

Specialized feeding of *Euconnus pubicollis* (Coleoptera: Staphylinidae: Scydmaeninae) on oribatid mites: Prey preferences and hunting behaviour

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Key words. Coleoptera, Staphylinidae, Scydmaeninae, Cyrtoscydmini, *Euconnus*, Palaearctic, prey preferences, feeding behaviour, Acari, Oribatida

Abstract. Prey preferences and feeding-related behaviour of a Central European species of Scydmaeninae, *Euconnus pubicollis*, were studied under laboratory conditions. Results of prey choice experiments involving 50 species of mites belonging to 24 families of Oribatida and one family of Uropodina demonstrated that beetles feed mostly on ptyctimous Phthiracaridae (over 90% of prey) and only occasionally on Achipteridae, Chamobatidae, Steganacaridae, Oribatellidae, Ceratozetidae, Euphthiracaridae and Galumnidae. The average number of mites consumed per beetle per day was 0.27 ± 0.07 , and the entire feeding process took 2.15–33.7 h and showed a clear linear relationship with prey body length. Observations revealed a previously unknown mechanism for capturing prey in Scydmaeninae in which a droplet of liquid that exudes from the mouth onto the dorsal surface of the predator's mouthparts adheres to the mite's cuticle. Morphological adaptations associated with this strategy include the flattened distal parts of the maxillae, whereas the mandibles play a minor role in capturing prey. Mechanisms for overcoming the prey's defences depended on the body form of the mite. When attacking oribatids that adopt the ptychoid defence (encapsulation) *Euconnus* opened the prodorsum and pressed the anal and genital plates deeply into the idiosoma, whereas it fed on all other mites by entering their bodies through small gnathosomal or/and genital openings, after breaking off mouthparts or/and genital plates. The preferential feeding of a specialized and locally abundant ant-like stone beetle on one family of Oribatida, documented here for the first time, has implications for the population dynamics of the prey and raises questions about predator-prey co-evolution and costs of an unusually prolonged period spent feeding when at risk from competition and attack by larger predators, typical of the habitats where Scydmaeninae occur.

INTRODUCTION

The subfamily Scydmaeninae (ant-like stone beetles) is a large lineage within the Staphylinidae, currently comprising nearly 4,900 species (Newton & Franz, 1998; Grebennikov & Newton, 2009). After two hundred years of study, the biology of Scydmaeninae is still exceptionally poorly known compared to many other subfamilies of rove beetles. Most published biological and synecological data is on the environments where ant-like stone beetles live and circumstances of collecting (briefly summarized by Newton & Franz, 1998 and O'Keefe, 2005) and associations with ants and termites (O'Keefe, 2000) or parasitic fungi (Scheloske, 1969; Tavares & Balazuc, 1989; O'Keefe & Monteith, 2001). Scarce but highly interesting observations on the feeding behaviour and prey preferences, reviewed by Jałoszyński (2012a) and recently supplemented with additional data (Jałoszyński, 2012b; Jałoszyński & Beutel, 2012; Jałoszyński & Kilian, 2012), provide data on feeding mechanisms and specializations not known in any other subfamily of the hyperdiverse Staphylinidae. The initial hypothesis that both larvae and adults of Scydmaeninae feed only on armoured oribatid mites, based on a notion expressed by Reitter (1909), observations of Schuster (1966a, b) and especially on experiments carried out by Schmid (1988), was only partly confirmed (e.g., Molleman & Walter, 2001). Cur-

rently it is known that in some taxa young larvae feed exclusively on a secretion deposited by a female together with eggs while mature larvae can feed on the soft tissues of dead caterpillars (De Marzo, 1983). In others larvae and adults readily accept live springtails and soft-bodied mites (Jałoszyński, 2012a; Jałoszyński & Kilian, 2012) but show no interest in oribatid mites. Moreover, there are reports of adults scavenging on various dead arthropods (Molleman & Walter, 2001; Jałoszyński, 2012b) and field observations of some Scydmaeninae carrying various Collembola in their mouthparts (Leleup 1968; O'Keefe & Monteith, 2001).

A possible strict specialization of larvae and adults of some genera or even large tribes of Scydmaeninae towards feeding on live mites with heavily armoured bodies (Oribatida, moss mites, armoured mites, beetle mites or box mites belonging to the superordo Acariformes, and to a less extent also Uropodina or tortoise mites belonging to Parasitiformes) deservedly attracted most interest. The cuticle of these mites is hardened by sclerotization or mineralization and often coarsely sculptured and bearing diverse setae or even special structures covering vulnerable body parts (e.g., pteromorphs protecting proximal leg articulations in Galumnoidea and other oribatids). Moreover, peculiar defensive mechanisms developed by some taxa protect them from many preda-

tors. Some oribatid mites (Ptyctima) are capable of retracting their legs into the idiosoma and “encapsulation” by flexing ventrally the large, shield-like prodorsum; this so called ptychoid defence mechanism enables them to protect soft and vulnerable body parts and expose to a predator only heavily sclerotized cuticle (Schmelzle et al., 2008, 2009, 2010). Other oribatids are known to have exocrine oil glands (or opisthonotal glands) that produce secretions, which in some taxa (belonging to families Collohmanniidae and Trhypochthoniidae) provide chemical protection against some beetle predators (Raspotnig, 2006; Heethoff et al., 2011; Heethoff & Raspotnig, 2012a, b). Recently Saporito et al. (2007, 2011) provided evidence that oribatids of the family Scheloribatidae contain toxic alkaloids. Since oribatid mites are common and highly abundant in a broad variety of habitats, including the soil, leaf litter and rotten wood (Wallwork, 1976), predators that evolved morphological and behavioural adaptations to overcome and breach the defence systems of Oribatida gained access to an enormously rich source of food. Evolving such adaptations might have played a crucial role in radiations of those Scydmaeninae that are known to feed mostly or exclusively on oribatid mites.

There are several detailed studies on Scydmaeninae that specialize on feeding on oribatids or uropodines, which focus on prey preferences and feeding mechanisms. Reitter (1909) mentions that ant-like stone beetles seem to feed on mites. Only more than a half century later Schuster (1966a, b) published the results of his experiments on the genus *Cephenium* Müller & Kunze (Cepheniini). He observed that these small (1.0–1.5 mm) beetles and their larvae choose oribatids from a broad spectrum of a potential prey, composed of various mites (Oribatida, Uropodina and other Mesostigmata), Collembola, Protura, oligochaete Enchytreidae and fly larvae. In addition to observing *Cephenium* predominantly feeding on Oribatida, Schuster records very few attacks on Uropodina and other Mesostigmata, and some cases of larval cannibalism. Schuster was also the first to describe some details of the mechanism utilized by *Cephenium* to overcome its hard-shelled prey. He observed larvae scraping the cuticle of a captured mite with their relatively short and blunt mandibles, which eventually resulted in drilling a hole in the integument of the mite (Schuster, 1966b). This mechanism, which he referred to as a “hole scraping technique” (O’Keefe’s 2005 translation of the German term “Lochschabetechnik” used by Schmid, 1988), was confirmed and further investigated by later authors. Schmid (1988) provides more detailed observations and reports that *Cephenium* uses paired labial suckers to capture and hold oribatid mites. Once the prey is immobilized on the suckers, the mandibles slowly grind a small hole in the prey’s cuticle, a process that can take several hours. There is a detailed study of the functional morphology of the specialized mouthparts of Cepheniini and possible evolutionary pathways of this peculiar prey-predator co-evolution (Jałoszyński & Beutel, 2012). This study reveals that *Cephenium* is a specialist predator of

armoured Oribatida and gives additional details of the way it captures and feeds on these mites. The highly modified labium of the adults of seven genera of Cepheniini studied bear four or six suckers on the prementum. Moreover, a histological examination of the head of adults of *Cephenium* and *Cephenodes* Reitter and larvae of *Cephenium* has shed new light on the way they hold their prey, which is based on contractions and relaxations of labial muscles attached to an integrated internal scaffold of the labium and hypopharynx, which change the shape of the anterior surface of the prementum. The paired circular or oval suckers of Cepheniini have a complex internal structure and are not known in any other beetles. They play a major role in capturing and holding a mite long enough for the mandibles to drill through the cuticle. When this is accomplished, digestive juices are injected into the prey and the liquefied soft tissues are ingested; abandoned empty mite shells show characteristic feeding damage in the form of a small hole in the idiosoma, while all other body parts remain intact (Jałoszyński & Beutel, 2012). This unique morphological adaptation is the only known example of a large tribe strictly specialized to feed on Oribatida; Cepheniini also includes the world’s smallest predacious beetles (Jałoszyński, 2011; Jałoszyński & Beutel, 2012).

Although Scydmaeninae belonging to some other tribes also feed on oribatid mites and one genus of Cyrtoscydmini also has labial suckers (Schmid, 1988), the “hole scraping technique” seems to be restricted to the Cepheniini. Cyrtoscydmini and some Scydmaenini utilize a “cutting technique” (O’Keefe’s 2005 translation of the German term “Schneidetechnik” used by Schmid, 1988). This mechanism was studied by Schmid (1988) and more recently by Molleman & Walter (2001). The beetle captures a mite using its protibiae, which bear adhesive (often spatulate) setae, and it breaches the armour of the prey by inserting a slender mandible into natural body openings in the mite such as the mouth, genital or anal valves. Movable structures around the penetration site (i.e., mouthparts, genital or anal plates) are removed and the predator can feed on internal tissues by producing digestive juices and ingesting the liquefied flesh. Schmid (1988) also mentions that the cyrtoscydmine genus *Neuraphes* Thompson cuts off the remarkably long legs of Damaeioidea oribatids in the initial stages of the attack using the mesal tooth (retinaculum) on its mandibles. Molleman & Walter (2001) report that in various genera of Australian scydmaenines this leg-cutting behaviour is frequent and independent of the length of mite’s legs.

The above-cited studies provide valuable observations and data on feeding mechanisms of those Scydmaeninae specialized (or most likely specialized) to feed on armoured mites but provide little information on their feeding preferences. Only high-rank taxon names of the prey (Oribatida, Uropodina) are cited in the papers of Schuster (1966a, b), Schmid (1988), although mentioning testing ca. 200 species of Oribatida and Uropodina did not publish any specific data, and Molleman & Walter (2001) identify the mite prey to superfamilies or families

and only in two cases to the genus level. They present scanning electron microscopy images of typical feeding damage to empty shells of undetermined Uropodidae, Galumnoidea, Oppioidea and *Hermanniella* sp. (Hermannelloidea), but do not associate particular mite remnants with any genus of the Australian Scydmaeninae studied. They only mention that one of the *Euconnus* species (Cyrtoscydmini) tested fed on the oribatid family Schelobatidae and others on unarmoured nymphs of *Galumna* (Galumnoidea), while beetles of the genus *Horaeomorphus* Schaufuss (also Cyrtoscydmini; but see problems with identity discussed previously by Jałoszyński, 2012a) consume only Oppioidea. In that study most of the Oribatida eaten by Scydmaeninae were Oppioidea plus a few successful attacks on “mites that exhibit conglobation” are recorded (Molleman & Walter, 2001), referring apparently to the typical defence mechanism of ptyctimous mites.

The poor knowledge of prey preferences and the feeding behaviour of Scydmaeninae prompted this study. We provide new data not only on the preferred prey but also on a previously unknown mechanism for capturing prey and details of a laboratory study of the entire feeding process of a common European species of an ant-like stone beetle, *Euconnus pubicollis* (Müller & Kunze). Schmid (1988) previously suggested that this species might be a predator that has specialized in feeding on ptyctimous Oribatida, but did not provide any details.

MATERIAL AND METHODS

Material

Adults of *Euconnus (Tetramelus) pubicollis* (Müller & Kunze, 1822) (Cyrtoscydmini) were collected at Promno near Poznań and Wrocław-Świniary, Poland, respectively in April and May, by sifting moist leaf litter in deciduous forests. 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 leaf litter *E. pubicollis* relatively quickly moves to the surface and, if undisturbed, the beetles spend most of the time walking on the 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. emerged onto the surface of the same sifted substrate. After the beetles were removed, sifted leaf litter samples were left in closed plastic containers (30 × 20 × 15 cm) and several pieces of white 60 g/m² printing paper, each ca. 8 × 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 *Euconnus*. In prey choice experiments the mites were collected by “sweeping” the surface of paper traps over a Petri dish with a brush; in feeding experiments only mites of particular taxa and body size were picked up with the aid of forceps.

Determinations

Beetles were identified by the first author; a distinct sexual dimorphism in the metaventricle (impressed in males) made it possible to separate males and females. The mites, including empty shells with feeding damage, preserved in 75% ethanol, were identified by the second author after clearing in lactic acid.

Prey choice experiments

Four study groups were established (duration of experiments in parentheses):

#1. 10 males (17.v.–15.vi.2011)

#2. 10 females (17.v.–15.vi.2011)

#3. 5 males and 5 females (06.iv.–05.v.2011)

#4. 5 males and 5 females (06.iv.–05.v.2011)

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) by filling with pressed and moist substrate (leaf litter sifted through 2 mm Ø mesh) for 24 h. This substrate was removed and each of the group of beetles studied was placed in a separate arena with a fresh substrate occupying ca. 1/3 of the surface to provide a three-dimensional environment and shelter for beetles; arenas were kept in the dark (except during observations and other manipulations, which were made under a dim light) at 22–24°C; the plaster was moistened every second day with 3–4 droplets of distilled water. A mixture of ca. 60 mites were 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 also recorded in our preliminary experiments) 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 30 days. This setup was adopted after a series of preliminary experiments with various numbers of beetles and mites in 1.5–10 cm large arenas. Small arenas with a relatively large number of beetles and Acari were found to be most suitable for obtaining conclusive data and recording a significant number of observations while disturbing the organisms as little as possible. Larger arenas proved impractical for observing the behaviour of the beetles, increased the chances of their escaping during the greater length of time it took to collect dead mites and moving the arena under a stereoscopic microscope in order to follow a beetle walking across the arena strongly disturbed the beetle; whereas with little movement it was possible to observe beetles in 35 mm-wide arenas. A smaller number of beetles and mites decreased the chance of observing interesting events during a 1-h session. Moreover, the high diversity of mites in the sifted litter samples, and therefore the large number of taxa tested (50 species belonging to 25 families; see Table 1) made it necessary to provide the beetles simultaneously with many Acari.

Feeding experiments

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 *Phthiracarus* sp. was placed in the middle of each arena and observed under a stereoscopic microscope until the mite was captured by the beetle. From this moment, the arena was inspected every hour (ceased during the night) and on reaching the final feeding stage (i.e., the head of beetle was inserted into the mite shell) the observation frequency was increased to once every 30 min. Prey of a wide range of body lengths were selected. In this experiment it was also possible to make detailed observations of consecutive feeding stages undisturbed by interactions with other beetles or mites present in the arena. There were forty five replicates of this experiment using 34 males and 11 females of *E. pubicollis*. In some cases the last stages of feeding took place during the night and the first inspection in the morning revealed the already abandoned remains of the prey. Such cases were

TABLE 1. Systematic list of the species of mites offered, accepted and rejected by *Euconnus pubicollis* in laboratory experiments.

Species	No. of mites		
	offered	accepted	rejected
Oribatida			
Achipterioidea			
Achipteriidae			
<i>Achipteria coleoptrata</i> (Linné, 1758)	1	1	0
<i>Achipteria nitens</i> (Nicolet, 1855)	3	3	0
<i>Achipteria sellnicki</i> van der Hammen, 1952	4	4	0
Carabodoidea			
Carabodidae			
<i>Carabodes areolatus</i> Berlese, 1916	1	0	1
<i>Carabodes coriaceus</i> C.L. Koch, 1835	4	0	4
<i>Carabodes ornatus</i> Štorkan, 1925	11	0	11
<i>Carabodes rugosior</i> Berlese, 1916	1	0	1
Ceratozetoidae			
Ceratozetidae			
<i>Trichoribates trimaculatus</i> (C.L. Koch, 1836)	1	1	0
Chamobatidae			
<i>Chamobates cuspidatus</i> (Michael, 1884)	5	5	0
<i>Chamobates subglobulus</i> (Oudemans, 1900)	8	2	6
Euzetidae			
<i>Euzetes globulus</i> (Nicolet, 1855)	40	0	40
Zetomimidae			
<i>Heterozetes palustris</i> (Willmann, 1917)	5	0	5
Crotonioidea			
Camisiidae			
<i>Heminothrus targionii</i> (Berlese, 1885)	10	0	10
<i>Platynothrus peltifer</i> (C.L. Koch, 1839)	7	0	7
Nothridae			
<i>Nothrus anauniensis</i> Canestrini & Fanzago, 1876	1	0	1
<i>Nothrus borussicus</i> Sellnick, 1928	1	0	1
<i>Nothrus palustris</i> C.L. Koch, 1839	43	0	43
Damaeidea			
Damaeidae			
<i>Damaeus gracilipes</i> (Kulczyński, 1902)	3	0	3
<i>Epidamaeus ?bituberculatus</i> (Kulczyński, 1902)	8	0	8
Damaeidae gen. sp.	35	0	35
Euphthiracaroidae			
Euphthiracaridae			
<i>Acrotritia ardua</i> (C.L. Koch, 1841)	5	0	5
<i>Euphthiracarus cribrarius</i> (Berlese, 1904)	17	1	16
Oribotritiidae			
<i>Mesotritia nuda</i> (Berlese, 1887)	3	0	3
Galumnoidea			
Galumnidae			
<i>Acrogalumna longipluma</i> (Berlese, 1904)	1	0	1
<i>Galumna obvia</i> (Berlese, 1914)	15	0	15
<i>Pergalumna nervosa</i> (Berlese, 1914)	174	1	173
Gustavioidea			
Liacaridae			
<i>Dorycranosus acutus</i> (Pschorn-Walcher, 1951)	9	0	9
<i>Liacarus coracinus</i> (C.L. Koch, 1841)	12	0	12
<i>Liacarus subterraneus</i> (C.L. Koch, 1841)	15	0	15
<i>Xenillus clypeator</i> Robineau-Desvoidy, 1839	52	0	52
<i>Xenillus tegeocranus</i> (Hermann, 1804)	91	0	91
Peloppiidae			
<i>Ceratoppia quadridentata</i> Haller, 1882	5	0	5
Tenuialidae			
<i>Hafenrefferia gilvipes</i> (C.L. Koch, 1840)	39	0	39

TABLE 1 continued.

Species	No. of mites		
	offered	accepted	rejected
Hermannielloidea			
Hermanniellidae			
<i>Hermanniella punctulata</i> Berlese, 1908)	112	0	112
Hypochthonioidea			
Hypochthoniidae			
<i>Hypochthonius rufulus</i> C.L. Koch, 1836	5	0	5
Nanhermannioidea			
Nanhermanniidae			
<i>Nanhermannia nana</i> (Nicolet, 1855)	2	0	2
Oribatelloidea			
Oribatellidae			
<i>Oribatella quadricornuta</i> (Michael, 1884)	11	2	9
Oripodoidea			
Schelorbitidae			
<i>Schelorbitates laevigatus</i> (C.L. Koch, 1836)	7	0	7
Phenopeloidea			
Phenopelopidae			
<i>Eupelops hirtus</i> (Berlese, 1916)	2	0	2
<i>Eupelops subuliger</i> (Berlese, 1916)	2	0	2
Phthiracaroidae			
Phthiracaridae			
<i>Phthiracarus clavatus</i> Parry, 1979	8	0	8
<i>Phthiracarus ?clavatus</i> Parry, 1979	9	9	0
<i>Phthiracarus crinitus</i> (C.L. Koch, 1841)	1	0	1
<i>Phthiracarus globosus</i> (C.L. Koch, 1841)	169	35	134
<i>Phthiracarus ?globosus</i> (C.L. Koch, 1841)	238	238	0
<i>Phthiracarus laevigatus</i> (C.L. Koch, 1841)	23	0	23
<i>Phthiracarus longulus</i> (C.L. Koch, 1841)	16	11	5
<i>Phthiracarus nitens</i> (Nicolet, 1855)	72	0	72
<i>Phthiracarus</i> sp.	4	4	0
Steganacaridae			
<i>Steganacarus magnus</i> (Nicolet, 1855)	28	0	28
<i>Steganacarus</i> sp.	3	3	0
Tectocephoidea			
Tectocephidae			
<i>Tectocephus velatus</i> (Michael, 1880)	2	0	2
Oribatida, juveniles, fam. indet.	24	0	24
Uropodina			
Uropodoidea			
Uropodidae			
<i>Oodinychus karawaiewi</i> (Berlese, 1903)	39	0	39
<i>Oodinychus ovalis</i> (C.L. Koch, 1839)	27	0	27
Total	1434	320	1114

excluded and therefore there were only 29 observations (based on 23 males and 6 females) of the end of feeding measured with an accuracy of 30-min. In 25 cases the moment of the opening of the encapsulated ptychoid mite by pulling away the flexed prodorsum was recorded.

Scanning electron microscopy (SEM)

The head and legs of disarticulated specimens of *E. pubicollis* were studied after a brief cleaning in a warm 10% solution of NaOH, thorough washing in distilled water, dehydration in isopropanol, drying in air and mounting on SEM stubs with carbon tabs. Feeding damage to empty mite shells abandoned by beetles of non-cleaned specimens collected into 75% ethanol, dehydrated in isopropanol, air-dried and mounted as above, were also studied. Dried remains of liquid produced by beetles and

present on the mites' cuticle were studied in *Phthiracarus* sp. mites taken away from predators five hours after capture, stored frozen at -20°C and after defreezing directly mounted on a carbon SEM tab. All specimens were sputter-coated with gold (Pirani 501, Edwards) and examined using an EVO LS15 (Carl Zeiss, Jena) scanning electron microscope.

Light photography and image processing

Photographs of feeding were taken using an Olympus C-750UZ digital camera with a Raynox MSN-202 close-up lens. Photographs of the habitus of mites were taken using a Nikon Coolpix 4500 camera mounted on a Nikon SMZ 1500 stereoscopic microscope. Image stacks were processed using Combine ZP (Hadley, 2010). Final image adjustments and annotations were made in Corel PhotoPaint.

Measurements

Two distinct morphological types of Oribatida were included in the experiments and as consequence were measured in different ways. Ptyctimous mites (represented in the study by the superfamilies Euphthiracaroida and Phthiracaroida) have laterally compressed bodies, which is an adaptation associated with the ptychoid defensive mechanism, and their body lengths in the open and closed position differ significantly. Feeding damage done by *Euconnus* to these mites in most cases makes it impossible to include the length of prodorsum in the measurements. Therefore, the length of Ptyctima is the length of the notogaster, measured in lateral view. All the other mites studied are incapable of flexing the anterior part of their bodies and changes in body length caused by feeding damage are negligible; their length was measured in a dorsal view, from the anterior margin of the capitulum to the posterior margin of the idiosoma.

Plots and statistics

The data were plotted using MS Office Excel 2003 and SigmaPlot 2004 v. 9.0 (Systat Software, USA). The linear and exponential regression analysis was conducted also in SigmaPlot; 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). Mean values with the standard deviation and median values with quartile 1 and 3 are given. Undetermined juvenile mites were not included in calculations of the preferred length of prey.

Terminology

"Accepted prey" are the mites that were found dead 24 h after placing in the 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. The "feeding time" refers to the time from attack to abandoning an empty mite shell; "access time" is the time it takes from the moment of the attack to the beetle making a noticeably wide opening in the prodorsum of its ptyctimous prey.

Source of errors

The experimental setup used in the present study was developed and optimized over a long period of time, but it is nevertheless a rather poor imitation of natural conditions, as some factors were intentionally adopted to make it easier to observe the beetles rather than create a small-scale copy of the natural environment (e.g., a high beetle density). It is almost certain the behaviour recorded was affected by the laboratory conditions.

The potential prey are not only small (a fraction of a millimetre) but often can only be identified by studying transparent

microscopic preparations of the mites as several externally similar species of mites occur in the same soil samples as the Scydmaeninae. This makes it almost impossible to study prey preferences in a strictly controlled way, i.e. by conducting a series of experiments, each with a different species of prey, and comparing the obtained feeding rates by statistical methods. Instead, in the present study prey choice experiments were conducted by presenting a broad range of mites simultaneously to the beetles and identifying the prey after harvesting dead and living mites. This could result in an overestimate of the number of prey eaten by scoring as accepted (i.e., eaten) mites that died for other reasons than being attacked by beetles. This undesired effect was minimized by the frequent collecting of dead mites and scoring only those with the characteristic feeding damage caused by beetles.

The accuracy of our observations (and also conclusions) was affected by difficulties in determining the species of several genera to which the empty mite shells belonged, especially those most frequently attacked by beetles. This problem forced us to present only tentative species determinations for some genera (marked with a question mark in Table 1) or to draw general conclusions based on both certain and tentative identifications.

Although a large number of beetles and prey were included in this study, different numbers of individuals of each mite species were collected from the substrate, and therefore in prey choice experiments it was not possible to provide the beetles with equal numbers of mites of each species. This 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 abundance of each species of mite placed in arenas was intended to reflect the corresponding abundance in the substrate from which both the beetles and mites were collected. However, the method adopted for collecting mites creates a bias towards those taxa that readily gathered on and under the "paper traps". It was only possible to estimate the direction of this bias for Phthiracaridae, which tended to walk on the walls of substrate containers and gathered not only on the traps, but also on the lid of the container. Therefore, the representation of this family in the samples of mites given to beetles was smaller than in the substrate. Other mites might have remained hidden in the substrate and avoided the traps, but this effect was not studied.

The method of measuring the mites and the calculations based on these measurements of body length may be another source of inaccuracy. A more suitable parameter would be body volume or even internal body volume (skeletal structures excluded). The very different body shapes of the prey (variability in body shape occurred even within some of the *Phthiracarus* spp. studied) make such calculations impractical. In the case of Phthiracaridae, results of the linear regression analysis based on body length, width and length \times width gave similar results and resulted in the same conclusions, therefore body length was used in all the calculations.

RESULTS

Prey choice

Species preferences (Table 1; Fig. 1)

A total of 1434 mites, representing 50 species (24 families of Oribatida and 1 family of Mesostigmata: Uropodina), were placed in arenas with *E. pubicollis* (Table 1). The 320 mites eaten by the beetles belonged to the following families and genera of Oribatida: Achipteridae (3 spp. of *Achipteria* Berlese); Chamobatidae (2 spp. of

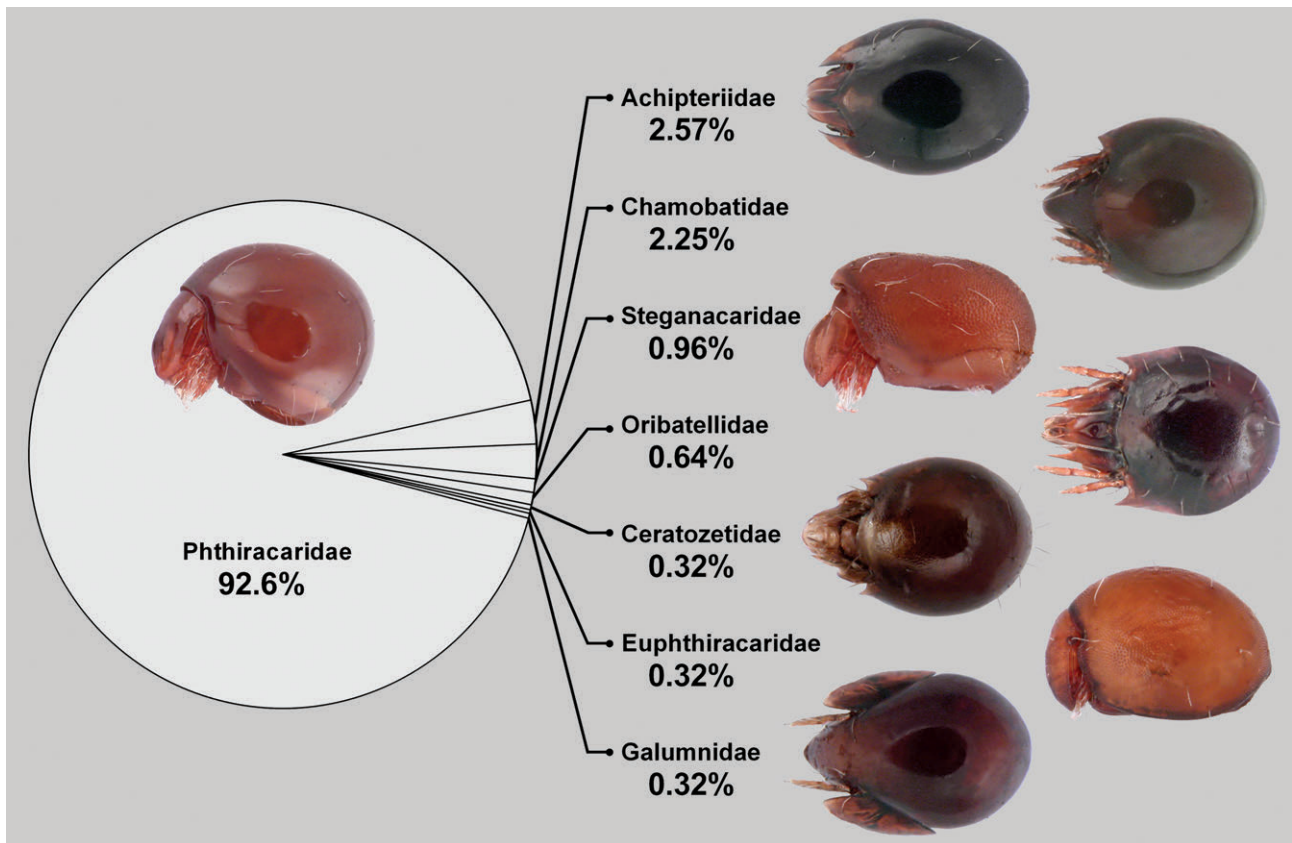


Fig. 1. Families of Oribatida eaten by *Euconnus pubicollis* in prey choice experiments, with examples of species belonging to each family: *Phthiracarus globosus* (Phthiracaridae), *Achipteria nitens* (Achipteriidae), *Chamobates subglobosus* (Chamobatidae), *Steganacarus* sp. (Steganacaridae), *Oribatella quadricornuta* (Oribatellidae), *Trichoribates trimaculatus* (Ceratozetidae), *Euphthiracarus cribrarius* (Euphthiracaridae) and *Pergalumna nervosa* (Galumnidae).

Chamobates Hull); Ceratozetidae (1 sp. of *Trichoribates* Berlese); Euphthiracaridae (1 sp. of *Euphthiracarus* Ewing); Oribatellidae (1 sp. of *Oribatella* Banks); Phthiracaridae (3 spp. of *Phthiracarus* Perty); Steganacaridae (1 sp. of *Steganacarus* Ewing); and Galumnidae (1 sp. of *Pergalumna* Grandjean). Individuals of the remaining 16 oribatid families (Carabodidae, Euzetidae, Zetomimidae, Camisiidae, Nothridae, Damaeidae, Oribotritidae, Liacaridae, Peloppiidae, Tenuialidae, Hermannelliidae, Hypochthoniidae, Nanhermanniidae, Schelolibatidae, Phenopelopidae and Tectocephidae) and the uropodines (Uropodidae) were not attacked. Some species belonging to Euphthiracaridae (*Acrotitia ardua*), Galumnidae (*Acrogalumna longipluma* and *Galumna obvia*), Phthiracaridae (*Phthiracarus crinitus*, *Ph. laevigatus* and *Ph. nitens*) and Steganacaridae (*Steganacarus magnus*) were also not attacked. Among the accepted mites, 92.6% belonged to the ptyctimous family Phthiracaridae represented by a single genus *Phthiracarus*; all the other mites eaten only made up a very small part of the diet, with only a few individuals of each family found dead and with the typical feeding damage 24 h after being placed with beetles. The majority of the Phthiracaridae eaten belonged to *Phthiracarus globosus* (and *Ph. ?globosus*) along with a small number of *Ph. ?clavatus* and *Ph. longulus*.

Body length of the mites eaten (Fig. 2)

Of all the mites provided (ranging in body length from 0.325 to 1.725 mm) only those with body lengths of 0.375–0.850 mm were accepted. The mites eaten ($n = 320$) had a median body length (quartiles in square brackets) of 0.625 mm [0.550, 0.675], which is significantly smaller ($U = 56700$; $p \ll 0.001$) than the median 0.750 [0.675, 0.925] of those not eaten ($n = 1037$). The accepted Phthiracaridae ($n = 297$) had a median body length 0.625 mm [0.550, 0.675], which is significantly smaller ($U = 11300$; $p \ll 0.001$) than the median of 0.750 [0.700, 0.850] of those rejected ($n = 257$). In the case of the most frequently eaten species *Phthiracarus globosus* (and *Ph. ?globosus*), the accepted mites ($n = 276$) had a median body length 0.625 mm [0.550, 0.700], which is significantly smaller ($U = 8489$, $p \ll 0.001$) than the median of 0.740 mm [0.675, 0.775] of the conspecific mites ($n = 276$) that were not eaten. There was no difference in the body lengths of the mites eaten by male (group #1) and female (#2) *E. pubicollis*, nor by each of separated genders and the mixed groups #3 and #4 ($p > 0.1$).

Number of eaten mites and feeding time

The males (group #1) ate 90 mites (83 Phthiracaridae), females (group #2) 103 mites (102 Phthiracaridae) and the two mixed groups #3 and #4 73 mites (63 Phthiracar-

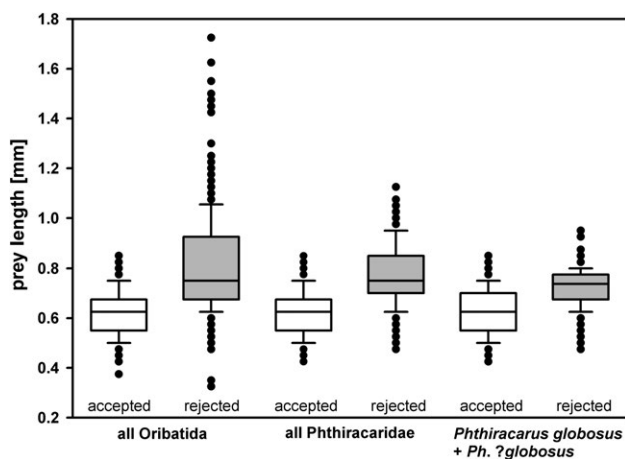


Fig. 2. Distributions of the body length of Oribatida accepted vs. rejected by *Euconnus pubicollis*; the median, 10th, 25th, 75th, 90th percentiles and outliers are shown.

idae) and 54 mites (49 Phthiracaridae), respectively. The consumption rates calculated as the number of mites consumed per beetle per day were 0.30 for males, 0.34 for females, and 0.24 and 0.18 for the mixed groups #3 and #4, respectively. The average number of mites consumed by one beetle per day was 0.27 ± 0.07 .

In the feeding experiments the time it took the beetles to eat *Phthiracarus* mites ranging in size from 0.425 to 0.675 mm in length was 2.15–33.70 h. There is a positive linear relationship between the prey body length and the feeding time (Fig. 3), with a regression coefficient $R^2 = 0.74$.

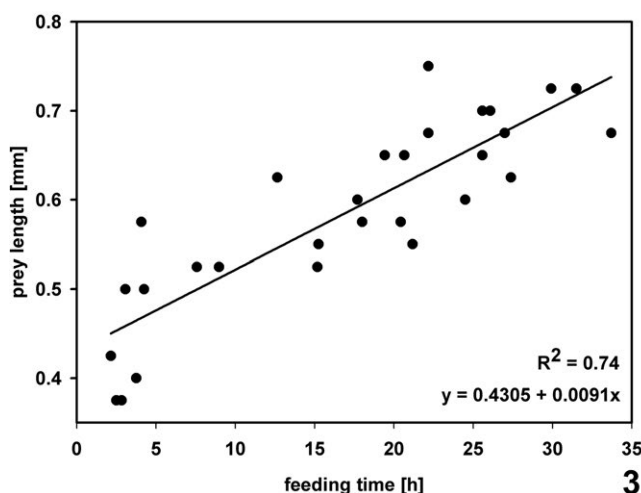
Feeding behaviour

Attack (Figs 5, 11–14)

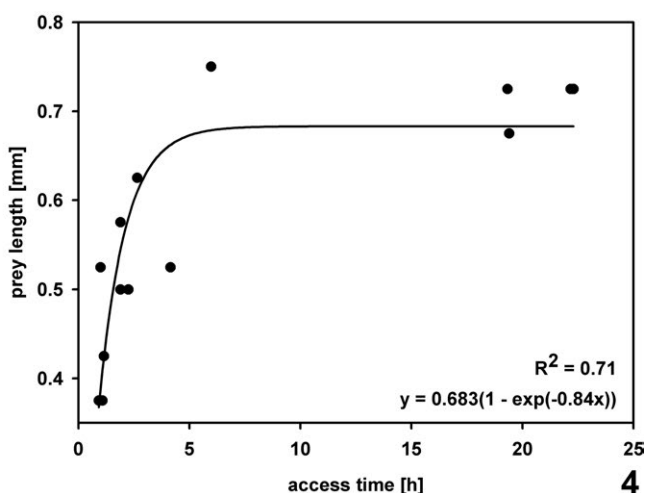
In the feeding experiments, *E. pubicollis* attacked *Phthiracarus* mites 0.5–65 min after they were placed in the middle of the arena. 40.91% of the attacks occurred within 1 min, 54.54% within 5 min and 79.54% within 10 min; only 9.09% of all attacks were initiated after 20 or more minutes. Beetles that encountered a mite during

patrolling the arena briefly palpated it with its antennae and then with the maxillary palps. Within the next 2–3 s the beetle rapidly moved its head and mouthparts towards the cuticle of the mite, exuded a droplet of liquid from its mouth and lifted the mite, typically using three points of contact: the droplet of liquid between the cuticle of the mite and the labrum, maxillae and labium of the predator (Fig. 11), and the internal surfaces of the apical parts of both protibiae, which are densely covered with spatulate setae (Fig. 22). In some cases the beetle lifted up its prey by means of the adhesive liquid on its mouthparts without using its fore legs.

The arrangement of the beetle's mouthparts during all the attacks was similar (Figs 11, 19–21): The anterior part of the labrum or its dorsal surface adhering to the mite cuticle by means of the liquid exuded from the mouth; the mandibles widely spread and touching the mite with dorsal surfaces of their apical halves; the maxillae protruded anteriorly with galea and lacinia covered with the liquid and adhering to the prey cuticle, maxillary palps spread laterally and occasionally touching the cuticle of the prey; the labium protruded anteriorly, its anterior part (prementum and possibly also the anterior part of hypopharynx) also covered with the liquid and adhering to the mite. The largest area of contact was formed by the flattened and broad galea and lacinia bearing dense setae (Fig. 21) covered with the liquid. During the lifting of the prey, beetles either adopted a posture of a raised head and prothorax while standing on middle and hind legs, or (in prey choice experiments carried out in arenas with particles of sifted leaf litter) utilized pieces of substrate to attack mites walking on the surface of the plaster from above, while standing head down, with hind and middle legs on the side of a particle of litter, and the anterior part of body with the mite hanging down above the ground. Only the distal parts of fore tibiae touch the cuticle of prey during its capture and manipulation, the fore tarsi being spread laterally. This technique was used independently of the size or shape of the mite and the first part of the mite contacted was usually a dorsal or lateral region



3



4

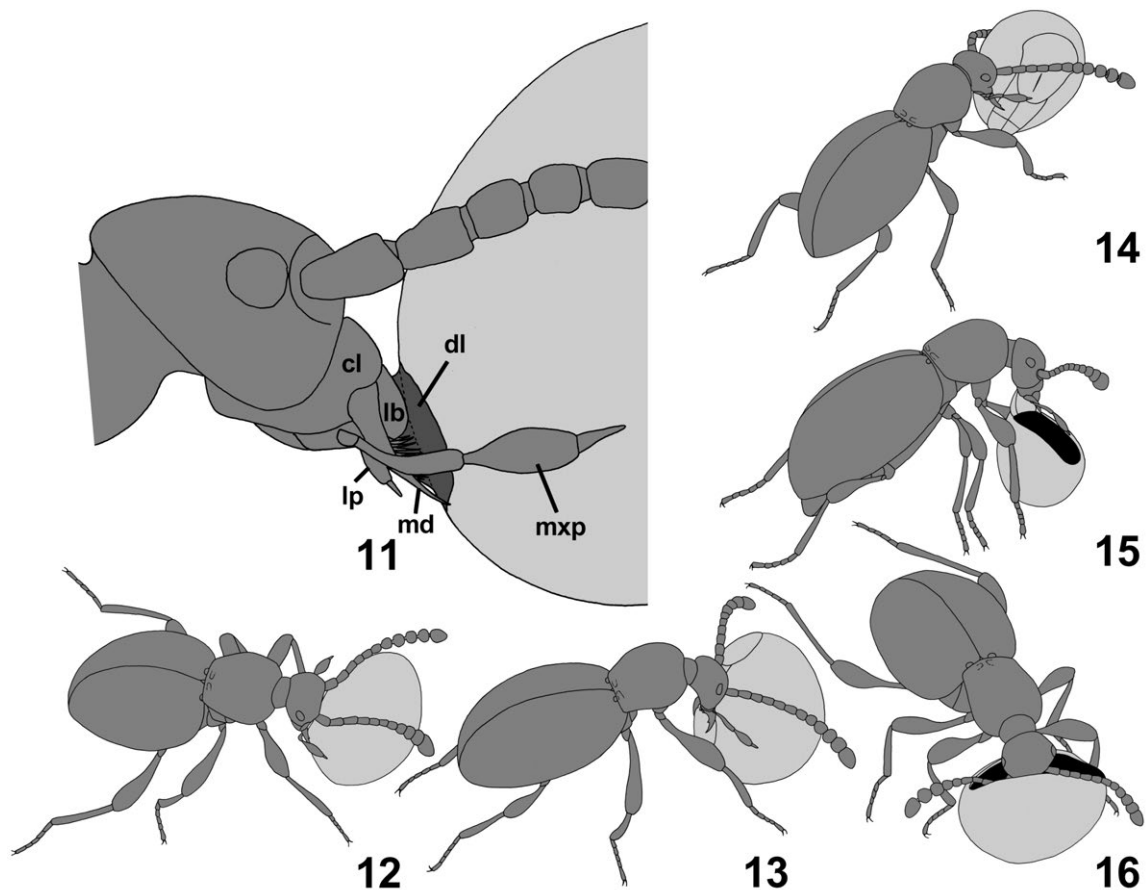
Figs 3–4. Relationship between the length of the prey and time spent feeding (with linear regression line) (3) and between the length of the prey and the access time (with exponential regression line) (4).



Figs 5–10. Photographs of *Euconnus pubicollis* feeding on mites of the genus *Phthiracarus*. Attack phase (5), prey lifted off the ground and carried in mouthparts (6–7), prey pressed against ground and manipulated with mouthparts and protibiae (8–9) and final phase of feeding, with prodorsum and ventral plates of prey removed and beetle feeding on soft tissues (10).

of the idiosoma. In the feeding time experiments, in which there was only one beetle in the arena not disturbed by any other organisms, the attack phase was immediately followed by manipulating the prey and searching for access to fragile or movable parts of the integument, and the time spent walking in the arena with the prey held in

the mouthparts took up only a minute fraction of the entire process. In the prey choice experiments, predators were frequently disturbed by other beetles and mites present in the arena, and were observed walking for prolonged periods of time (minutes to hours) around the entire arena with the prey held in mouthparts, searching



Figs 11–16. Schematic diagrams of the feeding stages and positions. Beetle walking with prey attached to a droplet of liquid exuded from mouth (11–14), manipulating the prey after the prodorsum has been opened and ventral plates pressed into idiosoma (15) and feeding on the prey that have had prodorsum and ventral plates removed (16). Abbreviations: cl – clypeus; dl – droplet of liquid; lb – labrum; lp – labial palp; md – mandible; mxp – maxillary palp.

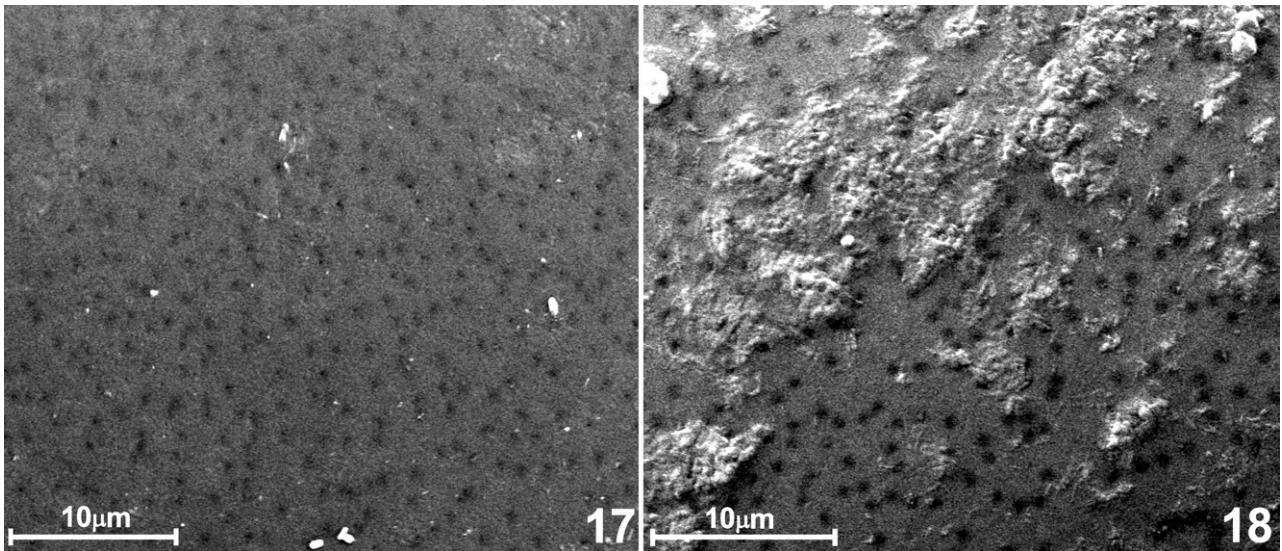
for shelter under litter particles or in narrow spaces between them, where, if undisturbed, they continued manipulating the mite to overcome its defence.

Breaching the prey's defence (Figs 15, 17–18)

The ptyctimous mites (Figs 23–24) reacted to an attack by adopting the ptychoid defence position, i.e., by flexing the prodorsum ventrad, retracting the legs and encapsulating (Fig. 24), while all other Acari only become more active to various extents and tried to escape, or ceased moving for a short period, when the beetle palpated them with its antennae and maxillary palps. Ptyctimous mites remained in the fully encapsulated state while being carried in the mouthparts and during all subsequent manipulations whereas other Acari showed various intensive leg movements. To gain access to soft body parts and the flesh of the armoured prey, beetles utilized one of two different techniques, depending on the body form of the prey.

The ptyctimous *Phthiracarus* oribatids were most frequently eaten and therefore the way they were attacked was the most thoroughly studied. In the encapsulated state (Fig. 24), the soft podosoma and legs are protected by the shield-like prodorsum and externally the mite exposes only heavily sclerotized body parts. Beetles that attacked Ptyctima were observed standing on their middle and

hind legs, either on the surface of the plaster arena or in various positions (often head down) on the sides of particles of litter, frequently turning and rotating the mite using their protibiae and often detaching and attaching their mouthparts to the prey. A relatively voluminous droplet of liquid was regularly produced and sucked back, in a cycle of about 2 s in which the droplet first increases in size followed by a rapid decrease in its volume. This was repeated over a prolonged period of time (from about 90 min to more than 20 h) during which the mites manipulated in this way remained motionless. The frequent changes in the way the beetles gripped their prey resulted after some time in the entire mite body surface appearing moist and covered with the liquid exuded by *Euconnus*. The cuticle of mites at this stage of the attack observed using SEM showed dried remnants of the liquid (Fig. 18). The moving and rotating of the mite was occasionally accompanied by movements of the mandibles, apparently searching for a grip on the margins of the closed prodorsum or the genital and anal plates. The moment when the prodorsum was at least partly lifted marked the end of this phase and the beginning of actual feeding. The attempts to lift up the flexed prodorsum were also accompanied by pressing on the genital and anal valves, and the genital and anal plates of mites taken



Figs 17–18. Cuticle of *Phthiracarus globosus*. Intact mite (17) and one attacked by *Euconnus pubicollis* and taken away from the predator five hours after it was captured, with dried remains of the fluid visible on the surface (18).

away from beetles at this time, with the prodorsum just opened, are clearly damaged (Figs 25–28).

The time from the attack to the lifting of the prodorsum and breaching of the defence of *Phthiracarus* (i.e., the access time) ranged from 0.92 to 22.3 h in the 24 cases observed. The relationship between prey length and access time (Fig. 4) was found to be exponential. In mites as large as 0.375–0.625 mm the access time ranged from about one and a half to five hours, while a further increase in the body length rapidly increased the access time to over 20 h.

A prolonged unsuccessful manipulation to gain access to soft body parts resulted in the prey being abandoned in four cases. These *Phthiracarus* mites had a body length 0.575–0.725 mm (the “edible” body length category) and were unsuccessfully manipulated for 23–28 h and then abandoned. These mites were collected and checked to determine whether they would show any movements if undisturbed. All four abandoned mites did not move for 24 h and were regarded as dead; their bodies remained in the encapsulated state and did not show any externally visible damage.

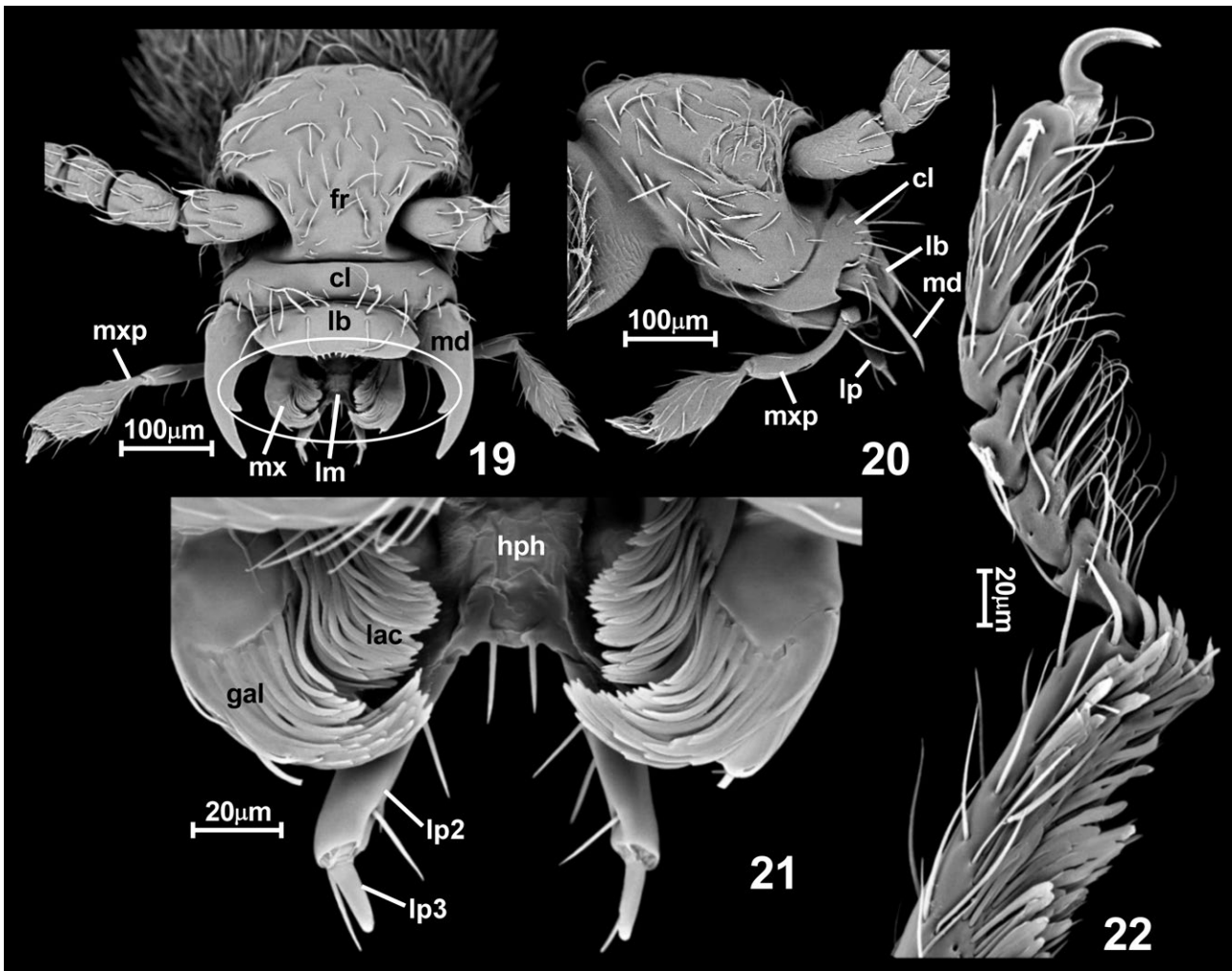
In 14 cases the predators, during manipulations of encapsulated mites, were disturbed by other beetles and left the prey, walked a short distance away, and then returned to the same mite and continued the struggle.

All other (i.e., not ptyctimous) mites attacked by beetles in the prey choice experiments (i.e., *Achipteria*, *Trichoribates*, *Chamobates*, *Oribatella* and *Pergalumna*) were not able to adopt the ptychoid defence. They were captured and lifted up in a similar way to the *Ptyctima*, but further manipulations were clearly different. The mite, moving its legs and adhering to the mouthparts and protibiae of *Euconnus*, was frequently moved and rotated, and often pressed against the ground or litter particles when the predator detached its tibiae of the surface of the prey to change its grip. It was observed that the beetle was trying to insert the slender and pointed tip of one

mandible into one of the natural body openings: into the gnathosoma, the genital or the anal valves. When successful, the leg movements of the prey stopped, and the beetle kept rotating the mite around the inserted mandible, frequently changing direction, which eventually resulted in breaking off and removing movable parts around the opening (i.e., the mouthparts, or genital or anal plates). The access time was not analyzed in detail, because the attacked prey belonging to Oribatida other than *Ptyctima* constituted only 6.1% of all the mites attacked and only three cases of feeding were observed in detail. In these the access time (defined as the time from the attack to inserting one mandible into the prey) was 25–190 min. Moreover, after inserting the mandible into the gnathosomal or genital opening and during feeding, beetles removed all or most of the legs of the mite. The legs were broken off near the end of feeding (in the last 5–20 min) by the mandible that was not inserted into the mite, during rotations and other manipulations; cutting off the legs with both mandibles was not observed. The legs were at least partly removed from all the empty mite shells of non-ptyctimous prey (Figs 29–32). In most observations, beetles took short breaks during the struggle with all types of prey. The mite was placed on the floor of the arena or on a particle of litter and the beetle spent 20 s to over 2 min grooming. The antennae and distal parts of fore legs were cleaned by passing them through their mouthparts, and middle legs cleaned the elytra; all grooming movements were repeated many times. Then the beetles resumed manipulating the prey. The grooming was observed to be repeated many times (at least 5) during this and the next phase.

Feeding (Figs 10, 16)

In order to gain access to the flesh of ptyctimous mites, beetles after opening the prodorsum continued pressing the ventral (genital and anal) plates. After ecptychosis (the opening of the mite) the beetles firmly gripped the

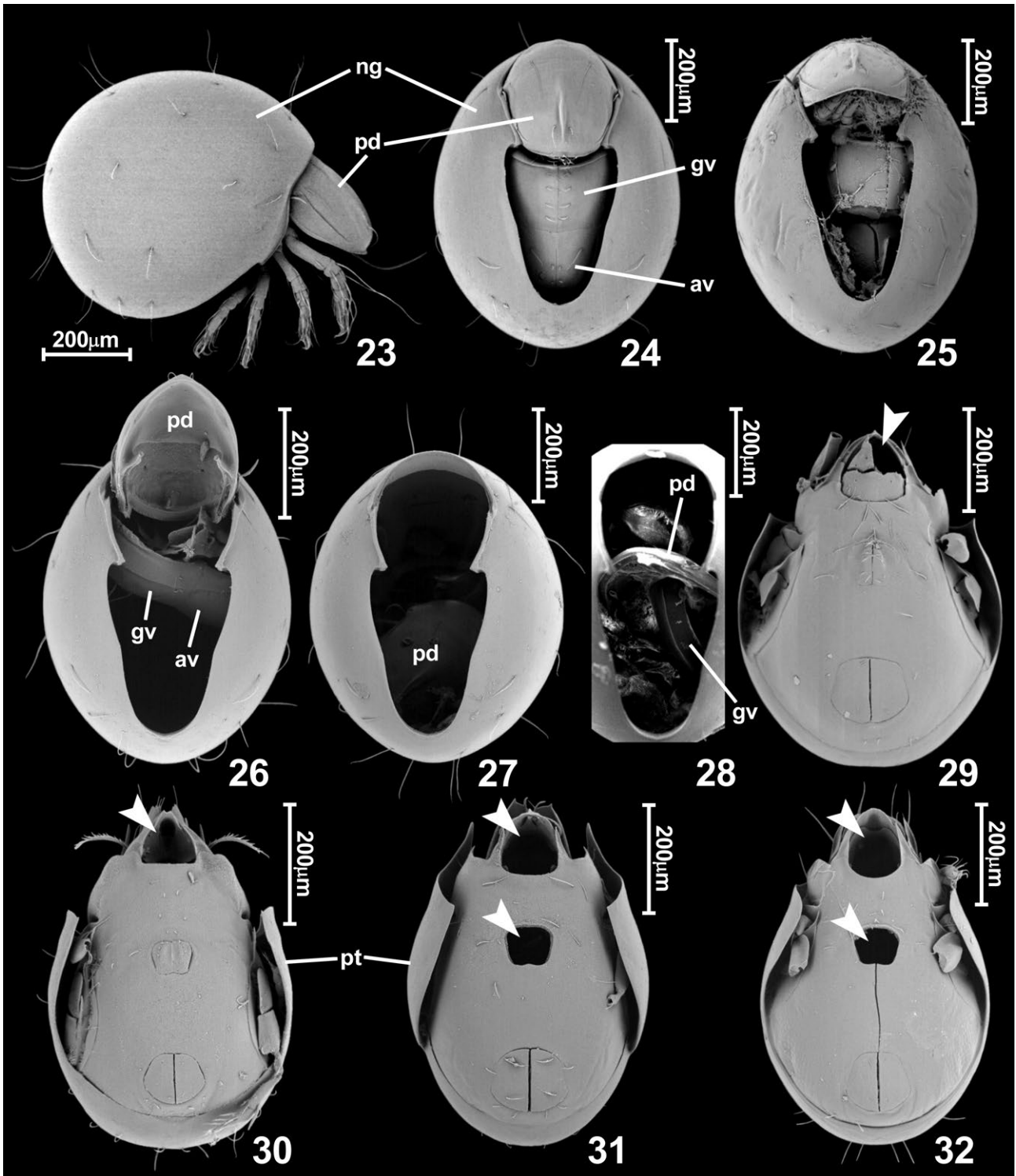


Figs 19–22. Structures of *Euconnus pubicollis* used to capture prey. Head in anterior (19) and lateral (20) view (contact zone in oval frame), distal parts of maxillae and labium in dorsal view (21) and distal part of left fore leg in mesal view (22). Abbreviations: cl – clypeus; fr – frons; gal – galea; hph – hypopharynx; lac – lacinia; lb – labrum; lm – labium; lp – labial palp; lp2–3 – labial palpomere 2–3; md – mandible; mx – maxilla; mxp – maxillary palp.

open prodorsum with their mandibles. The mite was usually pressed against the ground, the beetle adopted a posture with its head and pronotum lowered towards the prey while standing on all six legs, occasionally using its fore legs to rotate the mite. The mandibles were used to find a position to grip the margin of genital or anal valves, and gradually the entire complex of ventral plates was pressed into the notogaster, exposing the flesh. The mouthparts and nearly the entire head (with antennae bent latero-caudad) of *Euconnus* were gradually inserted deeper and deeper into the notogaster of large *Phthiracarus* (Figs 10, 16), during which the mandibles rapidly chewed away at the soft internal tissues. Small amounts of liquid were also exuded from the mouth at this stage. When the prey was too small for the beetle's head to be inserted into the opening, only mandibles (and sometimes just one mandible) were inserted into the mite's body. In such cases the mite was intensively manipulated, mostly rotated around the inserted mandible, and copious amounts of liquid were exuded from the mouth and then ingested.

Abandoned empty mite shells show characteristic feeding damage (Figs 25–28). The prodorsum and ventral plates of 76.55% of the empty *Phthiracarus* spp. shells were completely detached, of 21.61% the prodorsum was open but still attached to the idiosoma and of 1.83% the genital and anal plates were intact, while the prodorsum was open and still attached to the idiosoma. The prodorsum and the ventral plates of many of the empty shells were deeply pressed inside the idiosoma (Fig. 28).

In mites other than *Ptyctima*, the feeding took place through relatively small openings resulting from the removal of mouthparts (Figs 29–30), genital plates, or both mouthparts and genital plates (Figs 31–32). Beetles frequently rotated the prey around the inserted mandible and droplets of liquid were observed around the penetration site during this action. Because of the small size of non-ptyctimous prey it was not possible to observe the ingestion of liquefied tissues. Empty mite shells were abandoned 50–130 min after penetration.



Figs 23–32. Prey of *Euconnus pubicollis*, in 25–32 showing feeding damage. Intact *Phthiracarus globosus* in open (23) and encapsulated (24) position (the withdrawn position of the ventral plates is an artefact caused by fixation); *Ph. globosus* in early (25) and final (26, 27) stages of feeding; prodorsum and ventral plates visible inside idiosoma of consumed *Ph. globosus* (28); feeding damage (indicated by arrows) to empty shells of non-ptyctimous mites: *Chamobates cuspidatus* (29), *Oribatella quadricornuta* (30), *Achipteria coleoptrata* (31) and *Trichoribates trimaculatus* (32). Abbreviations: av – anal valve; gv – genital valve; ng – notogaster; pd – prodorsum; pt – pteromorph.

DISCUSSION

Of the mites belonging to 50 species and 25 families (Table 1) provided, *Euconnus pubicollis* most frequently attacked and ate Phthiracaridae (Ptyctima) (Fig. 1). Indi-

viduals of the genus *Phthiracarus* made up over 90% of the mites eaten and although some other ptyctimous mites (*Steganacarus*, *Euphthiracarus*) were also eaten they only made up a small percentage of the diet (1.28%). It is

noteworthy that the most frequently eaten species was *Phthiracarus globosus*, while the morphologically very similar congeners *Ph. clavatus* and *Ph. laevigatus* were not attacked (Table 1). The phthiracarids eaten by *E. pubicollis* have a glossy cuticle and a small number of moderately long setae, whereas the *Steganacarus* and *Euphthiracarus* eaten have a coarsely microsculptured cuticle. All these mites adopted the typical ptychoid defence position when attacked and their exoskeletons were damaged in the same way by the beetles: the prodorsum was opened, the ventral plates (genital and anal plates in Phthiracaridae, holovenral plates in Euphthiracaridae) removed or pressed inside the idiosoma and all the other vulnerable ventral structures (e.g., chelicerae, subcapitulum, legs) were missing from the empty mite shells studied. It seems that, in addition to possible chemical factors not included in this study, body size is an important criterion used by beetles to select suitable prey. Of the ptyctimous mites, the largest individual eaten was 0.85 mm in length. The maximum size of the prey may be limited by the peculiar mechanism the beetles use to capture prey. The gripping of the prey by means of a droplet of liquid exuded between the beetle's mouthparts and the mite's cuticle (apparently utilizing viscosity or/and capillary forces to maintain the adherence), observed in the present study (Fig. 11), has not been previously reported for mite-eating Scydmaeninae. The area on the mouthparts where the liquid spreads and forms a relatively small contact zone (Figs 11, 19) and presumably the forces generated may be insufficient to lift larger (heavier) prey. Previous authors (Schmid, 1988; Molleman & Walter, 2001) report that Scydmaeninae use their fore legs and mandibles to lift mites and that the spatulate setae on the distal parts of the tibiae played an important role in this process. Molleman & Walter (2001) even coined a term "tibial suckers". Similar observations were also made in the present study for ptyctimous mites and the SEM examination of the legs also revealed spatulate setae on the distal parts of the protibiae (Fig. 22). However, in contrast to Schmid's observations, in *E. pubicollis* the protarsi did not participate in capturing the prey and in all the cases observed were widely spread laterally, while the tibiae adhered to the prey. Incidentally, during collecting dead and surviving Acari it was noticed that *Phthiracarus* mites can be easily lifted as they adhere to entomological pins. The cuticular waxes of mites are sufficiently viscous to adhere to smooth objects, which may be the mechanism utilized by beetles, and may also account for how an Australian *Euconnus* sp. is able to lift a mite using only one leg (Molleman & Walter, 2001).

The large volume of liquid exuded from the beetle's mouth and sucked back in short cycles suggests a digestive juice rather than a glandular sticky secretion. Digestive or otherwise the noxious properties of this liquid together with the mechanical manipulations of the mandibles seem to be involved in the opening encapsulated ptyctimous mites. The increase in access time with the prey body length (Fig. 4) demonstrates that breaching the ptychoid defence is not an easy task for the beetles. The

encapsulation (or entptychosis) is achieved by a complex system of muscles and exoskeletal structures, which has been studied in detail in several ptychoid mites (Schmelzle et al., 2008, 2009, 2012). A mite must contract numerous muscle fibres to retract and properly position the various parts of its body, among others the coxisternum, podosomal membrane, subcapitulum, prodorsum, cheliceral and pedipalpal segments; also changes in hemocoel pressure play a role in the entptychosis (Schmelzle et al., 2009). Pouring copious amounts of digestive juices all over an encapsulated prey (Figs 17, 18) presumably weakens and eventually kills the mite and relaxes its muscles, enabling the beetle to open the prodorsum and gain access to the vulnerable and soft body parts of the prey. For mites 0.375 to ca. 0.65 mm in body length the time to open the prodorsum (the access time) was relatively short (0.90–4.15 h), while further increase in prey size was associated with an exponentially prolonged struggle, in some cases of more than 20 h (Fig. 4). However, the entire feeding time (from attack to abandoning an empty mite shell) increased linearly with prey body length (Fig. 3). The long time spent feeding (up to 33.70 h in this study) is interesting in terms of the energy expended vs. gained by consuming these mites. This may pose problems when the beetles are exposed to strong competition or threat from larger predators, as in leaf litter or soil inhabited by other scydmaenines and a large number of diverse staphylinids, carabids, ants and other predacious organisms. In the feeding experiments beetles spent most of the time processing captured prey, while in prey choice experiments they were frequently forced to move in search of shelter, as they were disturbed by other beetles and mites present in the arena. Under such conditions, the entire feeding process may be longer and prey frequently abandoned before completely eaten. Therefore, the feeding times recorded when a single beetle was provided with one mite may be the shortest possible time required. Differences in the number of mites eaten by the beetles in the different groups studied indicate that interactions between males and females of *E. pubicollis* should also be considered as a possible factor affecting feeding. Females (which are slightly larger than males) killed 103 mites, males 90 mites and the beetles in the two mixed groups, 73 and 54 mites, respectively. However, more beetles need to be studied in order to determine whether the sexes compete for food.

Non-ptyctimous mites eaten by the beetles made up a mere 6.10% of their diet (Fig. 1). Interestingly, all of them that belonged to the genera *Achipteria*, *Chamobates*, *Oribatella*, *Trichoribates* and *Pergalumna* (Table 1), have pteromorphs (Figs 30, 31), cuticular plates or folds protecting the proximal parts of the legs. Of the 30 species of non-ptyctimous mites that were not eaten, only 5 (belonging to the genera *Acrogalumna* Grandjean, *Galumna* von Heyden, *Euzetes* Berlese, *Hafenrefferia* Oudemans and *Scheloribates* Berlese) have pteromorphs. The small number of non-ptyctimous mites eaten resulted in insufficient observations on the way the beetles feed on these mites and in particular whether the pteromorphs are

used by the beetles during the attack (e.g., for gripping the mites), however, the asymmetry in the number of mites with and without pteromorphs eaten and not eaten is distinct and deserves further study.

The way of feeding on non-ptyctimous mites recorded in the present study is similar to that reported by Schmid (1988) and Molleman & Walter (2001), except that in all cases the penetration and feeding were via the gnathosomal or gnathosomal and genital openings, but not the anal opening (Figs 29–32). Schmid (1988) reports that Scydmaeninae belonging to the genus *Neuraphes* cut off legs of Damaeidae mites (which have the longest legs of all the mites tested in the present study and were not eaten by *E. pubicollis*), and Molleman & Walter (2001) record this leg-cutting behaviour as commonly occurring during the early stages of attack by most of the Australian Scydmaeninae taxa studied (including undetermined *Euconus* spp.). The legs of the prey were cut near their bases before penetration via the gnathosoma or valves and apparently this process was an important part of breaching the prey's defences. Although the legs of non-ptyctimous prey were removed by beetles in the present study, observations indicate that *Euconus* can efficiently deal with mites with intact legs and only near the end of feeding, when one mandible is deeply inserted into a body opening and the mite frequently rotated around the penetration site, would the other mandible break off (and not cut) the legs. Presumably at this stage most of the flesh is already dissolved and ingested and the legs, devoid of muscles and other internal tissues, are more fragile than in living mites and easily break off.

Scydmaeninae are common and relatively abundant inhabitants of litter on the forest floor in subtropical and tropical zones, and the cosmopolitan and enormously large genus *Euconus*, with nearly 2500 described species (Newton & Franz, 1998) and much higher number of yet undescribed species (Jałoszyński, unpubl. observ. based on museum collections) is one of the most common ant-like stone beetles in this habitat. Even in the temperate zone, there are dozens of individuals of species such as *E. pubicollis* in a few fistfuls of fallen leaves in alder woods and other deciduous and moist forests (Jałoszyński, unpubl. observ.), and this is not the only species of Scydmaeninae found in such places. Results of the experiments presented show that the average number of mites consumed by a beetle was 0.27 ± 0.07 per day (in other words, one beetle killed one mite every 3.7 days). Although this seems a relatively low number, in nature Scydmaeninae specialized to feed on oribatid mites may locally occur in high numbers and plausibly influence mite population dynamics. Acarologists have hypothesized that the defence systems of Oribatida evolved as a defence against predacious prostigmatan and mesostigmatan mites, and since this pressure is now low, armoured Acari now live in "enemy-free space" (Jeffries & Lawton, 1984). This hypothesis is further supported by other researchers, e.g. Peschel et al. (2006) who report that the predacious mesostigmatan mite, *Pergamasus septentrionalis* (Oudemans), in Germany strongly prefers

soft-bodied juvenile mites and only occasionally fed on armoured adult Oribatida. Interestingly, *Pergamasus* seems to utilize a similar mechanism to some Scydmaeninae, in cutting off the legs of its mite prey and penetrating its body through the gnathosoma or genital valves, leaving feeding damage that is similar to that caused by Scydmaeninae and illustrated by Molleman & Walter (2001) and recorded in the present study. Peschel et al. (2006) conclude that armoured Oribatida adults may indeed live in enemy-free space, "since few relevant predators at the study site are more abundant and powerful than *P. septentrionalis*". However, the authors suggest that springtails constitute a major part of the diet of *P. septentrionalis*, so their conclusions were drawn from a study of a predator specialized to feed on other kinds of prey than mites. Both previous (Schuster, 1966a, b; Schmid, 1988; Molleman & Walter, 2001; Jałoszyński & Beutel, 2012) and the present results concerning Scydmaeninae demonstrate that at least some of them are highly specialized to feed on Oribatida and have evolved a number of morphological and behavioural adaptations to breach the defences of such armoured prey. *Euconus pubicollis* is the first scydmaenine beetle for which there is strong evidence that it prefers to feed on a particular family of Oribatida, the phthiracarids that have evolved a method of defence that protects them from other predators. These findings suggest some interesting questions. Is the evolutionary success of Scydmaeninae (i.e., a large and diverse radiation) a result of gaining access to an abundant source of food unavailable to most other predators? How did Scydmaeninae develop such adaptations? Why have such feeding preferences developed in habitats rich in soft-bodied prey? How do Scydmaeninae avoid attacks by larger predators during the long periods they spend feeding? Do Scydmaeninae exert a significant effect on the population dynamics of Oribatida? Is the high abundance of certain mite taxa (e.g., Phthiracaridae) a measure evolved to counter the predation by specialized Scydmaeninae? Further studies on prey preferences, feeding rates and the adaptations of other taxa of ant-like stone beetles are necessary as the current level of our understanding of the behaviour of this cryptic and poorly known group of beetles does not allow us to formulate hypotheses to address these questions.

ACKNOWLEDGEMENTS. We are indebted to W. Niedbała and A. Napierała (Faculty of Biology, A. Mickiewicz University, Poznań, Poland) for identifying some of the ptyctimous and uropodine mites, respectively, and K. Kaliński (Wrocław University of Environmental and Life Sciences, Poland) for taking the SEM images.

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Received October 1, 2012; revised and accepted January 2, 2013