

Attack and defense in a gamasid-oribatid mite predator-prey experiment – sclerotization outperforms chemical repellency

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ABSTRACT — Oribatid mites represent a diverse group of soil micro-arthropods. They have evolved a broad range of defensive chemical and morphological traits (e.g. sclerotization, ptychoidy, biomineralization). Chemical defense, rather than sclerotization, can provide protection against large predators (staphylinid beetles) and many oribatid mite species are also well protected against gamasid soil mites using morphological traits ("enemy-free-space hypothesis"). However, since predatory mites and staphylinid beetles have different types of attacking and feeding, the adaptive values of chemical and morphological traits might differ accordingly. We used the oribatid model species *Archegozetes longisetosus* Aoki and the common gamasid mite *Stratiolaelaps miles* Berlese in a predator-prey experiment. We tested for effects of chemical defense (treatments with and without oil gland secretions) and sclerotization (treatments with unsclerotized tritonymphs and sclerotized adults) in an orthogonal design. In contrast to attacks by large predators, chemical defense was mostly ineffective against gamasid mites. Sclerotization, however, had a positive effect. Hence, in a natural environment with diverse types of predators, the "enemy-free space" seems only realizable by combinations of chemical and morphological protective traits.

KEYWORDS — Defensive mechanisms; Oribatida; Mesostigmata; soil food webs; attack type; chemical ecology

INTRODUCTION

Oribatid mites are among the most abundant and speciose arthropods in forest soil ecosystems all over the world (Schatz, 2004; Maraun *et al.*, 2007; Schatz *et al.*, 2011). Most of the species are particle-feeding saprophages and mycophages, inhabiting diverse microhabitats (Norton, 2007; Heethoff and Norton, 2009; Wehner *et al.*, 2016). The high number of individuals (up to several hundred thousand per square meter) and ubiquitous distribution render oribatid mites a potential resource for predators in terrestrial food webs (e.g., Hunt and Wall, 2002; Schneider and Maraun, 2009).

Oribatid mites can be consumed by numerous predators such as newts (Norton and MacNamara, 1976), salamanders (Maiorana, 1978; Walton *et al.*, 2006), caecilians (Kupfer and Maraun, 2003), poison frogs (Saporito *et al.*, 2007; Saporito *et al.*, 2009), ants (Masuko, 1994; Wilson, 2005), true bugs (Kott, 2015) and beetles (Riha, 1951; Schuster, 1966a; 1966b; Schmid, 1988; Molleman and Walter, 2001; Heethoff *et al.*, 2011; Jalszynski and Beutel, 2012; Jalszynski and Olszanowski, 2013; 2015). However, the most important predators of oribatid mites are most likely predatory mites (Mesostigmata, Gamasina) (Walter *et al.*, 1987; Norton, 1994; Koehler, 1997;

Koehler, 1999; Hunt and Wall, 2002; Schneider and Maraun, 2009). Gamasid mites are motile and agile predators of other soil micro-arthropods and therefore possess a key position in soil food webs (Koehler, 1997; Koehler, 1999; Berg *et al.*, 2001; Ruf and Beck, 2005). Their abundance in temperate forests can reach up to 25,000 ind/m², with an average between 4,000 and 10,000 ind/m² (Römbke *et al.*, 1997; Christian, 2000). Hence, gamasid mites outreach other soil predators in density and significantly contribute to below-ground energy flow (Luxton, 1982; Koehler, 1997; Koehler, 1999). They are eye-less, but light sensitive, and find their prey by chemical and/or mechanical stimuli (Koehler, 1999). Due to the fact that they digest their food pre-orally and suck it up for consumption (Koehler, 1997; Koehler, 1999), it was hypothesized that predatory mites may prefer prey with a thin, lightly sclerotized cuticle (Walter *et al.*, 1987). The density of unsclerotized juvenile oribatid mites, however, was not significantly reduced by high predatory mite densities in a microcosm experiment, while the density of adults of smaller and weaker sclerotized oribatid mites species was (Schneider and Maraun, 2009). Hence, a potential top-down control of soil micro-arthropods by gamasid predatory mites was suggested (Schneider and Maraun, 2009). These findings are in contrast to Peschel *et al.* (2006) who hypothesized that adult oribatid mites live in an "enemy-free space" [= conceptual ways of living that reduce or eliminate a species' vulnerability against their predators, (*sensu* Jeffries and Lawton, 1984)] while juveniles may not. Both studies (Peschel *et al.*, 2006; Schneider and Maraun, 2009) stated the lack of "experimental studies evaluating the effect of chemical defense against predators". Meanwhile studies have confirmed the opisthonotal glands (= oil glands) to be defensive glands in adults and juveniles (Heethoff *et al.*, 2011; Heethoff and Rasputnig, 2012a) against larger rove beetle (Staphylinidae) predators of the genus *Stenus* Latreille.

Rove beetles have a massive mechanical impact on oribatid prey and can crack sclerotized adults with their mandibles (Betz, 1998; Heethoff *et al.*, 2011). Here, chemical protection becomes an ef-

fective strategy to avoid the beetles from biting at the very first contact with the mouthparts (Heethoff *et al.*, 2011). Since gamasid mites have only small chelicerae and cannot crack a whole oribatid mite, a much more delicate attack type, which tackles soft, membranous elements, is mandatory (Walter *et al.*, 1987; Walter and Proctor, 1999). Peschel *et al.* (2006) showed that oribatid mites which did not expose membranous elements due to special adaption (e.g. ptychoidy) were well protected against gamasid predatory mites. Since predatory mites and staphylinid beetles have different types of attacking and feeding, the adaptive values of chemical and morphological traits might differ accordingly. Predatory mites cause a lower mechanical impact on their prey, hence their feeding success is presumably regulated by morphological traits such as sclerotization. Chemical secretions should be an effective strategy for defense of weakly sclerotized or unsclerotized prey. We tested these hypothesis by using adult (sclerotized) and juvenile (unsclerotized tritonymphs) oribatid mites (*Archeogozetes longisetosus* Aoki), each with and without defensive secretions, in a no-choice feeding experiment with the gamasid mite *Stratiolaelaps miles* Berlese (= *Hypoaspis miles*). We show that chemical defense was mostly ineffective against predatory mites while sclerotization had a positive effect in gamasid-oribatid mite feeding interactions.

MATERIALS AND METHODS

Animals

Specimens (adults and tritonymphs) of the laboratory culture *Archeogozetes longisetosus* ran (founded by Roy A. Norton; Heethoff *et al.*, 2007; Heethoff *et al.*, 2013) were used as prey, because their defensive gland chemistry is well known (Sakata and Norton, 2003; Rasputnig and Föttinger, 2008; Heethoff and Rasputnig, 2011). Furthermore, the species has been used in feeding experiments before (Heethoff *et al.*, 2011; Heethoff and Rasputnig, 2012a) and a functional response model of reservoir based chemical defense in predator-prey interactions has been described (Heethoff, 2012; Heethoff and Rall, 2015). The nymphs are unsclerotized and were used as

prey in comparison to sclerotized adults (Heethoff and Rasputnig, 2012a). Colonies of *A. longisetosus* were kept in constant dark at 28°C and 80–85% relative air humidity in plastic boxes (100x100x50 mm) grounded with a mixture of plaster of Paris and activated charcoal (9:1). Food (wheat-grass powder, Naturya, Bath, United Kingdom) on a 1 x 1 cm filter paper and water were provided *ad libitum* three times a week.

Adult specimens of the gamasid mite *Stratiolaelaps miles* were used as predators. Species of the genus *Stratiolaelaps* are common soil-dwelling predatory mites (e.g. Berndt *et al.*, 2003) with a broad feeding range on many different organisms (Enkegaard *et al.*, 1997), such as springtails, soil mites, nematodes, leaf-miners, thrips and small flies (e.g. Kevan and Sharma, 1964; Barker, 1969; Ragusa *et al.*, 1986; Epsky *et al.*, 1988; Gillespie and Quiring, 1990; Glockmann, 1992; Lesna *et al.*, 2000). Furthermore, *Stratiolaelaps* was selected as a "typical" soil predatory mite (Bakker *et al.*, 2003) with high consumption rates (Enkegaard *et al.*, 1997) and a body size comparable to that of oribatid mites - about 750 µm for *S. miles* (as *Laelaps miles*; Berlese, 1892). These predators were purchased from a commercial supplier (Schneckenprofi, Prime Factory GmbH & Co. KG, Hennstedt, Germany) and starved for one week (except for potential cannibalism) before starting the experiment. During this time *S. miles* were kept in plastic boxes (100x100x50 mm, the outer rim was impregnated with Fluon® PTFE resin) with moisturized vermiculite and no food.

Bioassays

No-choice feeding experiments were set up with one adult predatory mite and ten individuals of oribatid mites (adults or tritonymphs) as potential prey in squared plastic boxes (27x29x43 mm) grounded with a mixture of plaster of Paris and activated charcoal (9:1). Four different treatments were set up with 20 replicates for each treatment: chemically armed, undisturbed adults (ADU+) and tritonymphs (TRI+) as well as chemically disarmed adults (ADU-) and tritonymphs (TRI-) of *A. longisetosus* (for disarming protocol see Heethoff and Rasputnig, 2012b). Survival of prey (and predat-

tors) was recorded daily for five days and consumed prey specimens were not replaced. Dead oribatid mites were checked carefully under the microscope and only mites with feeding traces were counted for statistical analysis. Food (wheat-grass powder) on filter paper and water were provided *ad libitum*. The feeding experiments were performed at 23°C, 80–85% relative air humidity and constant dark for 22 h a day. Additionally, behavioral observations of *S. miles* focusing on attacking, handling and consuming behavior when dealing with chemically defended and disarmed *A. longisetosus* were carried out in a smaller plastic box (10x10x5 mm) grounded with plaster of Paris, using a Panasonic Lumix DMC-GH2 digital camera (Panasonic Deutschland, Hamburg, Germany) on a Zeiss Stemi 2000-C (Carl Zeiss AG, Oberkochen, Germany).

Chemical analysis

In a supporting experiment, individuals of *A. longisetosus* were paired with single individuals of *S. miles* to quantify discharge of defensive secretions during the predatory feeding process (n=55). Oribatid mites were carefully removed from the colony boxes and transferred to a small plastic arena (10x10x5 mm, grounded with a thin layer of plaster of Paris), equipped with one predator, by using a fine-brush. After *S. miles* attacked and fed on *A. longisetosus*, the released dead bodies of the prey were immediately submersed in 20 µl hexane (GC grade, 98% purity purchased from Merck, Darmstadt, Germany) with tetrade-cane (1 ng/µl as internal standard; ≥99.8%, analytical standard, purchased from Sigma-Aldrich, Munich, Germany) to extract potential residuals of the oribatid mites' defensive secretions. Furthermore, the defensive gland secretions of 25 actively moving, unattacked adults of *A. longisetosus* were extracted individually as a control. Defensive secretion amounts of both groups were analyzed by injecting 5 µl sample aliquots into a QP 2010 Ultra gas-chromatography mass-spectrometry system (GC-MS; Shimadzu, Duisburg, Germany) equipped with a ZB-5MS fused silica capillary column (30 m x 0.25 mm ID, df= 0.25 µm) from Phenomenex (Aschaffenburg, Germany). Chromatographic and

mass-spectrometric conditions were as follows: GC temperature was raised from 50°C for 5 min, to 250°C with a heating-rate of 8°C/min, to 320°C with a heating-rate of 25°C/min and an isothermal hold at 320°C for 5 min. MS spectra (electron impact) were recorded at 70 eV from m/z 40 to 240. The ion source and the transfer line were kept at 250°C. Quantification of absolute secretion amount was performed based on the peak area of detected compounds relative to a constant amount of the internal standard (5 ng tetradecane) expressed in [%] peak of this standard.

Mass and size measurements

Body mass of adults and tritonymphs ($n = 10$ each) was determined with a microbalance (Mettler Toledo, XS3DU, 0.1 µg readability and 1 µg repeatability). Size was measured as the length of the notogaster. Adults and tritonymphs ($n = 10$ each) were measured with a VHX-5000 digital microscope (Keyence Deutschland GmbH, Neu-Isenburg, Germany) using the VH-Z50L lens.

Statistical analysis

Statistical analyses were performed with R 3.2.1 (R Development Core Team, 2015). Prior to statistical analyses, consumption ($N_{\text{eaten}}/N_{\text{total}} \cdot 100\%$) was calculated and the absolute secretion amount in [%] of standard was normalized to 100 [%] in regard to the mean secretion of unattacked adults. Consumption between the different defense states (armed/disarmed) and developmental stages (adult/ tritonymph) and defensive secretion amounts between attacked and unattacked oribatid mites were compared using pairwise Mann-Whitney-U-tests (Mann and Whitney, 1947). Body mass and size of adults and tritonymphs were compared using Welch two-sample t-tests (Welch, 1947). In addition, counted data (N_{eaten} = oribatid mites eaten after five days) were analyzed with a generalized linear model using Poisson distribution (GLM) with N_{eaten} as response variable and chemical defense (armed/unarmed) as well as life-stage (tritonymph/adult) as explanatory variables. The significance of the effect terms in the GLM were tested using χ^2 -tests.

RESULTS

Feeding experiments

Considering all treatments, 23 (seven in ADU+, eight in ADU- and four each in TRI+ and TRI-) of the 80 *S. miles* ignored the prey, while the remaining 57 predators regularly fed on *A. longisetosus* regardless of the treatment. There was no difference in the consumption of chemically armed and disarmed adults (Mann-Whitney-U-test: $U_{40} = 216.5$; $p = 0.65$); about 9% of the disarmed and 12% of the chemically armed oribatid mites were consumed (Figure 1). In tritonymphs, 25% of the disarmed and 32% of chemically armed individuals were consumed (Figure 1), but the difference was also not significant (Mann-Whitney-U-test: $U_{40} = 231.0$; $p = 0.40$). However, feeding on adults and tritonymphs, either armed or disarmed, strongly differed (Mann-Whitney-U-test: $U_{80} = 442.0$; $p < 0.001$; Figure 1) and the relative consumption was almost three times higher on tritonymphs (28.5%; considering both treatments) than on adults (10.5%). These findings were supported by the results of the GLM (null-deviance = 184.5; deviance = 147.3) for counted oribatid mites eaten after five days (N_{eaten}). Life stage had a significant influence (deviance_{1,79} = 34.52; $p < 0.001$) on the number of consumed oribatid mites, chemical defense (deviance_{1,78} = 2.57; $p = 0.11$) and the interaction of both traits (deviance_{1,77} = 0.01; $p = 0.91$) were not significant. *S. miles* successfully attacked *A. longisetosus* by piercing their mouthparts into membranous elements of the gnathosoma (e.g. cheliceral sheath/frame; see supplementary video). Furthermore, the removal of the legs or attacks in the region of the genital/anal plates were observed. During the feeding process *S. miles* carried immobile prey specimens through the arena. If the predatory mites' mouthparts came into direct contact with the glandular region of the oribatid mites, the prey was quickly released and *S. miles* was disoriented and wobbly walked away from the prey (see supplementary video). After a short resting period (approximately 30 seconds to 1 minute) with intensively cleaning its mouthparts, *S. miles* were able to attack again.

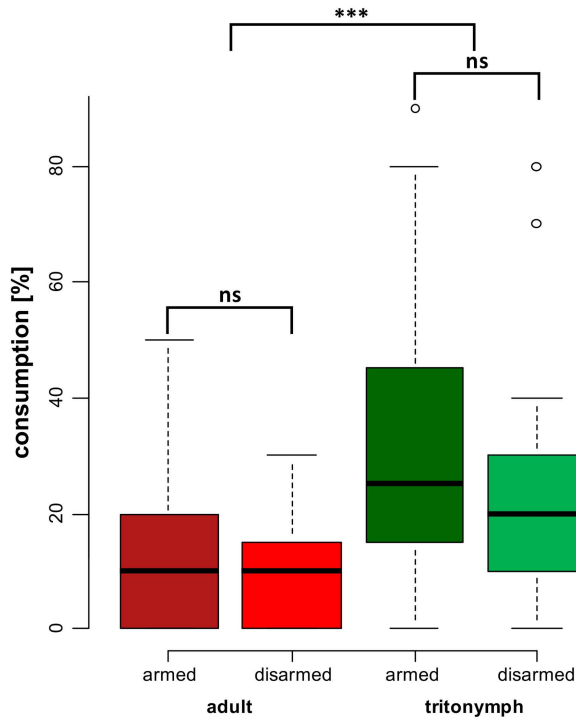


FIGURE 1: Consumption [%] of the predatory mite *Stratiolaelaps miles* feeding on differently treated adults and tritonymphs of *Archegozetes longisetosus* (armed= control group; disarmed= hexane treated specimens). Stars indicate significant differences (Mann-Whitney-U-test, *** $p < 0.001$).

Chemical analysis

Overall, 27 of 55 eaten *A. longisetosus* completely discharged their defensive secretions during the attack and feeding process of *S. miles*. The remaining 28 at least partly depleted their oil glands. The mean normalized secretion amount of the latter group was 40%, while the mean normalized amount of defensive secretion of all attacked and sucked up oribatid mites was 20%. Hence, attacked specimens expelled significant amounts of their secretions (Mann-Whitney-U-test: $U_{80} = 94.0$; $p < 0.001$; Figure 2).

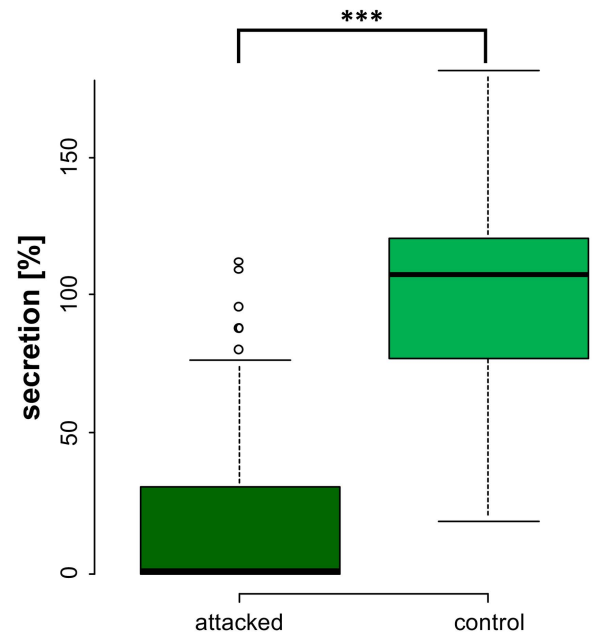


FIGURE 2: Normalized amount of defensive secretion of attacked and control group *Archegozetes longisetosus*. Stars indicate significant differences (Mann-Whitney-U-test, *** $p < 0.001$).

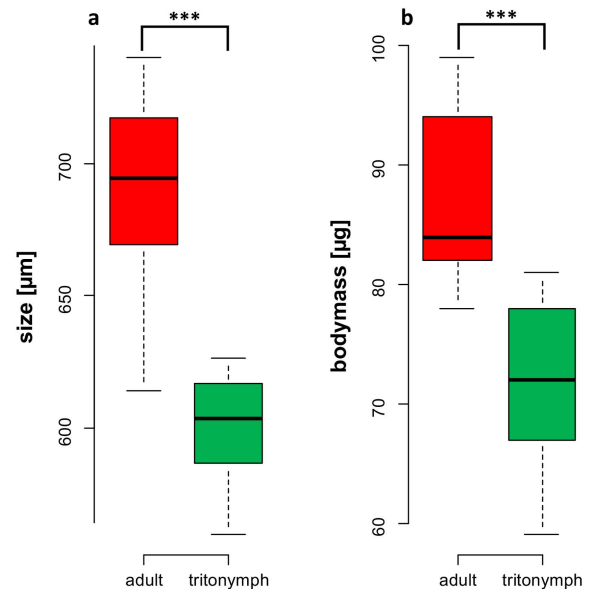


FIGURE 3: Body size and mass of adults and tritonymphs of *Archegozetes longisetosus*. Stars indicate significant differences (Welch two-sample t-test, *** $p < 0.001$).

Mass and size of oribatid mites

Size and body mass were significantly higher in adults than in tritonymphs (Figure 3). Adults were about 90 μm (15%) larger (mean: $691 \pm 34 \mu\text{m}$; $t\text{-test}_{(\text{size})}$: $t_{20}=6.8$; $p<0.001$) and 15 μg (20%) heavier (mean: $87 \pm 7 \mu\text{g}$; $t\text{-test}_{(\text{mass})}$: $t_{20}=4.8$; $p<0.001$) than tritonymphs (mean size: $602 \pm 19 \mu\text{m}$; mean mass: $72 \pm 7 \mu\text{g}$).

DISCUSSION

Understanding predator-prey links in soil is fundamental for our understanding of the enigmatically high diversity of soil animals (Anderson, 1975; Milton and Kaspari, 2007; Tylianakis *et al.*, 2008). Direct observation of predator-prey interactions of soil arthropods in the field, however, is impractical and very difficult due to the small size of the animals and the complexity of the habitat (Lister *et al.*, 1987). Hence, controlled laboratory feeding experiments are important tools to unravel trophic links among soil animals (e.g. Peschel *et al.*, 2006; Rall *et al.*, 2010; Heethoff *et al.*, 2011). Our experiments unexpectedly demonstrated that oil gland secretions of oribatid mites are mostly inefficient against the gamasid mite *S. miles* and, due to the conserved feeding mode (carrying the prey around or fixing it to the ground and piercing or cutting the cuticle with the chelicerae; Usher and Bowring, 1984; Koehler 1997), presumably also against other predatory mite species which belong to the same feeding guild as *S. miles* (polyphagous with unspecialized chelicerae; Eisenbeis and Wichard, 1985). Even if *A. longisetosus* expelled large amounts of their defensive secretions during the attack and feeding process, *S. miles* was not repelled. Only if the predatory mites came into direct contact with the glandular region of the oribatid mites, chemical protection became effectively repellent (see supplementary video). Attacking the opisthosoma does not seem to be, however, a common feeding strategy of predatory mites, since they prefer to attack areas with a thin cuticle (Walter *et al.*, 1987; Peschel *et al.*, 2006).

Juvenile specimens of *A. longisetosus* were chosen as a model for soft-bodied, unsclerotized mites,

given that the morphological characteristics that protect adult oribatid mites (and other heavily armed Oribatida) are lacking (Norton, 1994; 2007), but strong chemical defense is evident (Heethoff and Rasputnig, 2012a). Hence, these morphologically only weakly protected juveniles were preferably consumed by *S. miles*. Tritonymphs of *A. longisetosus* are smaller and lighter than adults – this may affect non-linear interactions strengths ("functional response") in predator-prey interactions (Brose *et al.*, 2006). Nevertheless, the size difference between tritonymphs and adults of *A. longisetosus* is small compared to the size spectrum of prey, which is regularly consumed by *S. miles* (ranging from about 100 μm up to 3000 μm , see material and methods for further information on prey spectrum). Body size is important, but does not explain everything (Kalinkat, 2014), and predator foraging traits (like the feeding type) and prey vulnerability traits (like chemical and morphological defense) have been neglected until recently (Boukal, 2014; Kalinkat *et al.*, 2015). Body size determines how predators affect prey communities on a large scale, while on a small scale (i.e. species-species) interactions specific traits (e.g., defensive strategies, attack/feeding type) may be more important than size, especially if the predator consumes a broad prey size spectrum (Rall *et al.*, 2011; Naisbit *et al.*, 2012; Klecka and Boukal, 2013; Rudolf *et al.*, 2014). Since the preferred sites of attacks in sclerotized adults were membranous regions (e.g. the sheath of the chelicerae, the joint membrane), unsclerotized tritonymphs or other soft-bodied oribatid mites (see Schneider and Maraun, 2009), should be accessible quicker and more effective to gamasid mites (Walter *et al.*, 1987). Hence, the higher consumption of tritonymphs could be explained by shorter handling times [= the time a consumer needs attack, overwhelm and ingest a prey (Holling, 1959; Jeschke *et al.* 2002)] item of *S. miles*. Our results support the conclusive hypothesis of Schneider and Maraun (2009) that chemical defensive secretions of oribatid mites may only be partly effective against gamasid mites. In accordance with the idea of sclerotization providing some mechanical protection against gamasid mite predation, but in contrast to the study of Schnei-

der and Maraun (2009), tritonymphs were more easily attacked and consumed than adults. In natural habitats, juvenile oribatid mites may colonize pores and other small scale shelters or have a specialized endophagous life-style which protect them from predators (Hansen, 2000; Norton, 2007; Schneider and Maraun, 2009), while in our experiments there was no shelter for the prey. Peschel *et al.* (2006) hypothesized an "enemy-free-space" for adult Oribatida based on morphological defense, and Heethoff *et al.* (2011) and Heethoff and Rasputnig (2012a) considered chemical defense to significantly contribute to the defensive potential of oribatid mites against large predators. The present study confirms that sclerotization is an important, but solitary insufficient, factor for oribatid mites to protect themselves against predatory mites (see discussion in Peschel *et al.* 2006). While chemical defense is effective against larger predators with an unspecific feeding mode (Heethoff *et al.*, 2011; Heethoff and Rasputnig, 2012a), some predators with more distinct and specialized feeding seem able to partially overcome the chemical protection. Evidently, the effectiveness of chemical defense in oribatid mites depends on the behavioral feeding mode of the predator species and the benefit of chemical defense should not be generalized. Predatory mites preferably attack at membranous body parts (Hartenstein, 1962; Walter *et al.*, 1987), like the cheliceral sheath, the joint membrane of the legs, or genital and anal plates (Peschel *et al.*, 2006), hence usually do not come in contact with the glandular region of attacked oribatid mites.

The solitary inefficiency of chemical defense against abundant soil predators may to some extent explain the evolution and diversification of other, morphological and behavioral defense mechanisms such as ptychoidy (Sanders and Norton, 2004; Schmelzle *et al.*, 2015), strong sclerotization and/or biomineralization of the cuticle (Norton and Behan-Pelletier, 1991a; 1991b; Alberti *et al.*, 2001), a cerotegumental layer (Alberti *et al.*, 1981), thanatosis in combination with the protection of legs under overlaying tecta (Schmid, 1988; Norton, 2007), pedofossae (= furrows in the notogaster where legs can be inserted) (Schmid, 1988), elongated setae

(Norton, 2001) and the ability to jump (Krisper, 1990; Wauthy *et al.*, 1998), especially in middle derived and higher glandulated Oribatida. For example, *S. miles* is not able to crack oribatid mites which do not expose membranous cuticle, such as, e.g., Ptyctima or Carabodidea (own observations). Furthermore, the predatory mite *Pergamasus septentrionalis* Oudemans (Parasitidae), which is larger than *S. miles* (about 1350 µm), is not able to crack and feed on heavily armed and extremely sclerotized oribatid mites like *Eupelops* Ewing (Phenopelopidae) or *Damaeus* C. L. Koch (Damaeidae) (Peschel *et al.*, 2006). Hence, morphological defense by hardened cuticle and hiding membranous regions seem to be most effective against small and abundant predators such as predatory mites (see also Schneider and Maraun, 2009). Larger predators, however, can also crack hard cuticle due to higher biting forces (e.g. Riha, 1951; Schmid, 1988; Masuko, 1994; Wilson, 2005; see also discussion in Peschel *et al.*, 2006), in this case chemical defense can be of outermost importance (Heethoff *et al.*, 2011). Therefore, the evolution of both - chemical and morphological defense – could be interpreted as a holistic defense which reduces top-down pressure by predators and results in an "enemy-free space" for such oribatid mite species.

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ETHICAL STATEMENT

There are no legal restrictions on working with mites.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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