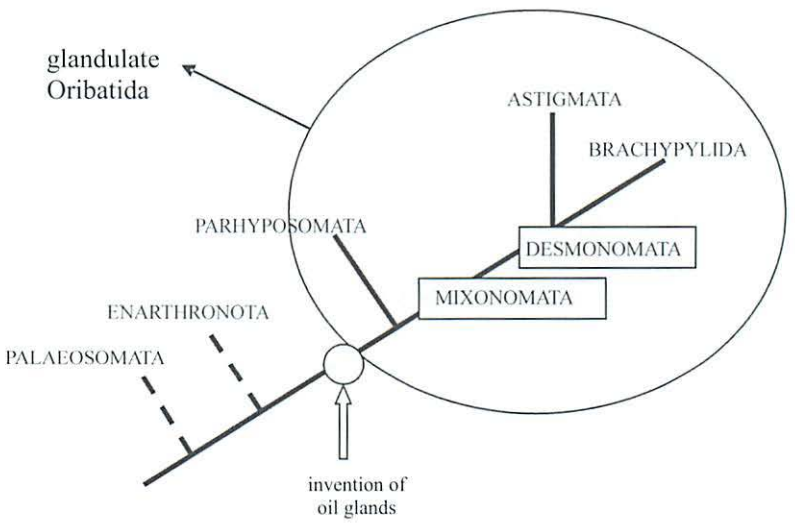

Fig. 2 The monophylum of glandulate Oribatida (according to NORTON 1998, modified). Note that groups in boxes (Mixonomata and Desmonomata) represent paraphyletic taxa.

Extraction procedure

In detail, extraction and analysis of oil gland secretions (at least as carried out by the author) involve the following steps, according to already described and standardised procedures (e.g. RASPOTNIG et al. 2001, 2004, 2005a, c): briefly, freshly collected, living individuals are extracted in hexane (one to ten individuals per 50 µl depending on body size) for a maximum of 30 min. Crude extracts are used for analysis.

Gas chromatography – mass spectrometry

The analytical instruments used included a Fisons 8000 gas chromatograph (GC) coupled to a Fisons MD 800 mass spectrometer (MS) from Thermo-Quest (Vienna, Austria). The GC-column (a DB-5MS fused silica capillary column: 30 m x 0.25 mm i.d., 0.25 µm film thickness from Fisons) was directly connected to the ion source of the MS. The splitless Grob injector was kept at 260 °C; helium was the carrier gas. Mainly, the following temperature program was used: initial temperature 50 °C for 1 min, followed by an increase of 10 °C/min to 200 °C, with 15 °C/min to 300 °C, and an isothermal hold for 5 min. The ion source of the mass spectrometer and the transfer line were kept at 200 °C and 310 °C, respectively. Electron impact (EI) spectra were recorded at 70 eV.

3. Results and Discussion

Classification of extract components

Access to oil gland secretions by the technique of whole-body extraction, as already mentioned above, requires an additional step for the discrimination between oil gland-derived extract components and components derived from other regions of the body. In a model study, using the giant oribatid mite *Collohmannia gigantea* Sellnick, 1922, whole-body-extracts of mite individuals with filled glands were compared to those that had their glands already depleted (RASPOTNIG et al. 2001). This investigation became possible as *C. gigantea* noticeably released its lemon-scented oil gland secretion in the case of mechanical irritation. Discharge of secretion could be induced for several times (e.g. by gentle shaking of mites in a jar) until the scent reserves were completely exhausted. In extracts of these individuals, after exhaustion of oil gland secretion reserves, several components disappeared in the chromatograms (= the oil gland secretion components!) while other extract components (derived from other body regions) remained unaffected. In fact, the stepwise (and proportionate!) decline of oil gland components after each event of discharge was chromatographically documented (Fig. 3). On the other hand, if using hexane as a solvent and if observing to short extraction times (see methods), only oil gland secretion components appeared in the chromatograms. Thus, the »hexane-method« allowed access to pure oil gland secretions without contaminations; this seemed to be true for other oribatid species as well (RASPOTNIG et al. 2004, 2005a, c). Oil gland secretions are obviously directly discharged into the solvent, making it possible to analyse their original (qualitative and relative quantitative) composition.

In addition, RASPOTNIG et al. (2001) – again on the model of *C. gigantea* – could demonstrate the presence of these designated oil gland secretion-components directly in the oil gland reservoirs by histochemical means: in detail, after treatment with a highly-sensitive aldehyde reagent (three components of the oil gland secretion of *C. gigantea* are aldehydes!), oil gland contents turned deeply black in individuals with filled reservoirs while no

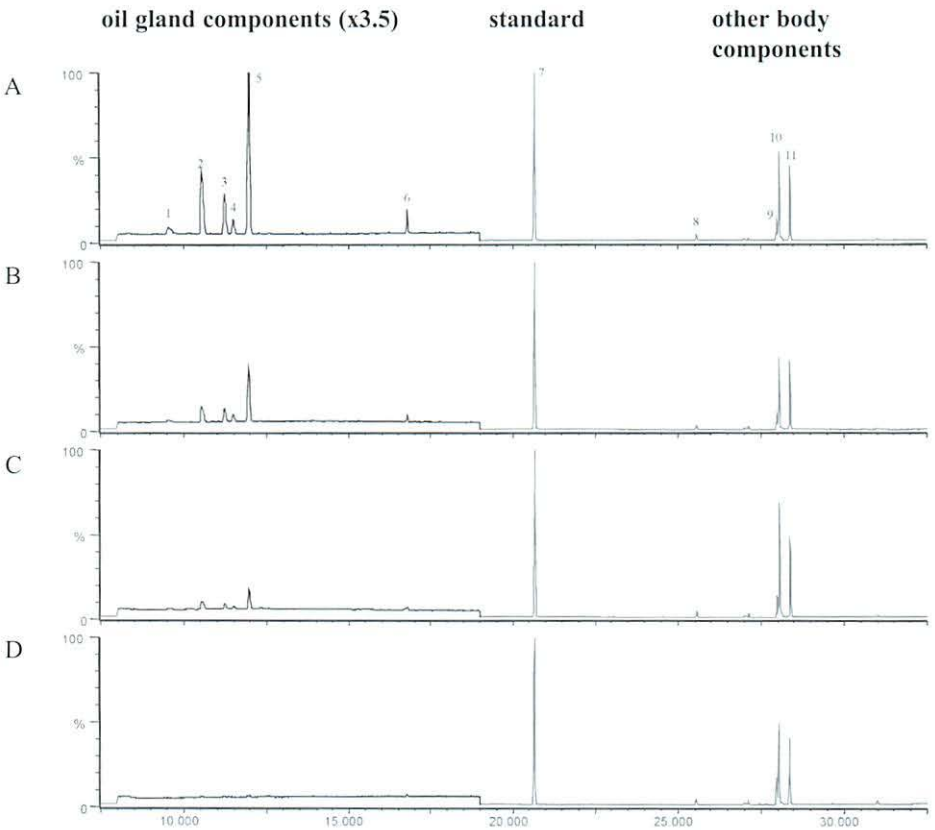

Fig. 3 Identification of oil gland secretion components in ethanolic whole-body extracts of *Collohmannia gigantea*. Stepwise and proportionate decrease of extractable amounts of oil gland secretion components paralleling events of secretion emission (due to irritation) while amounts of other extract components remain unaffected. (A) full oil gland reservoirs (= no irritation); (B) extracts after moderate irritation (and noticeable secretion emission); (C) extracts after heavy irritation (and repeated secretion emission); (D) extracts after complete exhaustion of oil gland reservoirs.

Extract components: (1) 2-hydroxy-6-methyl-benzaldehyde, (2) neral, (3) geranial, (4) neryl formate, (5) tridecane, (6) pentadecane, (7) tridecanoicacid ethyl ester was used as an internal standard for quantification, (8) hexadecanoic acid ethyl ester, (9) C18:2-carboxylic acid ethyl ester, (9) C18:1-carboxylic acid ethyl ester, (19) C18-carboxylicacid ethylester.

colouration could be observed in individuals after exhaustive discharge of secretion. Apart from *C. gigantea*, indications for the classification of certain extract components with the oil gland secretion arose from chemical investigations of exuviae of *Archegozetes longisetosus* Aoki, 1965: extracts of these exuviae, containing well-filled oil gland reservoirs, displayed the same set of components as whole-body extracts of intact individuals (SAKATA & NORTON 2003). These basic investigations, together with a large amount of chemical data from astigmatid mite oil glands (KUWAHARA 2004) led to the evaluation of a set of characteristic oil gland secretion components (see next paragraph), facilitating future classifications in extracts of other species. Furthermore, corroborative evidence came from chemical investigations of non-glandulate groups where the typical oil gland secretion components could not be detected (SAKATA & NORTON 2001).

Oribatid oil gland chemistry

Chemical data on oil gland secretions have been compiled for 21 oribatid species, though data for 6 species are preliminary and remain to be published (Tab. 1). In total, 30 different oil gland components have hitherto been elucidated (Fig. 4). All components belong to 4 distinct chemical classes, namely terpenes, aromatics, hydrocarbons, and – according to a most recent publication (TAKADA et al. 2005) – also alkaloids. This chemical »parsimony« results in a characteristic overall chemistry of secretions. Oil gland secretions, however, are multi-component systems comprising about 4 components (such as in *Parhypochthonius aphidinus* Berlese, 1904) and more than 10 components in Trhypochthoniidae. The specific combination of these compounds leads to species-specific profiles (Tab. 1).

On the other hand, the chemistry of oil gland secretions in Astigmata has extensively been investigated since 1975 by KUWAHARA and colleagues, showing comparable chemical compositions and representing a large chemical data base from a highly-derivative glandulate group (KUWAHARA et al. 1975, KUWAHARA 1991, 2004). In astigmatid mites, 67 components from 52 species have been identified (SAKATA et al. 2003).

Oil gland secretion profiles appear to be stable sets of characters: RASPOTNIG et al. (2001), in an extensive investigation of the chemical composition of the oil gland secretion of *Collohmannia gigantea* over a longer period, found nearly identical profiles irrespective of seasonal aspects and populations. In certain Desmonomata and Brachypylida, even juvenile profiles can clearly be distinguished from those of adults: examples are *Nothrus palustris* C. L. Koch, 1839, *Platynothrus peltifer* (C. L. Koch, 1839), *Hermannia convexa* (C. L. Koch, 1840), and *Scheloribates azumaensis* Enami, Nakamura & Katsumata, 1996, respectively (SHIMANO et al. 2002, RASPOTNIG et al. 2005a, c, TAKADA et al. 2005). In some species, however, profiles may exhibit a certain range of variability: for instance, even though multi-component profiles of adult *P. peltifer*, sampled from 9 different locations in Austria, generally showed a characteristic composition, they differed in one inconsistently occurring compound, namely γ-acaridial (RASPOTNIG et al. 2005c). Also a reinvestigation of the oil gland secretion profile of *Trhypochthoniellus crassus* (Warburton & Pearce, 1905) revealed certain differences (SAKATA et al. 1995, 2003): this latter inconsistency, however, possibly originated from the small number of individuals used for this investigation. Overall, and including profiles of astigmatid mites, compositions of oil gland secretions appear to be well suited as taxonomic characters, and even could successfully be applied to differentiate between morphologically similar species of certain genera such as *Oribotritia* Jacot, 1925 (RASPOTNIG, ined.) and *Tyrophagus* Oudemans, 1924 (LEAL et al. 1989a), respectively.

Tab. 1 Oribatid oil gland secretion profiles: Status quo

species	chemical profile of secretion[1]	references
cohort Parhyposomata		
Parhypochthonius aphidinus Berlese, 1904	5, 17, 18, 22	SAKATA & NORTON 2001
Gehypochthonius urticinus (Berlese, 1910)	4, 18, 20, 22, 23	
cohort Mixonomata		
Nehypochthonius porosus Norton & Metz, 1980	18, 19 + two unknowns (M=150, M=204)	
Perlohmannia sp. (undescribed)	2, 7, 9, 24	
Collohmannia gigantea Sellnick, 1922	1,(2), 6, 7, 9, 18, 19	RASPOTNIG et al. 2001
6 species of Oribotritiidae (*Oribotritia, Mesotritia*)	15, 16 + other components	RASPOTNIG, ined.
cohort Desmonomata		
Trhypochthonius japonicus Aoki, 1970	(1), 2, 9, 10, 11, 20, 23 + two unknowns	SAKATA et al. 2003
Trhypochthonius tectorum (Berlese, 1896)	1, 2, 7, 9, 10, 11, 19, 20, 23	RASPOTNIG et al. 2004
Trhypochthoniellus crassus (Warburton & Pearce, 1905) (syn. *Hydronothrus crispus*)	1, 2, 6, 7, 9, 18, 19, 20, 23, 24	SAKATA et al. 1995, 2003
Trhypochthoniellus sp. (undetermined)	2, 6, 7, 8, 9, 20, 23	SAKATA et al. 2003
Archegozetes longisetosus Aoki, 1965	1, 2, 6, 7, 9, 19, 20, 23, 24	SAKATA & NORTON 2003
Platynothrus peltifer (C. L. Koch, 1839)	(2), 3, 6, 7, 9, 20, 23	RASPOTNIG et al. 2005c
Nothrus palustris C. L. Koch, 1839	7, 9, 12, 21	SHIMANO et al. 2002
Hermannia convexa (C. L. Koch, 1840)	2*, 7*, 9*, 13**, 20, 23	RASPOTNIG et al. 2005a
cohort Brachypylida		
Scheloribates azumaensis Enami, Nakamura & Katsumata, 1996	2*, 7*, 14, 26, 28, 28'	TAKADA et al. 2005
Scheloribates sp. (undetermined)	25, 27, 29, 30 + seven unknowns	

[1]Numbers refer to components in Fig 4. Numbers in brackets indicate inconsistently occurring compounds
*Compounds present in juveniles only
**The classification of component no. 13 (1,8-cineole) with oil gland secretions is uncertain
Compound no. 28' is not fully characterised yet but chemically related to no. 28 (precoccinelline)

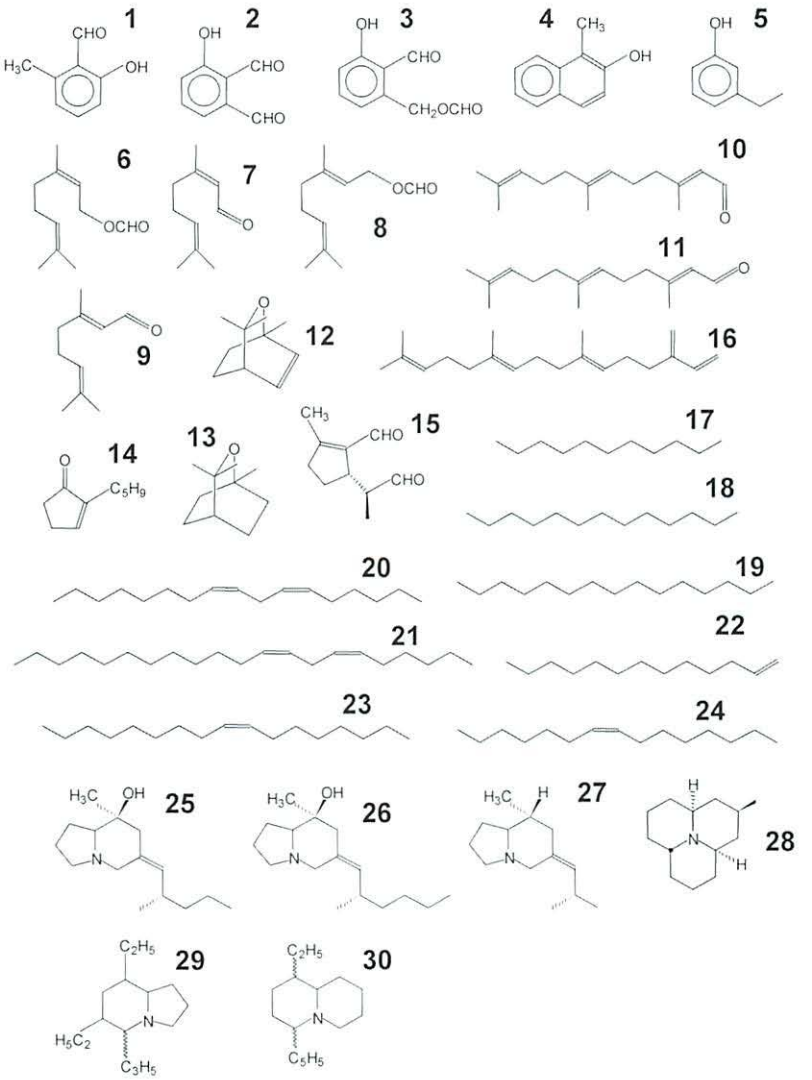

Fig. 4 Chemical constituents of oil gland secretions of Oribatida: status quo. (1) 2-hydroxy-6-methyl-benzaldehyde = 2,6-HMBD, (2) 3-hydroxybenzene-1,2-dicarbaldehyd = γ-acaridial, (3) rhizoglyphinyl formate, (4) 1-methyl-2-naphthol, (5) 3-ethylphenol, (6) neryl formate, (7) neral, (8) geranyl formate, (9) geranial, (10) (Z,E)-farnesal, (11) (E,E)-farnesal, (12) dehydrocineole, (13) 1,8-cineole (classification with oil gland secretion uncertain), (14) 2-(2-pentenyl)-2-cyclopenten-1-one, (15) chrysomelidial*, (16) ß-springene*, (17) undecane, (18) tridecane, (19) pentadecane, (20) 6,9-heptadecadiene, (21) heneicosadiene, (22) tridecene, (23) heptadecene, (24) pentadecene, (25) pumiliotoxin 237A, (26) pumiliotoxin 251D, (27) 8-deoxypumiliotoxin 193H, (28) precoccinelline, (29) 6,8-diethyl-5-propenylindolizidine, (30) 1-ethyl-4-pentenynylquinolizidine.

*preliminary data (RASPOTNIG, ined.)

Oil gland secretion profiles and oribatid phylogeny

Oil gland secretion profiles are devoted to evolutionary changes as any set of characters, and oribatid phylogeny is reflected as follows: Hydrocarbons are distributed in oil gland secretions of all species so far investigated, including Parhyposomata (the first group possessing oil glands), Mixonomata, Desmonomata and Astigmata. Thus, hydrocarbons are thought to represent ancient oil gland secretion components (= symplesiomorphic characters of glandulate Oribatida). No data on hydrocarbons, however, are available on Brachypylida. By contrast, sets of synapomorphic components characterise distinct groups within glandulate Oribatida: Naphthols and phenols are found in Parhyposomata only, and a large group from middle-derivative Mixonomata upwards is possibly characterised by so-called »astigmatid compounds«. SAKATA et al. (1995) and RASPOTNIG et al. (2001) noticed an »astigmatid mite-like« chemistry when investigating oil gland secretions of certain middle-derivative Oribatida. In fact, oil gland profiles from *C. gigantea* (Mixonomata) and *Hydronothrus crispus* (= *Trhypochthoniellus crassus*) (Desmonomata) strikingly resembled the oil gland secretion profiles from astigmatid mites, showing (in addition to hydrocarbons) a set of terpenes and aromatic components. Subsequently, SAKATA & NORTON (2001) evaluated a set of 5 terpenes and aromatics that were considered characteristic for Astigmata and a restricted set of middle-derivative Oribatida. These »astigmatid compounds« comprise neral, geranial, neryl formate, 2-hydroxy-6-methylbenzaldehyde (2,6-HMBD) and 3-hydroxybenzene-1,2-dicarbaldehyde (γ-acaridial). These are not found in early-derivative glandulate Oribatida such as Parhyposomata nor in early »mixonomatans« such as *Nehypochthonius porosus* Norton & Metz, 1980. Their hitherto known distribution strongly suggests that they arose stepwise in ancestors of middle-derivative Mixonomata: in *Perlohmannia* Berlese, 1916, only a part of them is present (SAKATA & NORTON 2001), but in *Collohmannia,* the full set of astigmatid compounds is already developed (RASPOTNIG et al. 2001, Fig. 5). Most probably, »astigmatid compounds« have evolved only once, and they are considered to have been transferred to all groups above Mixonomata; i.e. these components would characterise a large monophyletic unit within glandulate oribatids, the »astigmatid compounds-bearing« Oribatida (Fig. 6). In fact, besides Mixonomata, astigmatid compounds are well known from desmonomatan groups and are especially characteristic of Trhypochthoniidae. (In this respect, the evolutionary origin of astigmatid mites may be found in oribatid ancestors that already produced astigmatid compounds, underlining an idea of NORTON (1998) hitherto having been based on morphological evidence only). Results from recent investigations, however, indicate a wider distribution of astigmatid-compounds in Oribatida. These compounds, though reduced in richness, also occur in non-trhypochthoniids such as Nothridae (SHIMANO et al. 2002), and RASPOTNIG et al. (2005a, c) demonstrated their presence in desmonomatan Camisiidae and in »higher Desmonomata« such as Hermanniidae. In these groups, astigmatid compounds are subjected to reductions and replacements by other (apomorphic) components. Also in certain Brachypylida, at least in some juveniles, astigmatid compounds were detected (TAKADA et al. 2005) and further are to be expected (SAKATA & NORTON, pers. comm.). Thus, hitherto known data on the distribution of astigmatid compounds (Tab. 2), though being fragmentary yet, clearly support the above mentioned hypothesis of a large monophyletic group of astigmatid compounds-bearing Oribatida.

In addition, sub-groups (on any taxonomic level) within the astigmatid compounds-bearing Oribatida exhibit their own (additional) distinct chemistry.

In euphthiracaroid Mixonomata (4 species of *Oribotritia* Jacot, 1925 and 2 species of *Mesotritia* Forsslund, 1963 have preliminarily been investigated), astigmatid compounds tend to be reduced, but are replaced by a prominent and very unusual irodoid monoterpene (possibly chrysomelidial, but not yet fully characterised) and a diterpene (possibly ß-springene). Chrysomelidial and ß-springene are not only unique for oil gland secretions of all Sarcoptiformes (= Oribatida and Astigmata) but also for all arachnids: it is very likely that these compounds are synapomorphic for Oribotritiidae (RASPOTNIG, ined.).

In Desmonomata, oil gland secretion profiles in the genus *Trhypochthonius* Berlese, 1904 seem to be characterised by (apomorph) farnesals while these compounds are absent from

Tab. 2 Hitherto known distribution of »astigmatid compounds« within glandulate Oribatida

Species	astigmatid compounds	references
Mixonomata:		
Perlohmannia sp.	neral, geranial, γ-acaridial	SAKATA & NORTON 2001
Collohmannia gigantea	neral, geranial, neryl formate, 2,6-HMBD, γ-acaridial[1]	RASPOTNIG et al. 2001
Oribotritia banksi	neral, geranial	RASPOTNIG, ined.
Desmonomata:		
Trhypochthoniellus crassus (= *Hydronothrus crispus*)	neral, geranial, neryl formate[2], 2,6-HMBD, γ-acaridial[2]	SAKATA et al. 1995, 2003
Trhypochthoniellus sp.	neral, geranial, neryl formate, γ-acaridial	SAKATA et al. 2003
Trhypochthonius japonicus	geranial, (2,6-HMBD)[3], γ-acaridial	
Trhypochthonius tectorum	neral, geranial, 2,6-HMBD, γ-acaridial	RASPOTNIG et al. 2004
Archegozetes longisetosus	neral, geranial, neryl formate, 2,6-HMBD, γ-acaridial	SAKATA & NORTON 2003
Nothrus palustris	geranial	SHIMANO et al. 2002
Platynothrus peltifer	neral, geranial, neryl formate, γ-acaridial	RASPOTNIG et al. 2005c
Hermannia convexa[4]	neral, geranial, γ-acaridial	RASPOTNIG et al. 2005a
Brachypylida:		
Scheloribates azumaensis[4]	geranial, γ-acaridial	TAKADA et al. 2005

[1]Not mentioned in RASPOTNIG et al. (2001), but inconsistently present
[2]Profiles given in SAKATA et al. (1995, 2003) differ with regard to neryl formate and γ-acaridial
[3]2,6-HMBD was absent in one (of two) populations investigated
[4]Compounds present in juveniles only

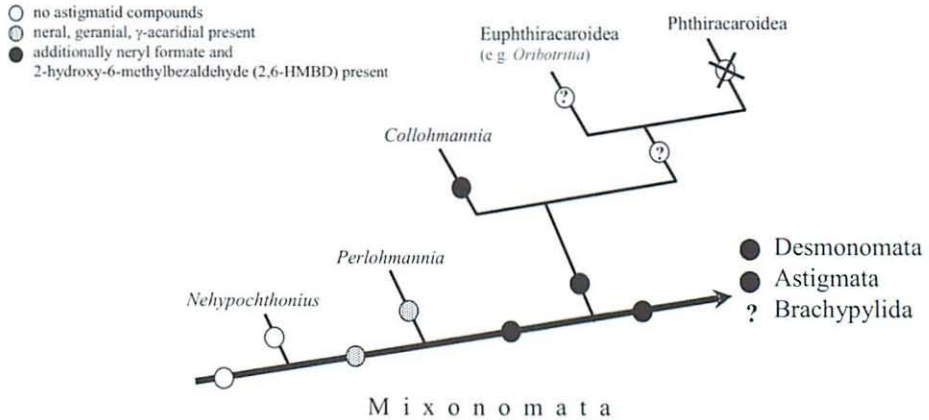

Fig. 5 Stepwise evolution of »astigmatid compounds« in mixonomatan Oribatida. White circles (astigmatid compounds not present yet), dotted circles (astigmatid compound partly present), black circles (full set of astigmatid compounds developed; reductions in Desmonomata, Astigmata and Brachypylida possible!). In Phthiracaroidea oil glands are reduced; in Euphthiracaroidea, a trend towards reduction and replacement of astigmatid compounds is obvious (see text).

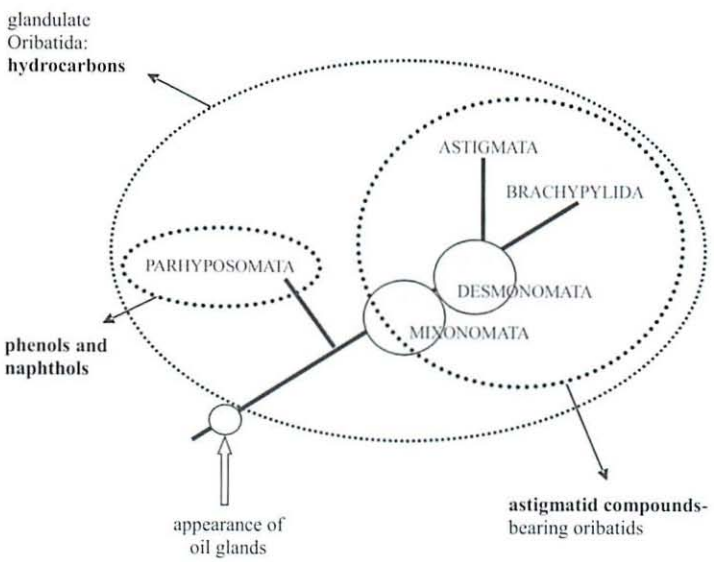

Fig. 6 Oil gland secretion profiles and oribatid systematics: the monophylum of »astigmatid compounds«-bearing Oribatida.

The monophyletism of Parhyposomata is not supported by oil gland chemistry: Parhypochthoniidae and Gehypochthoniidae each show autapomorph oil gland secretion profiles, the former phenols, the latter naphthols (SAKATA & NORTON 2001).

(possibly more basal) trhypochthoniids of genera *Trhypochthoniellus* Willmann, 1928 and *Archegozetes* Grandjean, 1931 (SAKATA & NORTON 2003, SAKATA et al. 2003, RASPOTNIG et al. 2004). Farnesals, on the other hand, were also detected in certain Astigmata, at least in the oil gland secretion of *Suidasia medaensis* Oudemans 1924 (LEAL et al. 1989b). Rhizoglyphinyl formate, found in the oil gland secretion of *Platynothrus peltifer* and hitherto also unique in Oribatida, may characterise certain Camisiidae (RASPOTNIG et al. 2005c) but, according to current knowledge, is also present in two astigmatid species (SATO et al. 1993, TARUI et al. 2002).

In adult Brachypylida, a fundamental change in the chemical compositions of oil gland secretions becomes obvious: a fourth distinct chemical class of oil gland secretion components, namely alkaloids, was demonstrated in the oil gland secretions of *Scheloribates azumaensis* and another (undetermined) *Scheloribates* species (TAKADA et al. 2005). Interestingly, remains of astigmatid compounds were still found in juveniles, further underlining a trend that was already observable in higher Desmonomata: i.e., a tendency to the reduction and replacement of astigmatid compounds in oil glands secretions of adults only and a hence resulting »chemical dimorphism« of juvenile and adult secretion profiles. Differentially composed secretions in juveniles and adults of the same species were reported from Nothridae (SHIMANO et al. 2002) and, in an extreme form, also from a species of Hermanniidae (RASPOTNIG et al. 2005a). Overall, this trend may characterise an evolutive lineage from higher Desmonomata to Brachypylida. In consistence, Hermannioidea are considered near-basal to Brachypylida also by morphological data (e.g. HAUMANN 1991).

4. Conclusion

Currently recognised taxonomic systems of Oribatida are artificial: not only the phylogenetic relationships of large oribatid groups, so-called »cohorts« (sensu GRANDJEAN 1969) have remained unclear but also the relationship of Oribatida to outgroups is still a subject of controversial discussion. Moreover, Oribatida contain a series of paraphyletic groupings, e.g. the Mixonomata and the Desmonomata represent (known) paraphyletic assemblages (e.g. NORTON 1998) and also the Poronota (or possibly the Brachypylida as a whole) may be paraphyletic (e.g. WOAS 1990). A similar situation, however, is true for many lower oribatid taxa: Many genera, families and super-families have remained monotypic (as they can not be classed with other groups), or, on the other hand, paraphyletic taxa have been generated (e.g. Trhypochthoniidae sensu WILLMANN 1931). Thus, current classifications actually represent keys for identification only, but conspicuously lack a phylogenetically founded basis (e.g. KRANTZ 1978, JOHNSTON 1982, BALOGH & BALOGH 1992).

Besides NORTON (e.g. 1998), only a few authors – such as the »grand seigneur« of Oribatidology, F. GRANDJEAN (e.g. 1969), but also G. HAUMANN (1991) and G. WEIGMANN (e.g. 1997) – have emphasised phylogenetic aspects: however, all of these studies are exclusively based on the evaluation of characters from traditional external morphology. In order to answer the problems mentioned above and to reach a sound basis for oribatid taxonomic research, a synopsis of characters from different sources is acutely needed. Thus, besides the application of newly arising molecular data (e.g. AVANZATI et al. 1994, SALOMONE et al. 1996, 2001, MARAUN et al. 2003, 2004), the chemistry of oil gland secretions provides a promising third and independent set of characters for a chemosystematic approach to oribatid phylogeny (SAKATA & NORTON 2001, 2003, RASPOTNIG et al. 2001, 2004, 2005a, c, SAKATA et al. 2003).

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