# Feeding of *Scydmaenus rufus* (Coleoptera: Staphylinidae: Scydmaeninae) on oribatid and uropodine mites: Prey preferences and hunting behaviour

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**Abstract.** Prey preferences and feeding-related behaviour of a Central European species of Scydmaeninae, *Scydmaenus rufus*, were studied under laboratory conditions. Results of prey choice experiments involving 22 identified species of mites belonging to 13 families of Oribatida and two families of Mesostigmata (Uropodina) demonstrated that this beetle feeds mostly on oribatid Scheloribatidae (60.38% of prey) and Oppiidae (29.75%) and only occasionally on uropodine Urodinychidae (4.42%) and oribatid Mycobatidae (3.39%); species belonging to Trematuridae (Uropodina), Ceratozetidae and Tectocepheidae (Oribatida) were consumed occasionally. The number of mites consumed per beetle per day was 1.42, and when *Oppia nitens* was the prey, the entire feeding process took 2.93–5.58 h. Observations revealed that mechanisms for overcoming the prey's defences depended on the body form of the mite. When attacking oribatids, with long and spiny legs, the beetles cut off one or two legs before killing the mite by inserting one mandible into its gnathosomal opening. Flattened and short-legged uropodines were killed in the same way but without cutting off their legs. More legs of the prey were removed during feeding, when the mite was already dead; in Oribatida additional damage included removal of genital plates, whereas the genital structures remained intact in Uropodina. *Scydmaenus rufus* was able to feed on potentially highly toxic Scheloribatidae, which raises questions about the efficiency of chemical defence in Oribatida.

## INTRODUCTION

The biology of the nearly 4900 currently known species of Scydmaeninae (Newton & Franz, 1998; Grebennikov & Newton, 2009) is still poorly known. As these beetles were observed feeding on armoured (Oribatida) and tortoise (Uropodina) mites, arthropods that play an important role in soil biology, their feeding habits attracted attention and were studied by several authors. Scydmaeninae are minute beetles (typically less than 2 mm in length) that inhabit mainly leaf litter and rotten wood in forests; their biology makes it nearly impossible to study their behaviour in nature and even laboratory studies are difficult.

Various aspects of the feeding behaviour, specialized morphological adaptations and prey preferences of Scydmaeninae were recently reviewed by Jałoszyński (2012a). After the pioneer observations of Schuster (1966a, b) and experiments carried out by Schmid (1988), more detailed data became available and prey preferences of ant-like stone beetles appeared more diverse than previously thought. De Marzo (1983) fed large scydmaenines belonging to the tribe Mastigini with dead caterpillars. Jałoszyński (2012a, b) and Jałoszyński & Kilian (2012) report that some Scydmaeninae ignore armoured mites and prefer to feed on soft-bodied arthropods (Acari and Collembola) and scavenge various dead soil organisms. Jałoszyński & Beutel (2012) give an account of the functional morphology of the specialized mouthparts of Cephenniini. Representatives of this scydmaenine tribe immobilize oribatid mites using paired labial suckers and a "hole scraping technique"

to penetrate the prey's cuticle and inject digestive juices (Schuster, 1966a, b; Schmid, 1988; Jałoszyński & Beutel, 2012). Molleman & Walter (2001) give a detailed account of the damage suffered by oribatid and uropodine mites when attacked by Scydmaeninae and "the cutting technique" used by some species of Cyrtoscydmini and Scydmaenini. These beetles remove the movable body parts of mites that cover natural openings (gnathosoma, genital and anal plates) and feed through the resulting holes. In addition, in some cases cutting off the prey's legs was found to be a prerequisite for killing the mite and feeding, as a mechanism for immobilizing armoured mites (Schmid, 1988; Molleman & Walter, 2001). More recently, Jałoszyński & Olszanowski (2013) studied in detail the prey preferences and feeding behaviour of a common Central European cyrtoscydmine species, *Euconnus pubicollis*, and report yet another way they capture prey. This species feeds predominantly on ptyctimous oribatids that are able to encapsulate, and exudes a droplet of digestive juice onto its mouthparts, which it uses as an adhesive to capture and lift its prey. Feeding takes place after the predator breaches the mite's defences by weakening the enptychosis (encapsulation) mechanism, by opening the prodorsum and pressing the genital and anal plates deeply into the idiosoma.

In the present study, we analyze the feeding preferences and hunting behaviour of yet another representative of the Scydmaeninae, the Central European ant-like stone beetle, *Scydmaenus rufus*. Other species of this genus feed on soft-bodied arthropods, while our preliminary observations indicated that *S. rufus* may specialize on oribatid mites.

TABLE 1. Systematic list of mite species offered, accepted and rejected by *Scydmaenus rufus* in laboratory experiments.

| Mite species | offered | accepted | rejected |
|---|---|---|---|
| **Oribatida** | | | |
| Achipterioidea | | | |
| Achipteriidae | | | |
| *Achipteria coleoptrata* (Linné, 1758) | 39 | 0 | 39 |
| *Achipteria nitens* (Nicolet, 1855) | 469 | 0 | 469 |
| Ceratozetoidea | | | |
| Ceratozetidae | | | |
| *Trichoribates trimaculatus* (C.L. Koch, 1836) | 7 | 7 | 0 |
| Mycobatidae | | | |
| *Punctoribates punctum* (C.L. Koch, 1839) | 41 | 23 | 18 |
| Crotonioidea | | | |
| Nothridae | | | |
| *Nothrus anauniensis* Canestrini & Fanzago, 1876 | 1 | 0 | 1 |
| Damaeoidea | | | |
| Damaeidae | | | |
| *Epidamaeus bituberculatus* (Kulczyński, 1902) | 1 | 0 | 1 |
| Galumnoidea | | | |
| Galumnidae | | | |
| *Galumna obvia* (Berlese, 1914) | 1 | 0 | 1 |
| Hypochthonioidea | | | |
| Hypochthoniidae | | | |
| *Hypochthonius rufulus* C.L. Koch, 1836 | 1 | 0 | 1 |
| Oppioidea | | | |
| Oppiidae | | | |
| *Oppia nitens* C.L. Koch, 1836 | 274 | 192 | 82 |
| *Ramusella mihelcici* (Pérez-Íñigo, 1965) | 10 | 10 | 0 |
| Oribatelloidea | | | |
| Oribatellidae | | | |
| *Oribatella quadricornuta* (Michael, 1884) | 3 | 0 | 3 |
| Oripodoidea | | | |
| Scheloribatidae | | | |
| *Liebstadia pannonica* (Willmann, 1951) | 2 | 2 | 0 |
| *Liebstadia similis* (Michael, 1888) | 258 | 258 | 0 |
| *Scheloribates laevigatus* (C.L. Koch, 1836) | 154 | 147 | 7 |
| *Scheloribates pallidulus* (C.L. Koch, 1840) | 3 | 0 | 3 |
| Phenopelopoidea | | | |
| Phenopelopidae | | | |
| *Eupelops occultus* (C.L. Koch, 1835) | 1 | 0 | 1 |
| Phthiracaroidea | | | |
| Steganacaridae | | | |
| *Steganacarus carinatus* (C.L. Koch, 1841) | 1 | 0 | 1 |
| Tectocepheoidea | | | |
| Tectocepheidae | | | |
| *Tectocepheus velatus* (Michael, 1880) | 6 | 1 | 5 |
| Oribatida indet. juveniles | 10 | 4 | 6 |
| **Uropodina** | | | |
| Uropodoidea | | | |
| Trematuridae | | | |
| *Trichouropoda karawaiewi* (Berlese, 1903) | 5 | 0 | 5 |
| *Trichouropoda orbicularis* (C.L. Koch, 1839) | 1 | 1 | |
| *Trichouropoda ovalis* (C.L. Koch, 1839) | 41 | 5 | 36 |
| Urodinychidae | | | |
| *Uroobovella pyriformis* (Berlese, 1920) | 39 | 30 | 9 |
| Total | 1368 | 680 | 688 |

Moreover, this species does not occur in the same habitat as the previously studied *Euconnus pubicollis*; it occurs in decomposing plant debris, most commonly in garden compost. Since a different community of mites occurs in this habitat than in the forest litter, we expected to record different prey preferences and possibly also behavioural or morphological adaptations not previously recorded.

## MATERIAL AND METHODS

### Material

Adults of *Scydmaenus* (*Parallomicrus*) *rufus* Müller & Kunze, 1822 (Scydmaenini) were collected at Włocławek, Central Poland on 01.ii.2013 and 26.vii.2013, by sifting the upper 10-cm layer of garden compost. The sifted material was transferred to the laboratory, placed in plastic containers and beetles emerging on the surface were manually picked up and placed in preconditioned observation arenas. During numerous previous field studies it was observed that in samples of sifted compost *S. rufus* relatively quickly moves up to the surface and, if undisturbed, the beetles spend most of the time walking on this substrate, where they hunt for Acari. Therefore, the potential prey was also selected from a broad variety of mites showing a similar tendency, i.e. active on the surface of the same sifted substrate. Once the beetles were removed, sifted samples were kept in closed plastic containers ($30 \times 20 \times 15$ cm) and several pieces of white 60 g/$m^2$ printing paper, each ca. $8 \times 5$ cm, were placed on the surface. Acari that gathered on both sides of these "traps" were collected every 5 days during the study and tested as potential prey for *Scydmaenus*. In prey choice experiments the mites were collected by brushing the surface of paper traps over a Petri dish.

### Mite cultures

For feeding experiments (i.e., detailed observations of attack and successive damage caused by feeding), *Oppia nitens* C.L. Koch, 1836 was selected as one of the most readily accepted species, which is not only possible to identify alive, but also has a unique morphology (long, spiny legs) indicating the possibility of observing capturing or feeding techniques not previously recorded for Scydmaeninae. Cultures of *Oppia nitens* collected from sifted compost were established in plastic containers, $12 \times 6 \times 6$ cm, filled to 1/4 of their depth with regularly moistened plaster of Paris. Small ($0.5–1$ cm$^3$) pressed baking yeast pellets were used as a source of food for the mites.

### Determinations

Beetles were identified by the first author. This species does not show any obvious sexual dimorphism (females are slightly larger than males, but this character is difficult to assess in living and quickly moving beetles), and therefore mixed groups were used in the experiments. The mites, including empty shells with feeding damage, were preserved in 75% ethanol, and were identified by the second author after clearing in lactic acid.

### Prey choice experiments

Three study groups were established (duration of experiments in parentheses), each comprising eight individuals:

#1 (06.ii–26.ii.2013)
#2 (31.vii–19.viii.2013)
#3 (31.vii–19.viii.2013)

Plastic vented Petri dishes (diameter 35 mm, height 10 mm; Nunc) half-filled with plaster of Paris were used as observation arenas, and were preconditioned as described previously (Jałoszyński, 2012a, b; Jałoszyński & Olszanowski, 2013) by filling with pressed and moist substrate (garden compost sifted through 3 mm ø mesh) for 24 h. This substrate was then removed and each group of beetles was placed in a separate empty arena; arenas were kept in the dark (except during observations and other manipulations, which were made under a dim light) at 22–24°C;
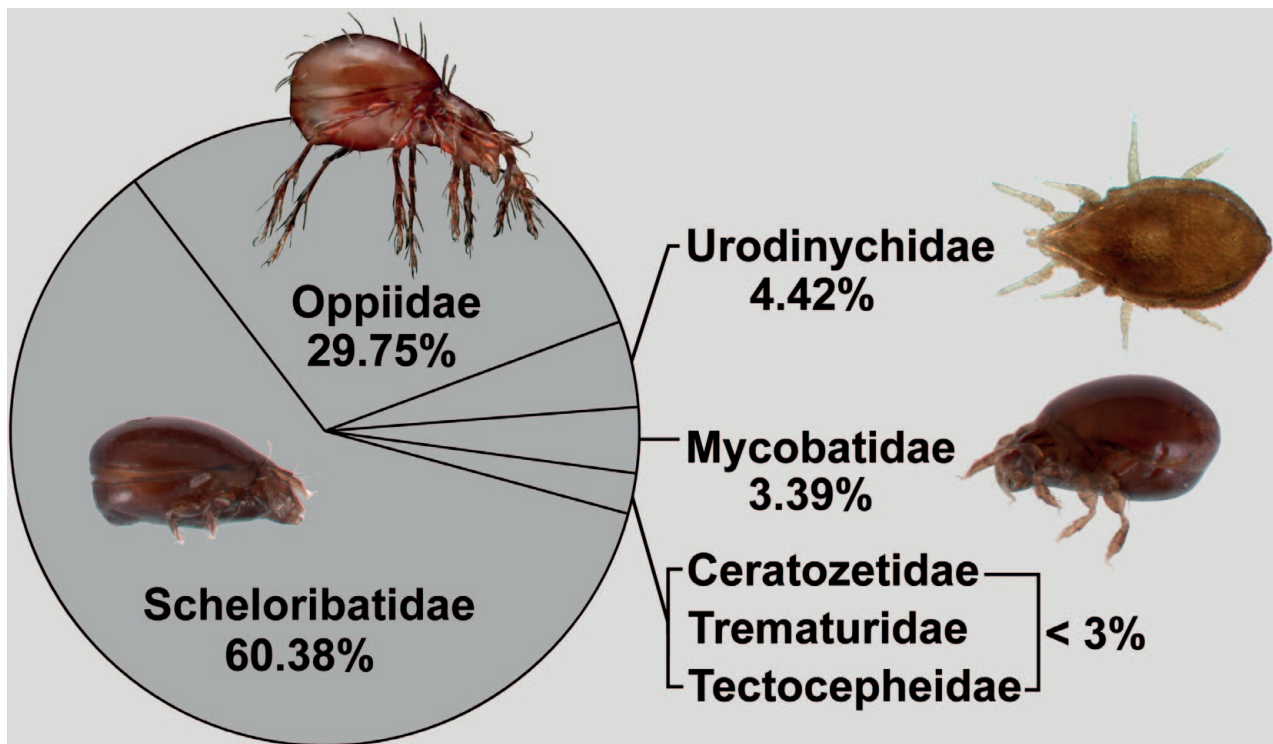
Fig. 1. Percentages of prey consumed by *Scydmaenus rufus* organized by taxon with examples of species belonging to each family: *Scheloribates laevigatus* (Scheloribatidae), *Oppia nitens* (Oppiidae), *Uroobovella pyriformis* (Urodinychidae) and *Punctoribates punctum* (Mycobatidae).

the plaster was moistened every second day with 3–4 droplets of distilled water. A mixture of ca. 100–120 mites was added to each group every 5 days and every day dead mites were collected and those showing characteristic feeding damage (described and illustrated by Molleman & Walter, 2001 and Jałoszyński & Olszanowski, 2013) were stored in ethanol for identification. Every 5 days all the living mites were collected and placed in ethanol and replaced with a fresh batch of potential prey. Observations were made every day for ca. one hour, usually in the morning, for 20 days. This setup was adopted from our previous study (Jałoszyński & Olszanowski, 2013), in which this size of arena proved most suitable for making observations.

**Feeding experiments**

Details of the attack, feeding damage and feeding time were recorded in separate experiments using *Oppia nitens* as prey. Beetles were kept without prey for 24 h and then placed individually in an empty and moistened 22 mm wide, 10 mm high arena (clear polystyrene containers for cosmetics purchased at a local store) half-filled with plaster of Paris, and preconditioned as described above. After 30 min a single *Oppia nitens* was placed in the middle of the arena and observed under a stereoscopic microscope. The entire feeding process of ten beetles was observed, from attacking the mite to abandoning its empty shell. In order to measure the time spent feeding, the same setup was used and five beetles were observed simultaneously in five separate arenas, each with a single *Oppia*. The beetles were observed until they attacked a mite and then every half an hour until they reached the final feeding stage (i.e., when all or most of the mite's legs had been removed and the beetle had inserted one mandible into the mite's genital opening) when the observation frequency was increased to once every 15 min. Twenty four beetles were observed, but only the results for twenty were included in the calculations because four beetles abandoned the prey after some time and then after 3–25 min picked up an apparently dead mite and continued

feeding. Such cases were not included in the calculation of the average time of continuous feeding. The same setup was used to determine the successive stages in the damage to the mite's body caused by the attack and feeding. The beetle in each arena was offered a single *Oppia nitens* and observed until the mite was captured. Mites were collected 10, 20, 30, 40, 60 and 100 min after being attacked, placed in 75% ethanol and observed under a compound microscope to evaluate the damage. For each interval of time ten beetles were used; they were randomly picked from a "stock" of ca. 40 individuals kept for 24 h without food in a plastic container similar to that used for rearing *Oppia nitens*. After collecting the mites, the beetles were returned to the same container.

**Scanning electron microscopy (SEM)**

The head and legs of disarticulated specimens of *S. rufus* were studied after brief cleaning in a warm 10% solution of NaOH, thorough washing in distilled water, dehydration in absolute ethanol, drying in air and mounting on SEM stubs with carbon tabs. Mites, including the empty shells abandoned by beetles, were dried directly from ethanol-stored samples without cleaning. Beetles during feeding were killed and preserved by pouring nearly boiling 75% ethanol onto the arena. In most cases the predator and its prey were not detached and the post-mortem position of mouthparts (holding the mite by a leg or with one mandible inserted into a body opening) was preserved. Such specimens were stored in ethanol only for a few minutes, then the beetles were briefly dried on a piece of a blotting paper and glued onto a mounting card in such a way that the mite in their mouthparts was above the card and not in contact with glued area. The beetles were immediately photographed under a light stereoscopic microscope and only then were left to dry for 1–2 weeks before the entire mounting cards were placed on SEM stubs with carbon tabs. All specimens were sputter-coated with gold (Pirani 501,

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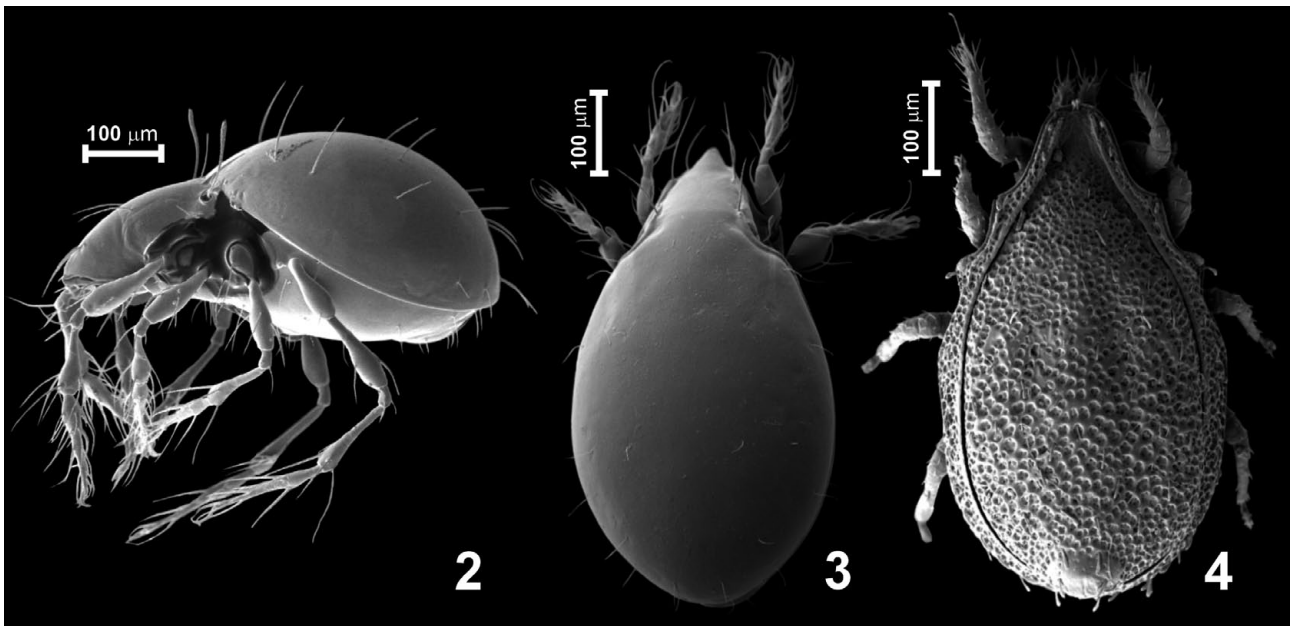
Figs 2–4. Examples of morphologies of the three different mites accepted by *Scydmaenus rufus*. 2 – convex body with long legs (*Oppia nitens*, Oppiidae); 3 – convex body with short legs (*Liebstadia similis*, Scheloribatidae); 4 – flattened body with short legs (*Uroobovella pyriformis*, Urodinychidae).

Edwards) and examined using an EVO LS15 (Carl Zeiss, Jena) scanning electron microscope at 10 kV.

**Light photography and image processing**

Photographs of feeding beetles were taken using a Panasonic DMC-FZ150 digital camera with a Raynox M-250 close-up lens. Photographs of specimens were taken using a JVC KY-F75U camera mounted on a Leica M205 C microscope. Image stacks were processed using CombineZP (Hadley, 2010). Final image adjustments and annotations were made in Corel PhotoPaint.

**Measurements**

The length of the mites was measured in a dorsal or lateral view and similarly intact specimens and empty mite shells, for comparison: Oribatida from the anterior margin of the rostrum to the posterior margin of the idiosoma and Uropodina from the anterior to the posterior margin of the idiosoma.

**Plots and statistics**

The data were plotted and a linear regression analysis was conducted using SigmaPlot 2004 v. 9.0 (Systat Software, USA). The differences in median body lengths of eaten and non-eaten prey were assessed using the Wilcoxon-Mann-Whitney two-sample rank-sum test in PAST 2.16 freeware (Hammer et al., 2001). Undetermined juvenile mites were not included in the calculations of the length of the preferred prey.

**Terminology**

Following Jałoszyński & Olszanowski (2013), the "accepted prey" are the mites that were found dead 24 h after placing in arenas with beetles and for which the feeding damage to their empty shells was similar to that described in the Results section. "Rejected prey" are mites still alive 5 days after being placed in Petri dishes with beetles, or dead but without typical feeding damage. The "feeding time" refers to the time from attack to the abandonment of the empty shell of the mite.

**Source of errors**

Potential sources of errors include the experimental setup not reflecting natural conditions; a possible overestimate of the number of prey eaten by scoring as accepted (i.e., eaten) some mites that died for other reasons than being attacked by beetles; different numbers of individuals of each mite species collected from the substrate and presented to beetles, which created a bias potentially resulting in overestimating the preferences for the most numerous species of prey and underestimating the preferences for the less numerous species of mites; the method adopted for collecting mites that created a bias towards those taxa that readily gathered on and under the "paper traps" leading to underestimating the preferences for mites that remained hidden in the substrate and avoided the traps. A discussion of each of these factors can be found in the previously published study (Jałoszyński & Olszanowski, 2013).

**RESULTS**

**Prey choice**

**Species preferences** (Table 1; Figs 1–4). A total of 1368 mites representing 22 species (13 families of Oribatida and 2 families of Mesostigmata: Uropodina) were placed in arenas with *S. rufus* (Table 1). The 680 mites eaten by the beetles belonged to the following taxa: Oribatida: Ceratozetidae (*Trichoribates trimaculatus*), Mycobatidae (*Punctoribates punctum*), Oppiidae (*Oppia nitens*, *Ramusella mihelcici*), Scheloribatidae (*Liebstadia pannonica*, *L. similis*, *Scheloribates laevigatus*), Tectocepheidae (*Tectocepheus velatus*); Uropodina: Trematuridae (*Trichouropoda orbicularis*, *T. ovalis*) and Urodinychidae (*Uroobovella pyriformis*). Individuals of the families Achipteriidae, Nothridae, Damaeidae, Oribatellidae, Phenopelopidae and Steganacaridae were not consumed. Also some species belonging to Scheloribatidae (*Scheloribates pallidulus*) and Trematuridae (*Trichouropoda karawaiewi*) were not eaten. Among the mites consumed (Fig. 1), 60.38% belonged to the family Scheloribatidae represented by two genera and three species, 29.75% to Oppiidae (two species in two
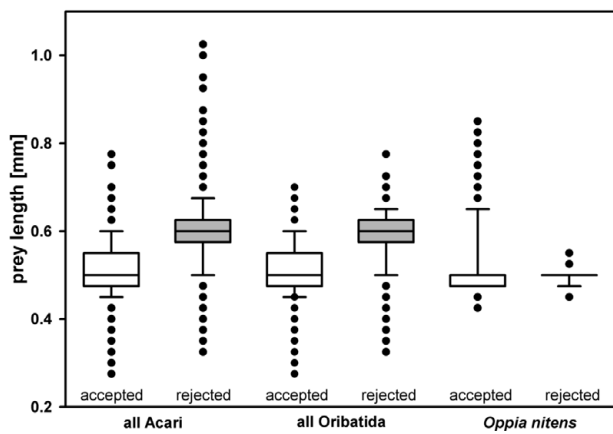
Fig. 5. Distributions of the body lengths of Acari eaten (accepted) vs. not eaten (rejected) by *Scydmaenus rufus*; the median, 10th, 25th, 75th, 90th percentiles and outliers are shown.

genera), 4.42% to Urodinychidae (one genus and species) and 3.39% to Mycobatidae (one genus and species); all the other mites eaten only made up a small part of the diet, with only a few individuals of each family (Ceratozetidae and Tectocepheidae of Oribatida and Trematuridae of Uropodina) being found dead and with typical feeding damage 24 h after being placed with beetles. The majority of the Scheloribatidae and Oppiidae eaten were the species *Liebstadia similis* and *Oppia nitens*, respectively.

The majority of the accepted mites can be classified into three morphological types (Figs 2–4). Oppiidae (Fig. 2) were represented by species with strongly convex and elongate bodies and long, spiny legs, with body surfaces glossy and covered with only sparse setae and pteromorphs absent. Ceratozetidae, Mycobatidae, Scheloribatidae (Fig. 3) and Tectocepheidae eaten were represented by species similar to Oppiidae but with much shorter and less spiny legs, pteromorphs were either absent (Tectocepheidae)

or present but relatively short (remaining families). Most readily accepted Uropodina (Urodinychidae) were flattened, short-legged and with coarse microsculpture (Fig. 4). Among mites totally rejected (Table 1) Achipteriidae predominated, which have relatively long pteromorphs.

**Body length of the mites eaten** (Fig. 5). Of all the mites provided (ranging in body length from 0.275 mm for the smallest species *Ramusella mihelcici* to 1.025 mm for the largest *Trichouropoda karawaiewi*) only those with body lengths of 0.275–0.775 mm were eaten. The mites eaten (n = 676) had a median body length (quartiles in square brackets) of 0.500 mm [0.475, 0.550], which is significantly smaller (U = 80363; p << 0.001) than the median 0.600 [0.575, 0.625] of those not eaten (n = 682). The Oribatida that were eaten (n = 640) had a median body length of 0.500 mm [0.475, 0.550], which is significantly smaller (U = 68669; p << 0.001) than the median of 0.600 mm [0.575, 0.625] of those (n = 632) not eaten. In the case of *Oppia nitens* (one of the most frequently eaten species and the only one with a sufficient number of rejected individuals for comparison), the eaten mites (n = 192) had a median body length of 0.500 mm [0.475, 0.500], which is not different from the median of 0.500 mm [0.500, 0.500] of the non-eaten conspecifics (n = 82).

**Number and time taken to eat the mites**

Twenty four beetles consumed 680 mites during the 20 days of the experiment. The average number of mites eaten per beetle per day was 1.42.

In the feeding experiments the time it took the beetles to eat *Oppia nitens* was 2.93–5.58 h. In 12 of 20 cases the feeding took four hours or less, with only four beetles feeding for more than five hours. There was no correlation between prey body length and feeding time (apparently because of the very uniform body length of *Oppia*).



Figs 6–7. Photographs of *Scydmaenus rufus* killed and preserved at different stages during feeding on *Oppia nitens*. 6 – initial stage of attack; 7 – late stage of attack.
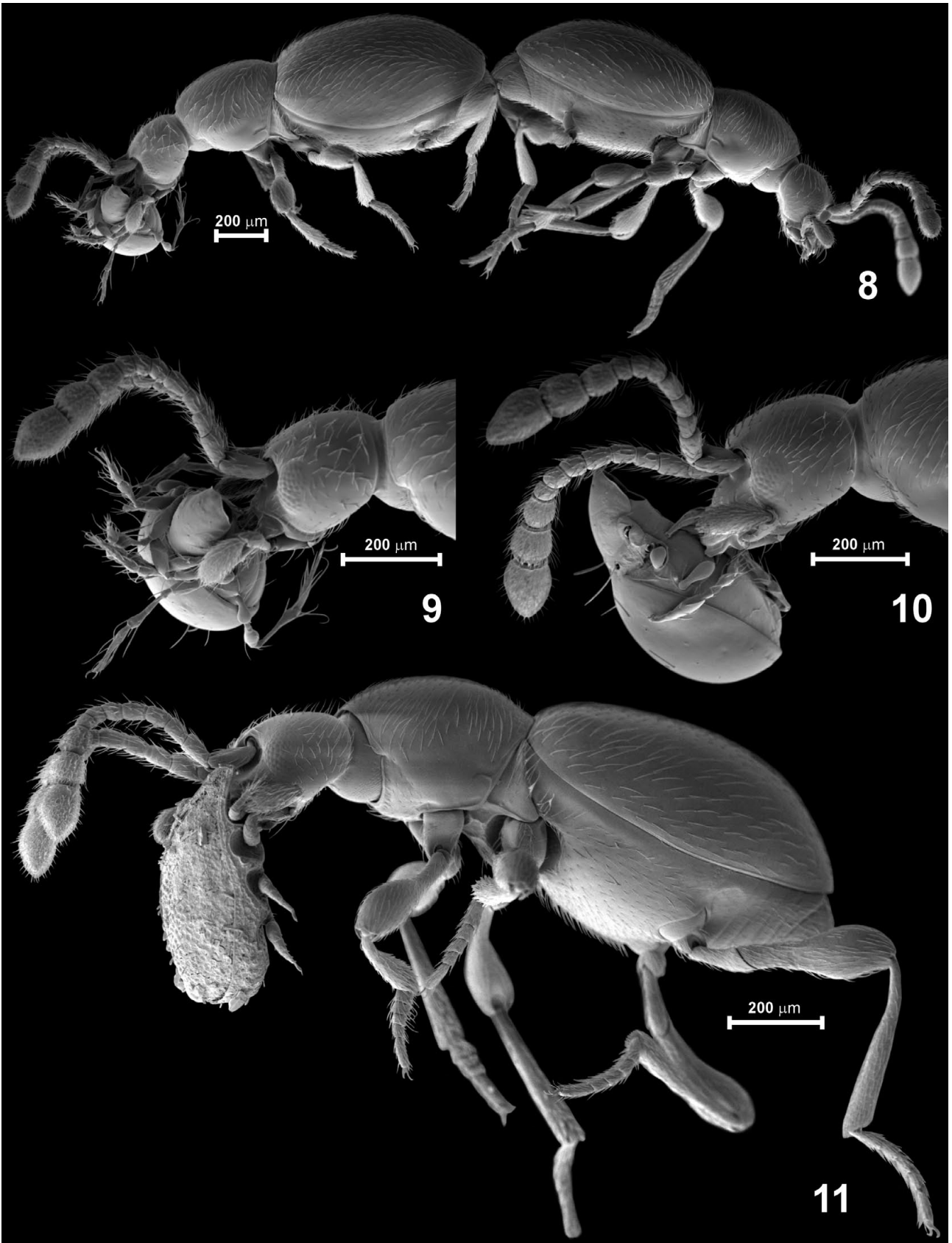
Figs 8–11. Scanning electron micrographs of *Scydmaenus rufus* killed and preserved during different stages of feeding on *Oppia nitens* (8–10) and *Uroobovella pyriformis* (11). 8 – a couple preserved during copulation, female with prey in mandibles; 9 – initial stage of attack; 10 – late stage of attack; 11 – feeding through gnathosomal opening.

Figs 12–17. Photographs of *Scydmaenus rufus*. 12, 13 – feeding on *Oppia nitens*; 14, 15 – feeding on *Uroobovella pyriformis*; 16, 17 – unsuccessfully attacking a large species of Liacaridae.

### Feeding behaviour

**Attack** (Figs 6, 18–19). In the feeding experiments, *S. rufus* attacked *Oppia nitens* 0.5–45 min after mites were placed in the arena. Eleven of 20 observed attacks occurred within 5 min and only 3 after 20 min or more. The first attack was usually successful; only two cases of three consecutive unsuccessful attacks repeated at 1–4-min intervals were observed, when beetles attacked and withdrew after a brief (less than a second) contact with *Oppia*. In each case the fourth attack was successful (i.e., led to feeding). Beetles that encountered a mite while patrolling the arena rapidly moved the head and mouthparts towards the cuticle of the mite, grabbing the prey by one of its legs; also apical parts of both protibiae were used by the predator to manipulate the prey. In feeding experiments with a single *Scydmaenus* per arena the next phase of attack frequently followed the capture immediately and occurred where the mite was encountered. In the prey choice experiments, predators were frequently disturbed by other beetles and mites present in the arena, and were observed walking for up to 30 min around the entire arena with the prey held in their mouthparts.

In the case of Oribatida, beetles hold the attacked prey by a proximal part of one of the legs (Fig. 6), often changing
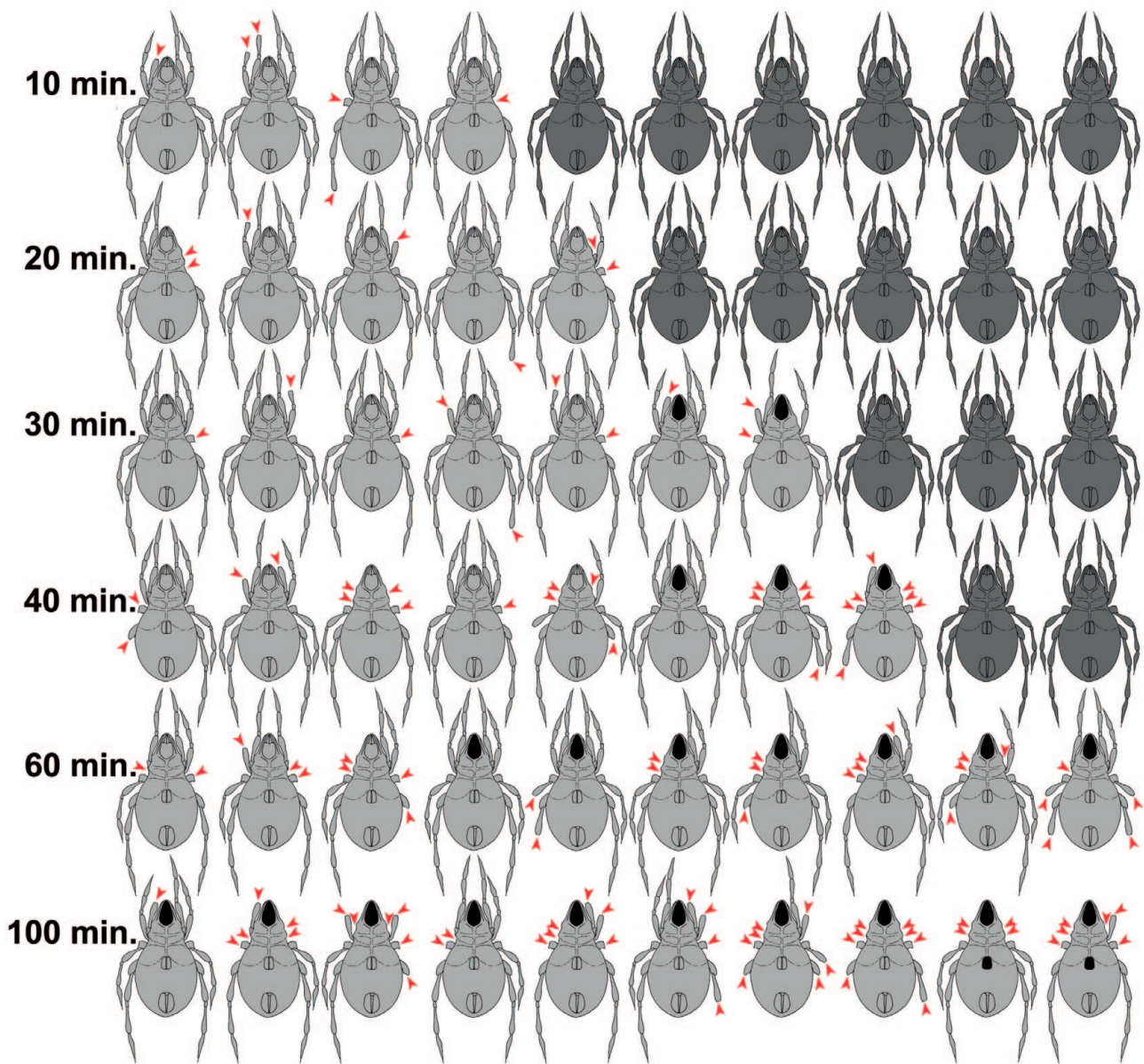
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Fig. 18. Time course of an attack and the early stages of feeding. Each mite represents a single experiment in which one individual of *Scydmaenus rufus* attacked an *Oppia nitens*, which was taken from the beetle after 10–100 min. Dark silhouettes represent mites without any damage and arrows indicate legs that have been cut off.

their grip. They used their mandibles to cut off the legs; within 10 min some legs of *Oppia nitens* were cut off and this damage continued to increase linearly over 100 min (Figs 18–19). Efforts of *Scydmaenus* were focused on positioning the prey vertically in such a way that the predator was able to insert one of its mandibles into the mites gnathosoma.

In the case of Uropodina (Figs 14–15), the first grip was on the anterolateral flattened edge of the idiosoma and the mite's legs were not cut off until the later stages of feeding. *Scydmaenus* within seconds positioned the mite vertically and attacked the gnathosoma.

During prey choice and feeding experiments, unsuccessful attacks were rarely observed. However, in a preliminary study, in which not only compost mites but also forest litter Oribatida were tested by exposing them to attack by several species of Scydmaeninae, two individuals of *S. rufus*

were observed unsuccessfully attacking large Liacaridae (Figs 16–17). This mite, which is about twice as large as *Oppia nitens*, was lifted by *Scydmaenus* and turned so that its legs were up; then the beetle directed its efforts to the genital opening of the prey. After 15–26 min of continuously struggling to insert a mandible into the genital opening, the beetles abandoned these mites, which were alive and apparently intact.

**Killing the prey.** When *Oppia nitens* is the prey, the earliest record of the next phase of the attack occurred after 30 min. The prey was positioned vertically, with the posterior margin of the idiosoma resting on the substrate, the gnathosoma facing up, and the prey's venter facing the predator. In this position *Scydmaenus* attacked the prey's mouthparts by inserting one mandible inside the gnathosoma; further manipulations and rotations (assisted by the protibiae) resulted in the removal of the entire
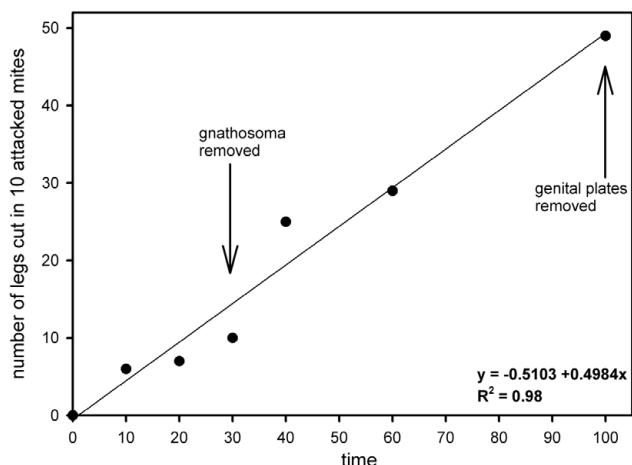
Fig. 19. Time course of an attack and the early stages of feeding. Each point represents ten experiments in which one individual of *Scydmaenus rufus* attacked an *Oppia nitens*, which was taken from the beetle after 10–100 min.

gnathosoma. Shortly after inserting the mandible into the gnathosoma the leg movements of the prey ceased. At this stage one or two legs of the prey were already partly cut off (Fig. 18). Only one case of a mite killed with all legs intact was observed (one of 10 mites collected from beetles after 40 min; Fig. 18). Two mites were found with their gnathosoma removed after 30 min; three after 40 min, seven after 60 min and ten after 100 min (Fig. 18). Cutting off some of the legs and then killing the mite by inserting a mandible into the mouthparts and removing the entire gnathosoma was a technique used independently of the size or shape of the oribatid mites attacked. In the case of the uropodine species *Uroobovella pyriformis* the mite was positioned vertically (gnathosoma up) within seconds of the first contact and one mandible was inserted into the prey's mouthparts. In ten such cases observed in detail, the gnathosoma of *Uroobovella* was removed within the first two minutes of the attack and all the legs remained intact at this stage (Fig. 11).

In prey choice experiments, it was observed seven times that a female with its mandible inserted into the gnathosoma of a dead mite was approached and mounted by a male, and copulation took place in the end-to-end position without the female losing its prey or ceasing feeding (Fig. 8).

When a mite was killed and its gnathosoma removed, beetles started the longest phase of the entire process, feeding on the soft internal tissues of the prey.

**Feeding** (Figs 7, 9–10, 12–13, 18–32). When the prey's gnathosoma was open, beetles continued rotating and manipulating the mite with one mandible inserted, and exuded copious amounts of liquid, apparently a digestive juice, from their mouth. The liquid covered the anterior part of the prey. During the following 60–100 min (Fig. 18) the mites had the gnathosoma removed and damage to the legs continued to increase (Figs 12–13). More legs were cut or broken off during further manipulations and after 100 min some of the *Oppia* mites also had their genital plates removed. After this time, some beetles were observed regularly exuding liquid onto the prey and then sucking it back,

while one mandible was inserted into the genital opening (Figs 7, 10).

In the case of uropodine *Uroobovella* mites, when the gnathosoma was removed the beetles fed by producing and sucking up droplets of liquid, and during further manipulations some legs were cut or broken off, starting with the anterior pair. Attempts to remove the genital plate were not observed.
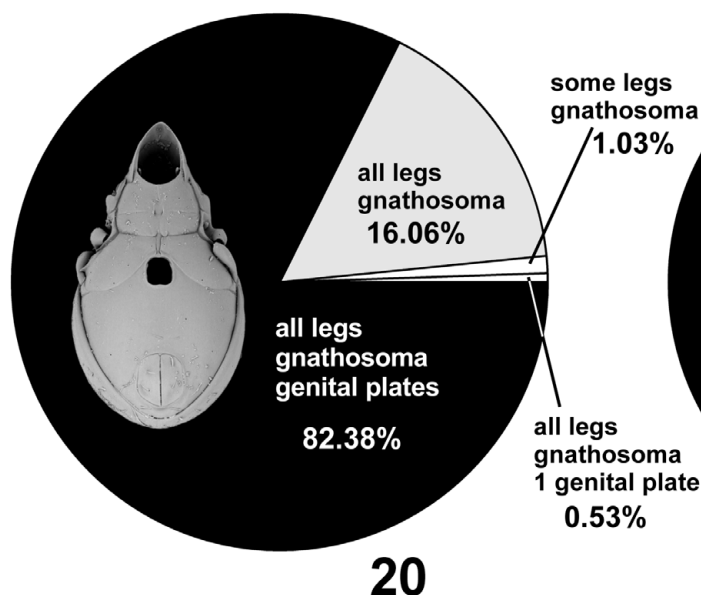
Abandoned empty mite shells show characteristic feeding damage (Figs 20–23, 24–32). In the four most frequently eaten mite species a distribution of damage was studied in detail by scoring damaged structures on all empty mite shells abandoned by beetles. In the oribatid species *Oppia nitens* and *Liebstadia similis* (Figs 20–21) most of the mites had all of their legs, gnathosoma and genital plates removed, and a much smaller fraction had only the legs and gnathosoma removed. In rare cases (below 2% of all eaten mites) the empty shells had only some legs, only one genital plate, or only the gnathosoma and genital plates (but not legs) removed. In the oribatid *Scheloribates laevigatus* (Fig. 22), the predominant damage was the removal of all legs and the gnathosoma, while in a smaller fraction of empty shells the genital plates were also missing. A different distribution of damage was recorded in the uropodine species *Uroobovella pyriformis* (Fig. 23), in which most of the abandoned remains lacked only some legs and the gnathosoma, rarely all legs and the gnathosoma were missing.

All or most legs were also removed from the other mites that were eaten, including all other Oribatida and Uropodina (Figs 24–32). Among Oribatida other than Oppiidae and Scheloribatidae the typical feeding damage was the removal of all legs, the gnathosoma and the genital plates; in only one case were some legs removed and the genital opening left intact (in *Trichoribates trimaculatus*; Fig. 29). In the uropodine Trematuridae eaten, all legs were cut off near their bases and the gnathosoma was removed, while the external genital structures remained intact (Fig. 32).
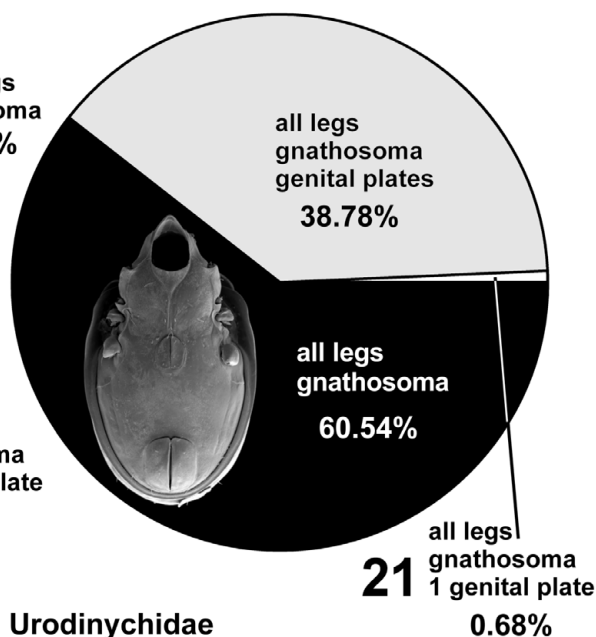
### Contact structures of *S. rufus*

The mouthparts of *Scydmaenus rufus* are directed anteroventrally (Fig. 33). The prey's legs are grabbed and then cut off by the asymmetrical mandibles (Fig. 35); the legs are held between the subapical mesal mandibular teeth or between the teeth and the broad mandibular base. Each mandible has a broad basal part with a densely setose mesal prostheca. The anterior margin of the labrum (Figs 33–34) has a pair of deep lateral emarginations and a row of long anteriorly directed setae. The epipharyngeal structures (Fig. 34) are composed of oblique lateral rows of dense trichia directed anteromesally and an arcuate median transverse row of seven long spines directed anteriorly and projecting beyond the anterior labral margin. The maxilla (Fig. 36) has a broad, flat and densely setose lacinia and galea, and a long maxillary palpus with broadened palpomere III and minute dome-shaped palpomere IV (typical of Scydmaenini, Fig. 33). The labium (Figs 36–37) has a broad prementum with a pair of anteriorly-directed setae and relatively long 3-segmented labial palpi. The hypopharynx (Fig. 37)
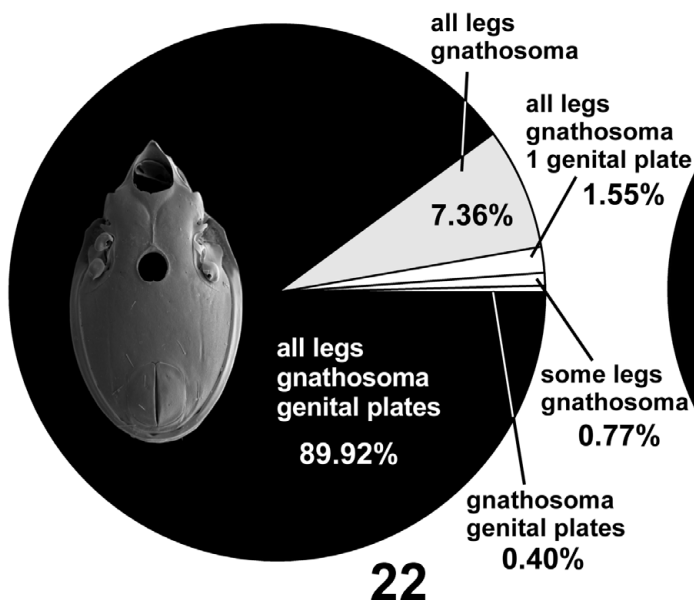
## Oppiidae
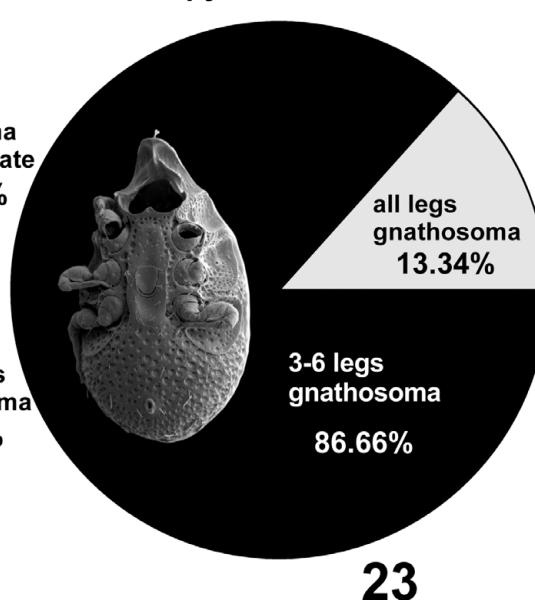### *Oppia nitens*



some legs gnathosoma **1.03%**

all legs gnathosoma **16.06%**

all legs gnathosoma genital plates **82.38%**

all legs gnathosoma 1 genital plate **0.53%**

**20**

## Scheloribatidae
### *Scheloribates laevigatus*



all legs gnathosoma genital plates **38.78%**

all legs gnathosoma **60.54%**

all legs gnathosoma 1 genital plate **0.68%**

**21**

## Scheloribatidae
### *Liebstadia similis*



all legs gnathosoma

all legs gnathosoma 1 genital plate **1.55%**

**7.36%**

all legs gnathosoma genital plates **89.92%**

some legs gnathosoma **0.77%**

gnathosoma genital plates **0.40%**

**22**

## Urodinychidae
### *Uroobovella pyriformis*



all legs gnathosoma **13.34%**

3-6 legs gnathosoma **86.66%**

**23**

Figs 20–23. Distribution of the feeding damage done by *Scydmaenus rufus* to abandoned mite "shells" of the most frequently consumed prey: 20 – *Oppia nitens*; 21 – *Scheloribates laevigatus*; 22 – *Liebstadia similis*; 23 – *Uroobovella pyriformis*. Structures removed are listed in respective fields; the most frequent type of damage is shown in SEM images.

has a pair of small elongate lateral lobes densely covered with mesally directed trichia. While lifting up and manipulating the prey, the beetles also used the distal portions of the protibiae (Fig. 38), which are covered with spatulate adhesive setae. The protarsi with modified adhesive setae were apparently not used to manipulate prey.

### DISCUSSION

Of the mites belonging to 22 species and 15 families (Table 1), *Scydmaenus rufus* most frequently attacked and ate representatives of two oribatid families: Scheloribatidae (mainly the common and abundant *Liebstadia similis* and

*Scheloribates laevigatus*, but also *L. pannonica*, which is rare in compost) and Oppiidae (*Oppia nitens* and *Ramusella mihelcici*). Some uropodines were also accepted, mainly Urodinychidae (*Uroobovella pyriformis*, Fig. 1). This is the first report of a representative of the genus *Scydmaenus* feeding on armoured Oribatida and Uropodina mites identified to species level. There are previous reports of an unidentified Australian *Scydmaenus* feeding on Oribatida, including Oppioidea (Molleman & Walter, 2001), the European *Scydmaenus* (s. str.) *tarsatus* Müller & Kunze, 1822 feeding on soft-bodied Acaridae and hypogastrurid springtails (Jałoszyński, 2012a) and also scavenging vari-
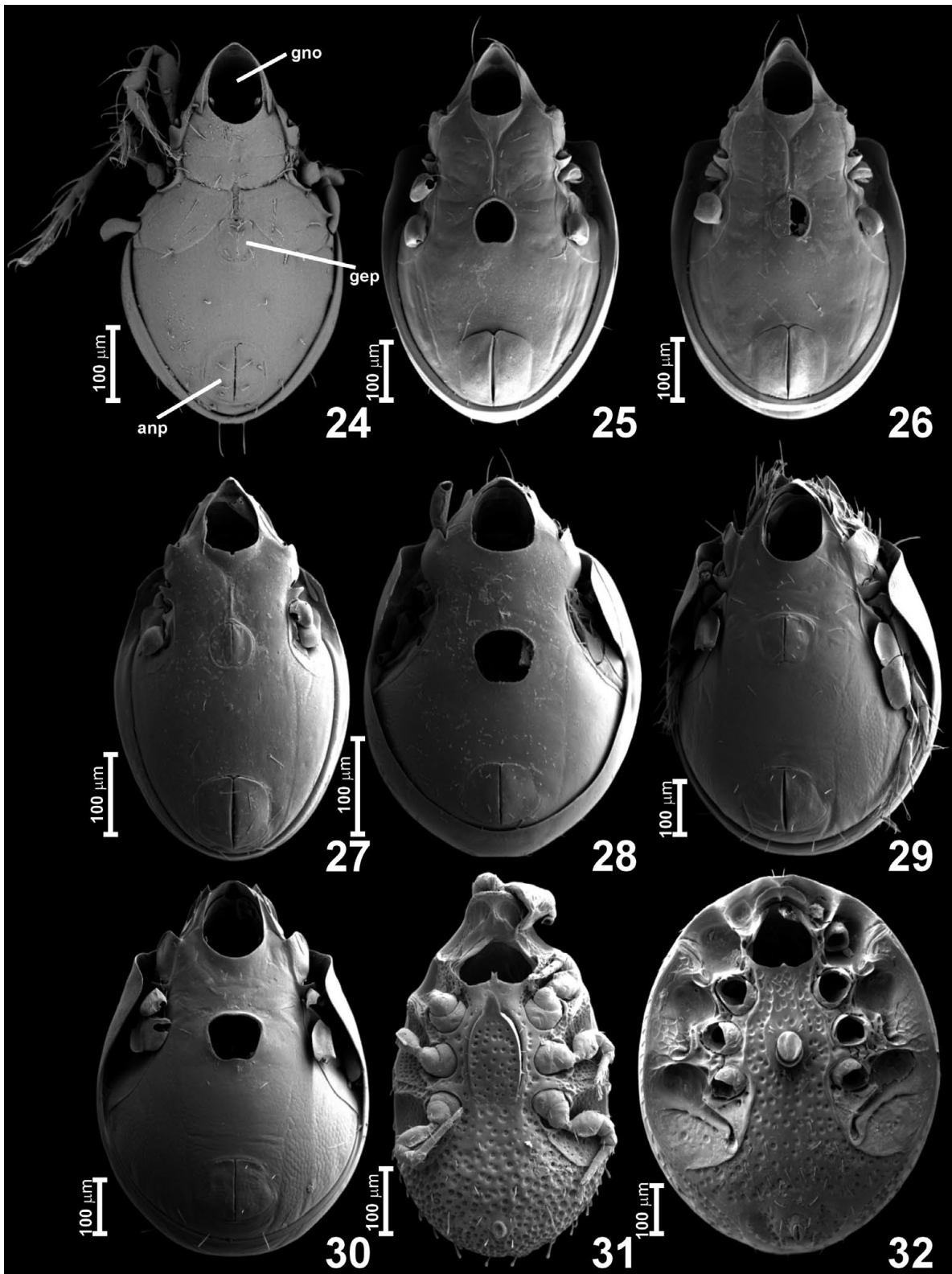
Figs 24–32. Prey of *Scydmaenus rufus* showing feeding damage. 24 – *Oppia nitens*; 25, 26 – *Scheloribates laevigatus*; 27 – *Liebstadia similis*; 28 – *Punctoribates punctum*; 29, 30 – *Trichoribates trimaculatus*; 31 – *Uroobovella pyriformis*; 32 – *Trichouropoda ovalis*. Abbreviations: anp – anal plate; gep – genital plate; gno – gnathosomal opening.

ous dead arthropods (Jałoszyński, 2012b), and the European *Scydmaenus* (*Cholerus*) *hellwigii* (Herbst, 1792) scavenging dead neanurine springtails. It is also possible to maintain long-term cultures of this species using living isotomids as a prey (Jałoszyński, 2012a). These observa-

tions were made on adult beetles; additionally it is known that larvae of *S. tarsatus* can feed on live Hypogastruridae and Tomoceridae springtails (Jałoszyński & Kilian, 2012).

The feeding preferences of *S. rufus* clearly differ from that of the forest cyrtoscydmine ant-like stone beetle
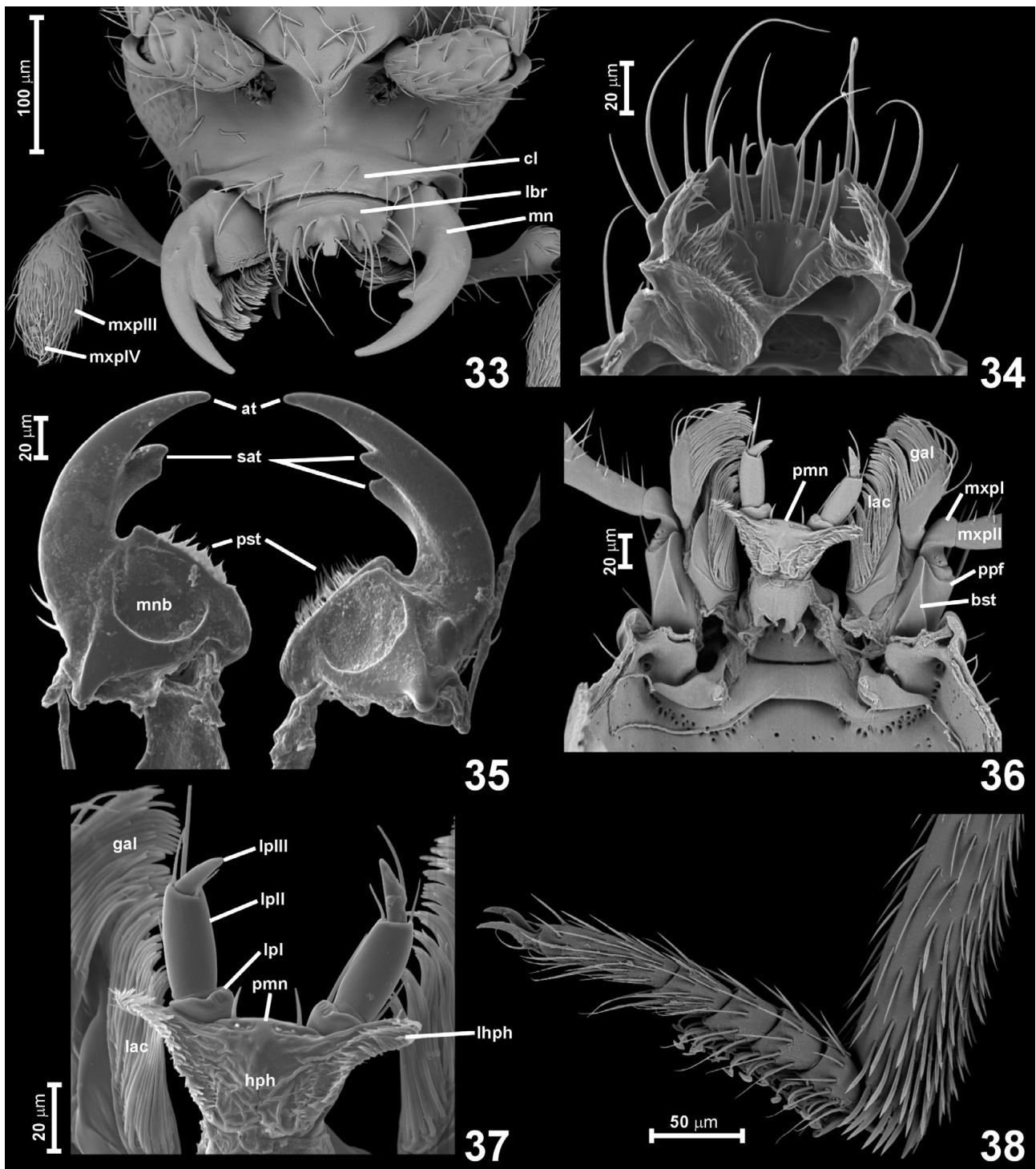
Figs 33–38. Structures of *Scydmaenus rufus* used to capture and consume prey. 33 – anterior portion of head in anterior view; 34 – epipharynx in ventral view; 35 – mandibles in ventral view; 36 – maxillae and labium in dorsal view; 37 – labium in dorsal view; 38 – distal part of right fore leg in mesal view. Abbreviations: at – apical mandibular tooth; bst – basistipes; cl – clypeus; gal – galea; hph – hypopharynx; lac – lacinia; lbr – labrum; lpI–III – labial palpomere I–III; lhph – lateral lobe of hypopharynx; mn – mandible; mnb – mandibular base; mxpI–IV – maxillary palpomere I–IV; sat – subapical mandibular tooth; pmn – prementum; ppf – palpifer; pst – prostheca.

*Euconnus pubicollis* (Jałoszyński & Olszanowski, 2013). The latter species predominantly feeds on ptyctimous mites of the family Phthiracaridae, and infrequently but successfully also attacks *Achipteria coleoptrata* and *A. nitens* (Achipteriidae), species that were offered in large numbers to *S. rufus* but rejected. *Euconnus* rejected the uropodine species *Trichouropoda ovalis*, occasionally accepted by *Scydmaenus*. The clear differences in their feeding preferences certainly reflect the fact that different species of mites are present in their respective habitats. *Euconnus* was fed with Acari collected from deciduous forest litter, and *Scydmaenus* with taxa co-occurring in a compost heap.

Phthiracarids are typical inhabitants of forest litter, while in compost they are absent or rare, while *Oppia nitens,* which is readily accepted by *S. rufus*, is abundant in compost and not present in forest litter (e.g., Beckmann, 1988).

Oribatids and uropodines accepted by beetles differ in their morphology (Figs 2–4). The eaten oribatids were smooth and convex, with the dorsum and venter of the idiosoma more or less broadly confluent laterally (Figs 2–3). The most frequently eaten uropodines were coarsely sculptured and strongly flattened, with a distinct lateral edge (Fig. 4). Long and spiny legs of oppiids (Fig. 2) make a direct attack on vulnerable body parts difficult and therefore beetles first grabbed such prey by one of the legs, cut off one or two legs, and only then focused their efforts on the gnathosomal opening. The dentate mandibles of *S. rufus* (Figs 33, 35) are a robust cutting tool, and a mite's leg is held either between the apical and subapical teeth or between the subapical teeth and the abruptly broadened mandibular base and then quickly cut off. The protibiae covered with spatulate adhesive setae (Fig. 38) assisted in capturing and lifting the prey. Interestingly, *Scydmaenus tarsatus* and *S. hellwigii*, species that do not feed on armoured mites but on soft-bodied soil arthropods (Jałoszyński, 2012a), have mandibles and protibiae nearly identical to those of *S. rufus* (P. Jałoszyński, unpubl. observ.). Therefore, even if asymmetrical mandibles and spatulate setae on the legs evolved in a common ancestor of these species as adaptations to capture and feed on a specific type of prey, at least the mandibles appear to be a rather universal and not specialized tool, which enables successful attacks on diverse arthropods such as Collembola, Acaridae, Oribatida and Uropodina.

The technique of lifting oribatid mites using an adhesive droplet of digestive juice exuded on the beetle's mouthparts, previously reported for *E. pubicollis* (Jałoszyński & Olszanowski, 2013), was not observed in *S. rufus*. Oribatids with short legs and a convex body (Ceratozetidae, Mycobatidae, Scheloribatidae, Tectocepheidae) were captured in a similar way to *Oppia*. Attacks on the uropodine species *Uroobovella pyriformis* were different; they primarily focused on securing a grip on the lateral body edge near the gnathosoma. The dorso-ventral flattening of the prey enabled the beetle's mandibles to lift the mite by directly holding the lateral margin of its idiosoma. The main attack on all mites focused on the gnathosoma and required that the prey be positioned vertically, with the anterior body part facing up, to gain access to the prey's mouthparts. Movements of the mite's legs ceased shortly after one mandible of *Scydmaenus* had been inserted into the gnathosomal opening, and further manipulations led to removal of the entire gnathosoma, cutting or breaking off of more legs, and feeding by exuding digestive juices and ingesting liquefied tissues of the prey. In Oribatida the genital plates were also usually removed and feeding took place through the genital opening; in uropodines the genital structures remained intact. A previous study indicates that *E. pubicollis* also feeds on non-ptyctimous Oribatida via the gnathosomal and genital openings and like *S. rufus*

does not remove the anal plates (Jałoszyński & Olszanowski, 2013). The latter structures are reported as a target for Scydmaeninae by Molleman & Walter (2001) in the case of oppioid Oribatida. These authors also report that all the legs are cut off by several genera of Australian Scydmaeninae (including *Scydmaenus* feeding on Oppioidea) before penetration through the gnathosoma. The leg-cutting in the case of *E. pubicollis* is an entirely secondary process that takes place after the prey is killed and during manipulations associated with feeding, especially when the legs become brittle after dissolution of the internal tissues and are then easily broken off (Jałoszyński & Olszanowski, 2013). In the present study the cutting off of the legs of prey was a routine procedure used to breach the defences of long-legged *Oppia*, but not short-legged *Uroobovella*. The beetles apparently did not cut the mite's legs in order to immobilize the prey and prevent its escape, but rather because the long and spiny legs protected vulnerable body parts and prevented access to the gnathosomal opening. Removing one or two legs was sufficient to reach the target structures. Once access to the gnathosoma was achieved, the removal of most or all other legs was accomplished by manipulations during feeding on the dead prey. It seems possible, however, that the initial attack on the legs is important, as Oribatida with leg bases well-protected by large pteromorphs (Achipteriidae) were not eaten (Table 1), while the accepted prey either did not have pteromorphs or they were relatively small.

For *E. pubicollis* and *S. rufus*, the size of the mite's body appears to be important in prey selection. *Scydmaenus* accepted prey with body lengths between 0.275 and 0.775 mm, but 50% of the mites eaten measured between 0.475 and 0.55 mm (Fig. 5). Attacks on Liacaridae (Figs 16–17) may have been unsuccessful because these mites are too large. However, it is worth recording that they did attack very large oribatids. An armoured body is not the only defence of the mites that were within the "edible" body length limits of *S. rufus*. There are alkaloids (pumiliotoxins, indolizidines and a coccinelline-like tricyclic compound) in the external secretion of the oil (opisthonotal) glands of the adults of *Scheloribates laevigatus*, one of the most preferred prey of *S. rufus* in our experiments (Saporito et al., 2011). Pumiliotoxins are highly toxic and oribatid mites, especially scheloribatid species, are believed to be a dietary source of these alkaloids for dendrobatid poisonous frogs (Saporito et al., 2007). Saporito et al. (2011) hypothesized that these alkaloids "may defend oribatid mites against predation". If the central European populations of *Scheloribates laevigatus* also contain these alkaloids, they certainly do not protect the mites against *Scydmaenus rufus*. Physiological and biochemical questions related to this phenomenon seem especially interesting; among others how an ant-like stone beetle deals with the toxic properties of the oil gland secretion of its prey and whether the predators are capable of sequestration of dietary toxins.

Jałoszyński & Olszanowski (2013) suggest that Scydmaeninae beetles may exert a significant effect on the population dynamics of mites. *Euconnus pubicollis* can be

locally abundant in deciduous forest leaf litter, and it feeds predominantly on the *Phthiracarus* oribatids (Jałoszyński & Olszanowski, 2013). In the case of *S. rufus*, the preferred habitat is the usually space-limited garden compost. *Scydmaenus rufus* occurs also in decaying plant matter in forests and even under the bark of dying trees, but it is only abundant in heaps of garden compost. The heap of compost from which the beetles and Acari were collected for the experiments presented here, was approximately $2 \times 1.5 \times 1.5$ m and contained in a wooden crate, and has been examined many times by the first author over nearly ten years of searching for interesting species of beetles. Samples were always collected from the upper 10–20 cm layer of relatively weakly decomposed garden remains (mostly stems and leaves of flowering plants and cut grass), and sometimes (especially during a warm spring season) more than 50 individuals of *S. rufus* were collected from ca. 10 l of compost. This species, as demonstrated by our results, fed faster than *E. pubicollis* (the time to eat *Oppia nitens* was 2.93–5.58 h, while for *Euconnus* beetles and *Phthiracarus* mites it was 2.15–33.70 h) and consumed more mites per unit time (1.42 mites per beetle per day compared with only 0.27 for *E. pubicollis*). Assuming that the beetles are active only during the warm season and feeding rates remain constant over time then one hundred beetles might consume nearly 26 thousand mites from April to September. This is a rough approximation, as the beetles are without doubt also active during the colder months and the feeding rates certainly depend on conditions different from those in the laboratory experiments. However, this calculation may give a general impression of how predation by *S. rufus* may influence the population dynamics of common compost mites such as Oppiidae and Scheloribatidae. Oribatids significantly alter the chemistry and nutrient cycling in decomposing plant matter (e.g., Wickings & Grandy, 2011). Moreover, the prey of *S. rufus* includes not only saprophagous oribatids but also uropodines that feed on nematodes (Athias-Binche & Habersaat, 1988). Therefore, the activity of this minute predacious beetle may be an important factor in shaping the complex network of compost ecology.

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