Occurrence, ecological function and medical importance of dermestid beetle hastisetae

Enrico Ruzzier Corresp., 1 , **Marcin Kadej** 2 , **Andrea Battisti** 1

1 Department of Agronomy, Food, Natural Resources, Animals and the Environment (DAFNAE), Università degli Studi di Padova, Legnaro (Padova), Veneto, Italy
2 Department of Invertebrate Biology, Evolution and Conservation, University of Wrocław, Wrocław, Poland

Corresponding Author: Enrico Ruzzier
Email address: enrico.ruzzier@phd.unipd.it

Hastisetae are a specific group of detachable setae characterizing the larvae of Megatominae (Coleoptera: Dermestidae), commonly known as carpet and khapra beetles. These setae are located on both thoracic and abdominal tergites and they are the primary defense of the larva against invertebrate predators. According to previous studies, the main purpose of hastisetae is to work as a mechanical obstacle, but they are also capable to block and kill a predator. Hastisetae, single or aggregate, function as an extremely efficient mechanical trap, based on an entangling mechanism of cuticular structures (spines and hairs) and body appendages (antennae, legs and mouthparts). It is believed that this defensive system evolved primarily to contrast predation by invertebrates, however it has been observed that hastisetae may affect vertebrates as well. Although information on the impacts of vertebrate predators of the beetles is lacking, hastisetae have been shown to be a possible threat for human health as an important contaminant of stored products (food and fabric), work and living environment. Review of old and recent literature on dermestid larvae has revealed that despite these structures indicated as one of the distinctive characters in species identification, very little is known about their ultrastructure, evolution and mechanism of action. In the present work, we will provide the state of the art knowledge on hastisetae in Dermestidae and we will present and discuss future research perspectives intended to bridge the existing knowledge gaps.

Occurrence, ecological function and medical importance of dermestid beetle hastisetae

Enrico Ruzzier[1], Marcin Kadej[2], Andrea Battisti[1]

[1] Department of Agronomy, Food, Natural Resources, Animals and the Environment (DAFNAE), Università degli Studi di Padova, Padova, Italy.

[2] Department of Invertebrate Biology, Evolution and Conservation, University of Wrocław, Wrocław, Poland.

Corresponding Author:
Enrico Ruzzier,
Department of Agronomy, Food, Natural Resources, Animals and the Environment (DAFNAE),
Viale dell'Università 16, Legnaro, 35020 Padova, Italy.
Email address: enrico.ruzzier@phd.unipd.it ; symphyla@gmail.com

Abstract

Hastisetae are a specific group of detachable setae characterizing the larvae of Megatominae (Coleoptera: Dermestidae), commonly known as carpet and khapra beetles. These setae are located on both thoracic and abdominal tergites and they are the primary defense of the larva against invertebrate predators. According to previous studies, the main purpose of hastisetae is to work as a mechanical obstacle, but they are also capable to block and kill a predator. Hastisetae, single or aggregate, function as an extremely efficient mechanical trap, based on an entangling mechanism of cuticular structures (spines and hairs) and body appendages (antennae, legs and mouthparts). It is believed that this defensive system evolved primarily to contrast predation by invertebrates, however it has been observed that hastisetae may affect vertebrates as well. Although information on the impacts of vertebrate predators of the beetles is lacking, hastisetae have been shown to be a possible threat for human health as an important contaminant of stored products (food and fabric), work and living environment. Review of old and recent literature on dermestid larvae has revealed that despite these structures indicated as one of the distinctive characters in species identification, very little is known about their ultrastructure, evolution and mechanism of action. In the present work, we will provide the state of the art knowledge on hastisetae in Dermestidae and we will present and discuss future research perspectives intended to bridge the existing knowledge gaps.

Subjects Evolutionary Biology, Morphology, Pest Management, Zoology

Keywords Allergy, Coleoptera, Dermestidae, Ecology, Health, Insects, Systematic, Zoology

Introduction

The cuticle plays a pivotal role in several aspects of arthropod biology, representing the interface between the living tissue and the external environment (Bereiter-Hahn *et al*., 1984). Thus, the cuticle displays structural specializations such as denticles, setae, setulae and spines, all with specific functions (Winterton, 2003). Correlations between structure and function were well studied especially in insects (Neville, 1975) and crustaceans (Garm, 2004a, b; Garm and Watling, 2013). Setae are multicellular protuberances on the cuticle, used primarily for mechanoreception (Steinbrecht, 1984; Keil and Steinbrecht, 1984; Keil, 1997; Winterton,2003; Barth, 2004). In all groups of arthropods, the role of setae has evolved from simple mechanoreception to various other functions, including defense (Battisti *et al.*, 2011), locomotion (Lebarque *et al.*, 2017), prey capture (Felgenhauer *et al.*, 1989), pheromone dispersal (Stainbrecht, 1984), sexual display (Perez-Miles *et al.*, 2005), preening (Felgenhauer *et al.*, 1989), and camouflage (Zeledon *et al*., 1973; Hultgren and Stachowicz, 2008; Stevens and Merilaita, 2009). Detachable setae are true setae characterized by the loss of the neural connection and the detachment of the base of the hair from the integument (Battisti *et al.*, 2011). The proximal end of each seta is attached to an integument stalk or inserted into a socket and can be easily removed with any kind of mechanical stimulation. This class of hairs has evolved as a defensive structure against predation at least four times in Arthropoda. The class is subdivided in two main morpho-ecological groups: urticating hairs and anchor-like setae. Urticating hairs are characterized in some Lepidoptera families such as the Nodotontidae (subfamily Thaumetopoeinae), Erebidae, Saturniidae and Zygenidae and the spider family Theraphosidae (sub. fam. Theraphosinae) (Battisti *et al.*, 2011). Whereas anchor-like setae are characterized in some larvae of Dermestidae (Insecta: Coleoptera) and Polyxenidae (Myriapoda: Polyxenida) (Eisner *et al.*, 1996). While urticating setae are described to protect from vertebrate predators (Battisti *et al.*, 2011; Bertani and Guadanucci, 2013), detachable setae of dermestids (Nutting and Spangler 1969) and polyxenids (Eisner *et al.*, 1996) work as entangling mechanism against invertebrates. Dermestid detachable setae (hastisetae) are used by the larvae as an active trapping system against arthropod predators (Nutting and Spangler 1969). These specialized setae are almost exclusively prerogative of Megatominae, the most species rich group in the entire family (Hava, 2015). The mechanism of action of hastisetae and their microstructure remains largely obscure and restricted to few case studies (Nutting and Spangler 1969; Mills and Partida, 1976);

furthermore, how the evolution of hastisetae is related to the biological success of the Megatominae remains unresolved. Although information on the impacts of hastisetae on vertebrate predators is lacking, dermestid larvae and Megatominae in particular have been documented as possible source of allergens in human (Mullen and Durden, 2009). Hastisetae and integument fragments carrying them can be contaminants of stored commodities and are present in working and living environments (Hinton, 1945). Hastisetae seem to be involved in allergic reactions through skin contact, ingestion or inhalation; symptoms can vary accordingly to exposition and consist of skin rushes, asthma, conjunctivitis and digestive system inflammation (Gorgojo *et al.*, 2015; MacArthur et al. 2016). Correlation between the presence of hastisetae and the incidence of allergies in humans exists but the scarce and incomplete information available do not allow to consider hastisetae as a major hazard in living and working places. The aim of this review is to synthesize the knowledge on the hastisetae of dermestid beetles, to evaluate their occurrence in the group and their ecological importance, and to assess their possible implications in the human health. Finally, future perspectives on the study of the hastisetae with special emphasis on Megatominae are envisaged.

Survey methodology

In order to compile and then review the most exhaustive literature on hastisetae we performed a careful and reiterated research in Google Scholar and Scopus through the use of keywords such as “hastisetae”, “Dermestidae”, “defense”, “larva”, integrated by the usage the Boolean operators AND, OR, NOT and the use of " " for specific word combinations. The literature not available online has been recovered thanks to Network Inter-Library Document Exchange (NILDE), a web-based software for the service of Document Supply and Inter-Library Loan, managed by the Italian National Research Council. Our research has enabled the collection of more than a hundred publications, of which ninety were considered in the realization of this review. The library created was comprehensive of literature in English, German and French.

Results

Hastisetae, structure and function

Hastisetae (or hastate setae) have been cited in several papers dealing with Dermestidae systematics (Rees, 1943; Kiselyova and McHugh, 2006), species identification (Booth *et al.*

1990; Peacock, 1993), and product contamination (Bousquet, 1990) however, the amount of information available concerning their microstructure (Elbert, 1976; 1978), function (Nutting and Spangler, 1969; Mills and Partida, 1976) and evolution (Zhantiev, 2000; Kiselyova and McHugh, 2006) is quite scarce. These hairs, located on the dorso-lateral surface of the tergites of larvae and pupae (Fig. 1) (Rees, 1943; Beal, 1960; Kiselyova and McHugh, 2006; Kadej, 2012a, Kadej, 2012b; Kadej and Jaroszewicz 2013, Kadej, *et al*. 2013; Kadej and Guziak 2017; Kadej 2017; 2018a, b), are generally quite small with an estimated length, according to the literature, between 150 and 900 µm. Density and distribution of the hastisetae vary substantially not only among genera and species but also among tergites of the same species. The hastisetae of the thoracic segments are generally scattered and in low numbers in respect to the other parts of the body. While the abdominal tergites present a wider distribution pattern, from hastisetae covering the major part the tergal disc up to proper setae fields located at the posterior corners of tergites (i.e. *Reesa*, *Trogoderma*). In some larvae, the hastisetae give origin to real tufts of hairs located on the posterior corners of the terga IV-VII (i.e. *Ctesias*) or V-VII (i.e. *Anthrenus*) (Mroczkowski, 1975; Kadej *et al*. 2013; Kadej 2017; 2018a, b). The hastisetae are inserted in setal sockets on the integument and are connected to the tormogen cell trough the pedicel (Elbert, 1978). The pedicel is the breaking point of the shaft which allows the detachment of the hastiseta (Elbert, 1978). Hastisetae microstructure consists of two main parts: the shaft and the apical head (Fig. 1). The shaft is long and filiform, subcylindrical in section. It is made by repeated modules, from 5 to 77, each of them constituted by one cylindrical segment provided with one wreath of spines/scales in the distal part (Elbert, 1978). These spines/scales are postero-laterally oriented and can vary in number from five to seven (Elbert, 1978). The last module of the shaft is generally bigger and thicker than the previous and can slightly vary in general shape to the others; this structure, however, has not been characterized yet. The head of the seta is a subconical anchor-like, spear-shaped structure subdivided longitudinally in sections; apex blunt (Elbert, 1976; 1978) (Fig. 1). The head consists of five to seven longitudinal, circularly arranged, elements separated from each other by one deep groove, connected to the stem in the upper half by cross-bracing and free in the lower part. The “anchor-like head”, set against the thorns of the last shaft module, is involved in entangling invertebrate body parts (Nutting and Spangler, 1969), functioning as trap for antennae, legs, mouthparts, setae and spines (Mills and Partida, 1976). This structure is apparently species specific, varying in shape and length between taxa (Elbert, 1976; Kiselyova and McHugh, 2006; Kadej *et al.* 2013; Kadej 2017; 2018a). The shaft allows setae to cluster together amplifying the "trapping" effect and the spines increases friction and entangling among hastisetae and between setae and body parts. The combined action of several hastisetae affects small predators (Nutting and Spangler, 1969) and possibly food competitors (Kokubu and Mills, 1980). These setae are hollow (Elbert, 1976; 1978) and could potentially contain proteins or chemical secretion involved in the defense. Hastisetae morphology and distribution, combined together with other characters, constitute a useful tool for species identification (Rees, 1943; Beal, 1960; Peacock, 1993, Kadej, 2012a, b; Kadej and Jaroszewicz 2013, Kadej, *et al.,* 2013; Kadej and Guziak 2017; Kadej 2017; 2018a, b).

Hastisetae in the systematic and ecology of Dermestidae

Dermestidae is a cosmopolitan, comparatively small family of Coleoptera, regarded as 'a well-defined, monophyletic group' (Lawrence and Newton, 1982), consisting of six subfamilies: Orphilinae, Thorictinae, Dermestinae, Attageninae, Trinodinae and Megatominae (Hava, 2015) (Fig. 2). Dermestids are homogeneous only in general appearance, hiding a complex and rich diversity in term of morphological, ecological and ethological aspects. Specific traits and evolutionary tendencies could be observed in several lineages, associated to ecological groups and niches (Zhantiev, 2009); these traits can be observed at adult (Zhantiev, 2000) and larval stage (Kiselyova and McHugh, 2006). Orphilinae are mycetophagous, with sclerotized burrowing larvae (Lenoir *et al*., 2013). Thorictinae are myrmecophilous and larvae protection is provided by the associated ant species (Lenoir *et al*., 2013). Dermestinae, the basal group of the "necrophagous clade" (*sensu* Zhantiev, 2009), have larvae feeding on fresh or relatively humid animal remains (over 15% in water content) (Zhantiev, 2009). Since Dermestinae food resource is highly perishable, the larvae develop rapidly and persist only for short periods. The oblong, sub-cylindrical and sclerotized larvae of this subfamily can dig through the feeding substrate and live in butyric fermentation condition, under animal remains. It's is plausible that the absence of hastisetae on larval tergites is directly attributable to their burrowing lifestyle. Anchor-like detachable setae could be disadvantageous to move within the substrate. Hastisetae would in fact create friction and would be systematically lost, requiring an important energy expenditure necessary for their replacement. The defensive strategy Dermestinae is based on the fast escape behavior and the sclerotized integuments of the body. The larvae specifically require the pupation chamber to molt and they are capable to dig into soil and/or substrate in case of lacking suitable places where to hide. The pupae of this subfamily present gin-traps on the integuments, as a defensive system against predators (Hinton, 1946; Kiselyova and McHugh, 2006) (Fig. 2). Attageninae have burrowing larvae associated to wood dust, fissures of rocks and sandy environments and feed of insects and other arthropods remains; the larvae are oblong-fusiform with integuments covered of three different kind of hairs (Zhantiev, 2000; Kiselyova and McHugh, 2006). The larvae show a fast escape behavior, similar to Dermestinae. Attageninae prefer to pupate in hidden niches and are usually present gin-traps (Zhantiev, 2000). Trinodinae are inquiline of animals' nets: rodent borrows with larvae phoretic on mammal (Zhantiev, 2009) or larvae associated to spider nests (Beal, 1959; Kadej, 2011). The hastisetae, with the single exception of the genus *Trinodes* (Trinodinae), in which modified hastisetae are described (Kiselyova and McHugh, 2006), are prerogative of the Megatominae larvae and they are strictly associated to larval and pupal morphology and behavior (Kiselyova and McHugh, 2006; Zhantiev, 2009) (Fig. 2). Megatominae is the richest in species subfamily within Dermestidae and its biological success is most probably attributable to the hastisetae occurrence. Amber fossils indicate that hastisetae morphology is highly conserved and remained virtually unchanged since late Cretaceous (Poinar and Poinar, 2016). This group shows a remarked investment on hastisetae as a defensive tool (Nutting and Spangler 1969; Mills and Partida, 1976), exploiting their resistance and durability over time to protect both larvae and pupae (Kiselyova and McHugh, 2006; Zhantiev, 2009). Megatominae is the clade within the xerophilous necrophagous dermestids (*sensu* Zhantiev, 2009), which can survive on low-water food resources, especially chitinous and keratinous remains (Armes, 1990; Beal, 1998; Zhantiev, 2009). These substrates are capable to stand in the environment for a long time but the poor nutrients prolong the duration of larval development, with major implications on morphology, ethology and defensive behavior. Lengthening of the larval phase and its persistence in the environment for a long time has promoted the evolution of morphological and ethological features in Megatominae that otherwise would have been disadvantageous in a different lifestyle. The inability of the larvae to delve into the living substrate (Zhantiev, 2009) favored the evolution of defensive structures (hastisetae) with low energy investment for their synthesis and to remain functional even after being dispersed in the environment. Over time, energetic investment in cuticularized integuments in larvae and gin-traps in pupae shifted to the morphology of hastisetae and its defense mechanisms. Hastisetae provide protection in both larvae and pupae, favoring a positive energy trade-off in larval development. All the larvae of this subfamily are stout, feebly sclerotized, slow moving and present an aggressive-non escaping defensive behavior (Kiselyova and MchHugh, 2006). In a disturbance, the larva stops moving, arches its body and spread the hastisetae, frequently from the posterior part of the body where it is densely packed with hastisetae towards the stimulus (Kiselyova and MchHugh, 2006). In general, Megatominae do not make pupation chambers or hide, but simply pupate where they have been feeding. Pupae completely lack gin-traps and remain protected inside the last larval exuvia, completely covered in hastisetae (synapomorphy of Trinodinae + Megatominae) (Kiselyova and McHugh, 2006) (Fig. 2). Megatominae have been able to adapt against interspecific and intraspecific competition for food resources. They evolved specialized larvae that are capable to use a wide range of trophic resources that are poor in nutrients and water content in association with an energy-efficient and effective defensive mechanism. A common trait associated with the evolution of the hastisetae in the dermestids is, in the necrophagous clade, the transition from scavenger habits of adults to anthophily or aphagy (Zhantiev, 2009) (Fig. 2).

Hastisetae and human health

The capability to feed on a wide range of food resources scarce in water content and to resist to prolonged starvation makes Megatominae larvae the perfect candidate to inhabit public and private spaces such as houses and working environments. In addiction, due to their slow movements and cryptic behavior these larvae result difficult to detect and remove. For this reason, some species are now synanthropic and cosmopolitan (Bouchet *et al.,* 1996; Gamarra *et al.,* 2009), having been spread all over the world with trade. These species became serious pests, causing considerable loss and damage to stored goods of both animal and plant origin (Hinton, 1945; Burges, 1959; Kantack and Staples, 1969; Mroczkowski, 1975; Beal, 1991; Veer *et al*., 1991a, b; Veer and Rao, 1995; Veer *et al*., 1996; Imura, 2003; Rajendran and Hajira Parveen, 2003; Lawrence and Slipinski, 2010) and to objects of organic origin in museums of cultural and natural history (Jurecka, 1987; Zaitseva, 1987; Armes, 1988; Bousquet, 1990, Pinniger and Harmon, 1999; Stengaard Hansen *et al*., 2012; Quarner, 2015). The hastisetae released by the larva throughout its entire development and abandoned in the environment in association to the exuviae are an important contaminant in dwelling, public spaces as well as food stuff (Gorham, 1979; 1989; Burgess, 1993) and can contribute as allergens in humans (Wiseman *et al*., 1959; Johansson *et al.,* 1985; Baldo and Panzani, 1988; Burgess, 1993; Gorgojo *et al*., 2015; McArthur *et al*., 2016): chitin, likely the main constituent of the hastisetae, is in fact a powerful and widely recognized allergen, and its interaction with Th2 lymphocytes and human chitinases enhances the inflammation process (Brinchmann *et al.,* 2011; Bucolo *et al.,* 2011; Mack *et al.,* 2015). However, it is still unclear whether the inflammatory effect of the hastisetae is attributable to the mechanical action of the seta and its penetration through the epithelia or if it is associated to the presence of specific molecules capable to start an immunological reaction. Hastisetae have been directly linked to occupational diseases in working environments (Loir and Legagneux 1922; Renaudin, 2010), especially when processing organic materials such flour, wool, silk and other commodities (Veer *et al*., 1996; Brito *et al*., 2002), or stored objects of organic origin in museums and art galleries (Siegel *et al*. 1991). The exposure to and inhalation of hastisetae, even in the form of dust, are reported to cause rhinoconjunctivitis (Brito *et al.*, 2002) and asthma (Cuesta-Herranz *et al*., 1997; Brito *et al*., 2002; Bernstein *et al*., 2009). Megatominae are also one of the arthropod groups most commonly recorded inside houses (Gamarra *et al.,* 2009; Bertone *et al*., 2016; Madden *et al.* 2016); the larvae persist in these environments for months, even for years, feeding on food (Gorham, 1979; 1989; Hirao, 2000), pet food (Rudolph *et al.,* 1981), dust, insect remains and clothes, especially wool fabric (Bouchet *et al.,* 1996). This prolonged presence inside houses together with the persistence of the hastisetae in the environment greatly increase the possibility for the humans to come into contact and develop a sensitization to these detachable hairs (Wiseman *et al*., 1959; Kaufman *et al.*, 1986; Burgess, 1993; Jakubas-Zawalska *et al.,* 2016). The direct exposure of hastisetae to the skin, maybe due to contaminated bed or clothes, causes severe dermatitis (Sheldon and Johnston, 1941; Cormia *et al.*, 1945; Okamura, 1967; Ahmed *et al.*, 1981; Alexander, 1984; Johansson *et al.,* 1985; Southcott, 1989; Horster *et al.*, 2002; Zanca *et al.*, 2012; Hoverson *et al*., 2015; McArthur *et al*., 2016), while the prolonged inhalation can determine the insurgence of asthma (Cuesta-Herranz *et al.*, 1997; Brito *et al.*, 2002; Bernstein *et al*., 2009). Food contamination and hastisetae ingestion has been proved to cause the inflammation of the digestive system, manifesting through nausea, fever, diarrhea (Hirao, 2000), proctitis and perianal itching (Krause *et al.*, 1998). Unusual, and apparently asymptomatic findings of hastisetae have been done on sputum (Johnson and Batchelor, 1989) and cervical specimens (Bechtold *et al.*, 1985; Bryant and

Maslan, 1994; Williamson *et al*., 2005). The incidence of pathologies associated with Dermestidae and Megatominae in particular, seems to be considerably reduced in recent decades probably due to the increased degree of attention regarding the presence of contaminants in food and the marked improvement in the processes of conservation and storage of raw materials; the development of adequate plans for monitoring and management of pests and the general improvement in the quality of life of people associated with greater healthiness of the houses have contributed further to the imitation of the impact (Athanassiou and Arthur, 2018). However, there is also the possibility that many domestic cases of exposure to hastisetae, especially in the case of skin rushes (erythematobullous reactions) may be under-recognized and underdiagnosed, due to similar effects to attacks by other arthropods (Burgess, 1993; McArthur *et al*., 2016). Furthermore, almost all the cases reported in the medical literature regard developed countries while the effect of hastisetae on human health in developing countries remains almost obscure and widely understudied. Undoubtedly, a better knowledge of the inflammation caused by hastisetae would allow the formation of medical personnel able to provide early diagnosis and to administer quickly appropriate therapies. Moreover, a close collaboration between occupational physicians, entomologists and immunologists could be of great help for the development of new surveillance programs and new health and safety guidelines for workers and people most at risk.

Conclusions

The scant information about the fine morphology and the ecological roles of hastisetae, and their implications in human health opens a whole horizon of research possibilities. Hastisetae morphology is undoubtedly the starting point for any future study. The characterization of hastisetae through electron microscopy and micro-CT is the basic and fundamental step to understand their functional morphology. The identification of specific morphological traits in the hastisetae will help to solve Megatominae systematics, highlighting the evolution of these structures in relation to phylogeny and biology. A detailed knowledge of hastisetae morphology will allow us to understand the defensive mechanism and if it acts similarly in all Megatominae. Comparing reactions of different predators to hastisetae will be useful to evaluate the different effects and particularly if this defensive system is primarily directed towards invertebrates and/or to vertebrates. Are humans or other vertebrates possible targets of hastisetae, and if so what are the causes of the unpleasant side-effects in humans? Is it the penetration of these setae trough epithelia the main cause of inflammation and are there any particular substance inducing the reaction, as it has been showed in Lepidoptera? Chemical analysis of secretions can identify and characterize the compounds responsible of the inflammation in humans and clarify their possible role as adjuvants in defense against the threats. Understanding the causes of allergic responses in humans will allow the development of specific medical therapies. Hastisetae could become an important addition in species identification, with relevant application in forensic entomology and pest management on stored products. Furthermore, the creation of a molecular fingerprint based on hastisetae content can aid in developing tools to detect insect fragments in contaminated stored products, especially food.

Acknowledgements

Thanks to Mizuki Uemura (Università degli Studi di Padova) for language editing, to Paolo Paolucci (Università degli Studi di Padova) and Michał Kukla (University of Wrocław) for images realization, to Antonio Masi (Università degli Studi di Padova) and three anonymous referees for useful suggestion provided during manuscript realization.

References

Ahmed R, Moy R, Barr R, Prince Z. 1981. Carpet beetle dermatitis. *Journal of the American Academy of Dermatology* 5: 428-432. 10.1016/S0190-9622(81)70104-X

Alexander JD. 1984. *Arthropods and human skin*. London: Springer.

Armes NJ. 1988. The seasonal activity of *Anthrenus sarnicus* Mroczkowski (Coleoptera: Dermestidae) and some other beetle pests in the museum environment. *Journal of Stored Products Research* 24: 29-37. 10.1016/0022-474X(88)90006-9

Armes NJ. 1990 The biology of *Anthrenus sarnicus* Mroczkowski (Coleoptera: Dermestidae): I. Egg and larval development. *Journal of Stored Products Research* 26: l-22. 10.1016/0022-474X(90)90033-O

Athanassiou C, Arthur F. 2018. *Recent Advances in Stored Product Protection*. Springer, Berlin, Heidelberg. 10.1007/978-3-662-56125-6

Ayres S, Mihan R. 1967. Delusions of parasitosis caused by carpet beetles. *JAMA* 199: 675. 10.0.3.233/jama.1967.03120090117036

Baldo BA, Panzani RC. 1988 Detection of IgE Antibodies to a Wide Range of Insect Species in Subjects with Suspected Inhalant Allergies to Insects. International Archives of Allergy and Immunology 85:278–287 10.1159/000234518

Barth FG. 2004. Spider mechanoreceptors. *Current Opinion in Neurobiology* 14: 415-422. 10.1016/j.conb.2004.07.005

Battisti A, Holm G, Fagrell B, Larsson S. 2011. Urticating hairs in arthropods: their nature and medical significance. *Annual Review of Entomology* 56: 203-220. 10.1146/annurev-ento-120709-144844

Beal RS. 1959. Notes on the biology and systematics of the dermestid beetle genus *Apsectus* with descriptions of two new species. *Annals of the Entomological Society of America* **52**: 132-137. 10.1093/aesa/52.2.132

Beal RS. 1960. Descriptions, biology, and notes on the identification of some *Trogoderma* larvae (Coleoptera, Dermestidae). United States Department of Agriculture. *Technical Bulletin* 1228: 1-26.

Beal RS. 1991. Dermestidae (Bostrichoidea) (including Thorictidae, Thylodriidae). In: Stehr, FW, ed. *Immature Insects. Vol. 2*. Dubuque: Kendall/Hunt, IA, 434-439.

Beal RS. 1998. Taxonomy and biology of nearctic species of *Anthrenus* (Coleoptera: Dermestidae). *Transactions of the American Entomological Society* 124: 271-332.

Bechtold E, Staunton CE, Katz SS. 1985. Carpet beetle larval parts in cervical cytology specimens. *Acta Cytologica* 29: 345-352.

Bereiter-Hahn J, Matoltsy AG, Richards KS. 1984. *Biology of the integument, Vol. 1. Invertebrates*. Berlin: Springer-Verlag.

Bernstein JA, Morgan MS, Ghosh D, Arlian L. 2009. Respiratory sensitization of a worker to the warehouse beetle *Trogoderma variabile*: An index case report. *Journal of Allergy and Clinical Immunology* 123: 1413-1416. 10.1016/j.jaci.2009.04.006

Bertani R, Guadanucci JPL. 2013. Morphology, evolution and usage of urticating setae by tarantulas (Araneae: Theraphosidae). *Zoologia* 30: 403-418. 10.1590/S1984-46702013000400006

Bertone MA, Leong M, Bayless KM, Malow TLF, Dunn RR, Trautwein MD. 2016. Arthropods of the great indoors: characterizing diversity inside urban and suburban homes. *PeerJ* 4:e1582 h10.7717/peerj.1582

Booth RG, Cox ML, Madge RB. 1990.*Guides to insects of importance to man. No. 3. Coleoptera*. Wallingford: CAB International.

Bouchet F, Lavaud F, Deschamps F. 1996. Coléoptères synanthropes des moquettes et autres textiles domestiques. *Revue Française d'Allergologie et d'Immunologie Clinique* 36: 765-770. 10.1016/S0335-7457(96)80063-3

Bousquet Y. 1990. *Beetles associated with stored products in Canada: An identification guide*. Ottawa: Canadian Government Publishing Centre.

Brinchmann BC, Bayat M, Brøgger T, Muttuvelu DV, Tjønneland A, Sigsgaard T. 2011. A possible role of chitin in the pathogenesis of asthma and allergy. Annals of Agricultural and Environmental Medicine 18: 7–12.

Brito F, Mur P, Barber D, Lombardero M, Galindo P, Gómez E, Borja J. 2002. Occupational rhinoconjunctivitis and asthma in a wool worker caused by Dermestidae spp. *Allergy* 57: 1191-1194. 10.1034/j.1398-9995.2002.23676.x

Bryant J, Maslan A. 1994. Carpet beetle larval parts in pap smears: report of two cases. *Southern Medical Journal* 87:763-764.

Bucolo C, Musumeci M, Musumeci S, Drago F. 2011. Acidic mammalian chitinase and the eye: implications for ocular inflammatory diseases. *Frontiers in Pharmacology* 2: 1-4. 10.3389/fphar.2011.00043

Burges HD. 1959. Studies on the dermestid beetle, *Trogoderma granarium* Everts: Ecology in malt stores. *Annals of Applied Biology* 47: 445-462. 10.1111/j.1744-7348.1959.tb07278.x

Burgess I. 1993. Allergic reaction to Arthropods. *Indoor and Built Environment* 2: 64-70. 10.1177%2F1420326X9300200202

Cormia FE., Lewis GM. 1948. Contact dermatitis from beetles, with a report of a case due to the carpet beetle (*Anthrenus scrophulariae*). *New York state journal of medicine* 48: 2037l-2039.

Cuesta-Herranz J, de las Heras M, Sastre J, Lluch M, Fernández M., Lahoz C, Alvarez-Cuesta E. 1997. Asthma caused by Dermestidae (black carpet beetle): A new allergen in house dust. *Journal of Allergy and Clinical Immunology* 99: 147-149. 10.1016/S0091-6749(97)70311-7

Eisner T, Eisner M, Deyrup M. 1996. Millipede defense: use of detachable bristles to entangle ants. *Proceedings of the National Academy of Sciences of the United States of America* 93: 10848-10851. 10.1073/pnas.93.20.10848

Elbert A. 1976. Elektronenmikroskopische untersuchungender pfeilhaare verschiedener arten der Anthreninae (Col. Dermestidae). *Anzeiger Schadlingskunde Pflanzenschutz Umweltschutz* 49: 81-83. 10.1007/BF01985639

Elbert A. 1978. Die pfeilhaare der Megatominae (Col., Dermestidae): ein abwehrsystem. *Anzeiger Schadlingskunde Pflanzenschutz Umweltschutz* 51: 109-110. 10.1007/BF01903308

Felgenhauer EB, Watling L, Thistle AA. 1989. *Functional morphology of feeding and grooming in crustacea*. (Crustacean Issues 6. General editor: Frederick R. Schram). Rotterdam: Brookfield, A. A. Bakema.

Gamarra P, Outerelo R, Hernández JM. 2009. Coleópteros en las viviendas de la zona centro de España (Insecta, Coleoptera). Boletín de la Real Sociedad Española de Historia Natural. Seccion Biologica 103: 87-101.

Garm A, Watling L. 2013. The crustacean integument: setae, setules, and other ornamentation. In: Watling L, Thiel M, ed. *Functional Morphology and Diversity*. *The Natural History of the Crustacea series*, *volume 1*. Oxford: Oxford University Press, 167-198

Garm A. 2004a. Mechanical functions of setae from the mouth apparatus of seven species of decapod crustaceans. *Journal of Morphology* 260: 85-100. 10.1002/jmor.10213

Garm A. 2004b. Revising the definition of the crustacean seta and setal classification systems based on examinations of the mouthpart setae of seven species of decapods. *Zoological Journal of the Linnaean Society* 142: 233-252. 10.1111/j.1096-3642.2004.00132.x

Gorgojo IE, De Las Heras M, Pastor C, Cuesta Herranz J, Sanz Maroto A. 2015. Allergy to Dermestidae: A new indoor allergen? *Journal of Allergy and Clinical Immunology* 135: Supplement, Page AB105. 10.1016/j.jaci.2014.12.1278

Gorham JR. 1979. The significance for human health of insects in food. *Annual Review of Entomology* 24: 209-224. 10.1146/annurev.en.24.010179.001233

Gorham JR. 1989. Foodborne Filth and Human Disease. *Journal of Food Protection* 52: 674-677. 10.4315/0362-028X-52.9.674

Hava J. 2015. World catalogue of Insects. Volume 13. Dermestidae (Coleoptera). Leiden/Boston: Brill.

Hinton HE. 1945. *A Monograph of the Beetles Associated with Stored Products. Vol. 1.* London: British Museum (Natural History).

Hinton HE. 1946. The "gin traps" of some beetle pupae; a protective device which appears to be unknown. *Transactions of the Entomological Society of London* 97: 473-496. 10.1111/j.1365-2311.1946.tb00273.x

Hirao M. 2000. Warehouse Beetle, *Trogoderma variabile* Baillon (Coleoptera: Dermestidae), Associated with Stored Product Pest and Human Illness. *Urban Pest Management* 22: 8-21. [in Japanese]

Horster S, Prinz JC, Holm N, Wollenberg A. 2002. *Anthrenus*-dermatitis. Hautarzt, 53: 328-331.

Hoverson K, Wohltmann WE, Pollack RJ, Schissel DJ. 2015. Dermestid dermatitis in a 2-Year-old girl: case report and review of the literature. *Pediatric Dermatology* 32(6): 228-233. 10.1111/pde.12641

Hultgren KM, Stachowicz JJ. 2008. Alternative camouflage strategies mediate predation risk among closely related co-occurring kelp crabs. *Oecologia* 155, 519-528. 10.1007/s00442-007-0926-5

Imura O. 2003. Insect pests of stored products in East Asia (Japan and Korea). In: Prakash A, Rao J, Jayas DS, Allotey J, ed. *Insect Pests of Stored Products: A Global Scenario*. Cuttack: Applied Zoologists Research Association, 203-216.

Jakubas-Zawalska J, Asman M, Kłyś M, Solarz K. 2016. Sensitization to *Sitophilus granarius* in selected suburban population of South Poland. *Journal of Stored Products Research* 69: 1-6. 10.1016/j.jspr.2016.05.006,

Johansson SG, Wüthrich B, Zortea-Caflisch C. 1985. Nightly asthma caused by allergens in silk-filled bed quilts: clinical and immunologic studies. *Journal of Allergy and Clinical Immunology* 75: 452-459 10.1016/S0091-6749(85)80017-8

Johnson FP, Batchelor J. 1989. Carpet beetle larval hairs in a sputum cytology specimen. *Acta Cytologica* 33:286.

Jurecka W, Gebhart W, Mainitz M. 1987. *Anthrenus* sp. The paraffin block eater bug. *The American Journal of Dermatopathology* 9: 204-207.

Kadej M, Guziak J. 2017. Description of the larva of *Globicornis emarginata* (Gyllenhal, 1808) (Dermestidae: Megatominae). *Annales Zoologici* 67: 749-757. 10.3161/00034541ANZ2017.67.4.010

Kadej M, Jaroszewicz S. 2013. Detailed morphological description of the mature larva of *Globicornis corticalis* (Eichhoff, 1863) (Dermestidae: Megatominae) with comparisons to related species. *Zootaxa* 3686: 556-564. 10.11646/zootaxa.3686.5.4

Kadej M. 2012a. Detailed morphological description of the mature larva *of Anthrenus latefasciatus*Reitter, 1892 (Dermestidae: Megatominae: Anthrenini) with comparisons to related species. *Zootaxa* 3270: 31-40. 10.11646/zootaxa.3270.1.2

Kadej M. 2012b. Detailed description of the morphology of the last instar larva of *Trogoderma megatomoides* Reitter, 1881 (Dermestidae: Megatominae: Megatomini) with comparison to related species. *Journal of the Kansas Entomological Society* 85: 5-13. 10.2317/JKES110707.1

Kadej M. 2017. Larva and pupa of *Megatoma* (s. str.) *undata* (Linnaeus, 1758) with remarks on biology and economic importance (Coleoptera, Dermestidae). *Zookeys* 698: 54-79. 10.3897/zookeys.698.14049

Kadej M. 2018a. Contribution to knowledge of the immature stages of Dermestidae with special emphasis on the larval morphology of the genus *Anthrenus* Geoffroy, 1762 (Megatominae: Anthrenini). Poznan: Polish entomological Monographs.

Kadej M. 2018b. *Larva* and *pupa* of *Ctesias* (*s.str.*) *serra* (*Fabricius*, *1792*) with *remarks* on *biology* and *economic importance*, and *larval comparison* of *co-occurring genera* (*Coleoptera*, *Dermestidae*). *ZooKeys* 758: 115-135. 10.3897/zookeys.758.24477

Kadej M. Jaroszewicz, S, Tarnawski D. 2013. Comparative morphology and biology of mature larvae in the genus *Anthrenus* (Dermestidae: Megatominae: Anthrenini) with comparisons to related species. *Annales de la Société Entomologique de France* 49: 244-256. 10.1080/00379271.2013.845472

Kantack BH, Staples R. 1969. The biology and ecology of *Trogoderma glabrum* (Herbst) in stored grains. Lincoln: *Research Bulletin 232. Lincoln, Nebraska,* University of Nebraska.

Kaufman GL, Bado BA, Tovey ER. 1986. Inhalant allergy following occupational exposure to blow flies. Clinican and experimental Allergy 16: 65-71. **10.1111/j.1365-2222.1986.tb01955.x**

Keil TA, Steinbrecht RA. 1984. Mechanosensitive and olfactory sensilla of insects. In: King RC, Akai H, ed. *Insect Ultrastructure, Vol. 2*. New York: Plenum Press, 477-516.

Keil TA. 1997. Functional morphology of insect mechanoreceptors. *Microscopy Research and Technique* 39: 506-531 10.1002/(SICI)1097-0029(19971215)39:6%3C506::AID-JEMT5%3E3.0.CO;2-B

Kiselyova T, McHugh JV. 2006. A phylogenetic study of Dermestidae (Coleoptera) based on larval morphology. *Systematic Entomology* 31: 469-507. 10.1111/j.1365-3113.2006.00335.x

Kokubu H, Mills RS. 1980. Susceptibility of thirteen stored product beetles to entanglement by *Trogoderma* hastisetae. *Journal of Stored Products Research* 16: 87-92. 10.1016/0022-474X(80)90002-8

Krause R, Reisinger EC, Zenahlik P, Krejs GJ. 1998. The beetle *Anthrenus verbasci* causing proctitis and perianal itching. *Scandinavian* Journal of *Gastroenterology* 33: 894-895.

Labarque FM., Wolff JO, Michalik P, Griswold CE. Ramirez MJ. 2017. The evolution and function of spider feet (Araneae: Arachnida): multiple acquisitions of distal articulations. *Zoological Journal of the Linnean Society* 181: 308-341. 10.1093/zoolinnean/zlw030

Lawrence JF, Slipinski A. 2010. Dermestidae Latreille, 1804. In: Leschen RAB, Beutel RG, Lawrence JF, ed. *Coleoptera, beetles. Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformiapartim)*. Berlin: Walter de Gruyter, 198-206.

Lawrence JF. Newton AF. 1982. Evolution and classification of beetles. *Annual Review of Ecology and Systematics* 13: 261-290. 10.1146/annurev.es.13.110182.001401

Lenoir A, Háva J, Hefetz A, Dahbi A, Cerdá X, Boulay R. 2013. Chemical integration of *Thorictus* myrmecophilous beetles into *Cataglyphis* ant nests. *Biochemical Systematics and Ecology* 51: 335-342. 10.1016/j.bse.2013.10.002

Loir A, Legagneux H. 1922. Accidents du travail occasionnés par les coléoptères. *Bulletin de l'Académie nationale de médecine* 88: 68-72.

MacArthur KM, Richardson V, Novoa RA, Stewart CL, Rosenbach M. 2016. Carpet beetle dermatitis: a possibly under-recognized entity. *International Journal of Dermatology* 55: 577-579. 10.1111/ijd.12952

Mack I, Hector A, Ballbach M, Kohlhäufl J, Fuchs KJ, Weber A, Mall MA, Hartl D. 2015. The role of chitin, chitinases, and chitinase-like proteins in pediatric lung diseases. Molecular and Cellular Pediatrics 2: 1-8. 10.1186/s40348-015-0014-6

Madden AA, Barberan A, Bertone MA, Menninger HL, Dunn R, Fierer N. 2016. The diversity of arthropods in homes across the United States as determined by environmental DNA analyses. *Molecular Ecology* 25: 6214–6224 doi: 10.1111/mec.13900.

Mills RB, Partida GJ. 1976. Attachment mechanisms of *Trogoderma* hastisetae that make possible their defensive function. *Annals of the Entomological Society of America* 69: 29-33. 10.1093/aesa/69.1.29

Mullen G, Durden I. 2009. *Medical and Veterinary Entomology, Second Edition*. London: Academic.

Mroczkowski M. 1975. *Dermestidae, Skórnikowate (Insecta:* Coleoptera). *Fauna Polski. Tom 4*. Warsaw: Polska Akademia Nauk. [In Polish]

Neville C. 1975. *Biology of the arthropod cuticle*. Berlin: Springer Verlag.

Nutting WL, Spangler HG, 1969. The hastate setae of certain dermestid larvae: an entangling defense mechanism. *Annals of the Entomological Society of America* 62: 763-769.

Okumura GT. 1967. A report of canthariasis and allergy caused by *Trogoderma* (Coleoptera: Dermestidae). *California Vector Views* 14: 19-22.

Pauli GJ, Bessot C. 2009.Rare indoor allergens. *European Annals of Allergy and Clinical Immunology* 41: 99-105. 10.1053/ai.1994.v94.a56012

Peacock ER. 1993. *Adults and larvae of hide, Larder and carpet beetles and their relatives (Coleoptera: Dermestidae) and of derodontid beetles (Coleoptera: Derodontidae), Handbooks for the Identification of British Insects.* London: Royal Entomological Society of London.

Perez-Miles F, Montes De Oca L, Postiglioni R, Costa FG. 2005. The stridulatory setae of *Acanthoscurria suina* (Araneae, Theraphosidae) and their possible role in sexual communication: an experimental approach. *Iheringia* 95: 365-371. 10.1590/S0073-47212005000400004

Pinniger DB, Harmon JD. 1999. Pest management, prevention and control. In: Carter D, Walker A, eds. *Care and Conservation of Natural History Collections*. Oxford: Butterwoth Heinemann, 152 - 176.

Poinar GO Jr, Poinar R. 2016. Ancient hastisetae of Cretaceous carrion beetles (Coleoptera: Dermestidae) in Myanmar amber. *Arthropod Structure & Development* 45: 642-645. 10.1016/j.asd.2016.10.012

Querner P. 2015. Insect pests and integrated pest management in museums, libraries and historic buildings. *Insect,* 6: 595-607. 10.3390/insects6020595

Rajendran S, Hajira Parveen KM. 2005. Insect infestation in stored animal products. *Journal of Stored Products Research* 41: 1-30. 10.1016/j.jspr.2003.12.002

Rees BE. 1943. Classification of the Dermestidae (larder, hide and carpet beetles) based on larval characters, with a key to North American genera. *United States Department of Agriculture, Miscellaneous Publications* 511: 1-18.

Renaudin J-M. 2010. *Allergie aux insects piqueurs et maladie professionnelle*. *Revue Française d'Allergologie* 50: 137-140.

Rudolph R, Blohm B., Kunkel G, Mast H, Muckelmann R, Schniggenberg E. 1981. Futtermittelallergien bei Tierhaltern. In: Christophers E, Goos M eds. *XXXII. Tagung gehalten in Westerland/Sylt vom 16. bis 20. September 1980. Verhandlungen der Deutschen Dermatologischen Gesellschaft, vol 32*. Springer, Berlin, Heidelberg 10.1007/978-3-642-81671-0_42

Sheldon JM, Johnston JH. 1941. Hypersensitivity to beetles (Coleoptera). Report of a case. *Journal of Allergy and Clinical Immunology* 12: 493-494. 10.1016/S0021-8707(41)90228-9

Siegel S, Lee N, Rohr A, Ank B, Rachelefsky G, Spector S, Siegel J. 1991. Evaluation of dermestid sensitivity in museum personnel. *Journal of Allergy and Clinical Immunology 1:190*. 10.1016/0091-6749(91)91488-F

Southcott RV. 1989. Injuries from Coleoptera. *Medical Journal* of *Australia* 151: 654-659. 10.5694/j.1326-5377.1989.tb139642.x

Steinbrech RA. 1984. Arthropoda: chemo-, thermo, and hygroreceptors. In: Bereiter-Hahn J, Matoltsy AG, Richards KS, ed. *Biology of the integument, Vol 1. Invertebrates*. Berlin: Springer Verlag, 532-553.

Stengaard H, L., Akerlund M, Grontoft T, Rhyl-Svendsen M, Schmidt A, Bergh J, Vagn Jensen, K. 2012. Future pest status of an insect pest in museums, *Attagenus smirnovi*: distribution and food consumption in relation to climate change. *Journal of Cultural Heritage* 13: 22l-27. 10.1016/j.culher.2011.05.005

Veer V, Negi BK, Rao KM. 1996. Dermestid beetles and some other insect pests associated with stored silkworm cocoons in India, including a world list of dermestid species found attacking this commodity. *Journal of Stored Products Research* 32: 69-89. 10.1016/0022-474X(95)00032-3

Veer V, Prasad R, Rao KM. 1991a. Taxonomic and biological notes on *Attagenus* and *Anthrenus* spp. (Coleoptera: Dermestidae) found damaging stored woollen fabrics in India. *Journal of Stored Products Research* 27: 189-198. 10.1016/0022-474X(91)90044-D

Veer V, Prasad R, Rao KM. 1991b. Studies on insect proofing of woollen fabrics with EulanWA New and permethrin. In: Ramachandran PK, Sukumaran D, Rao SS, ed. *Entomology for Defense Services. Proceedings of the Symposium, September 1990*. Gwalior, India, 244-253.

Veer V, Rao KM. 1995. Taxonomic and biological notes on three *Attagenus* spp. (Coleoptera: Dermestidae) not previously recorded as pests of stored woollen fabrics in India. *Journal of Stored Products Research* 31: 211-219. 10.1016/0022-474X(95)00016-Z

Williamson BA, Nicolas MM, Nayar R. 2005. Unusual finding in cervical smear. *Archives of Pathology & Laboratory Medicine* 129: 809-809.

Winterton S. 2009. *Scales and setae*. In: Resh VH, Cardé RT, ed. *Encyclopedia of Insects, 2nd ed*. 901-904.

Wiseman RD, Woodin WG, Miller HC, Myers MA. 1959. Insect allergy as a possible cause of inhalant sensitivity. *Journal of Allergy* 30: 191-197.

Zaitseva GA. 1987. Protection of museum textiles and leather against the dermestid beetle (Coleoptera, Dermestidae) by means of antifeedants. *Studies in Conservation* 32: 176-180. 10.1179/sic.1987.32.4.176

Zanca A, Zanca A, Cassisa A. 2012. A case of carpet beetle dermatitis. *Giornale Italiano di Dermatologia e Venereologia* 147: 216-218.

Zeledón R. Valerio CE, Valerio JE. 1973. The camouflage phenomenon in several species of Triatominae (Hemiptera, Reduviidae). *Journal of medical Entomology* 10: 209-211. 10.1093/jmedent/10.2.209

Zhantiev RD. 2000. Classification and phylogeny of dermestids (Coleoptera, Dermestidae). *Entomological Review* 80: 1115–1129.

Zhantiev, R. D. 2009. Ecology and classification of dermestid beetles (Coleoptera, Dermestidae) of the Palearctic fauna. *Entomological Review* 89: 157-174. 10.1134/S0013873809020055

Figure 1

Hastisetae structure and distribution on Megatominae larvae (general scheme):

(a). Example of Megatominae larva (Megatoma undata (Linnaeus, 1758)), dorsal view. T1-T3: thoracic segments; A1-A8: abdominal segments. (b). Tuft of hastisetae on abdominal segments. (c). Hastisetae, lateral view. (d). Head of the hastiseta (subconical anchor-like, spear-shaped head). Image credit: Paolo Paolucci, Michał Kukla.

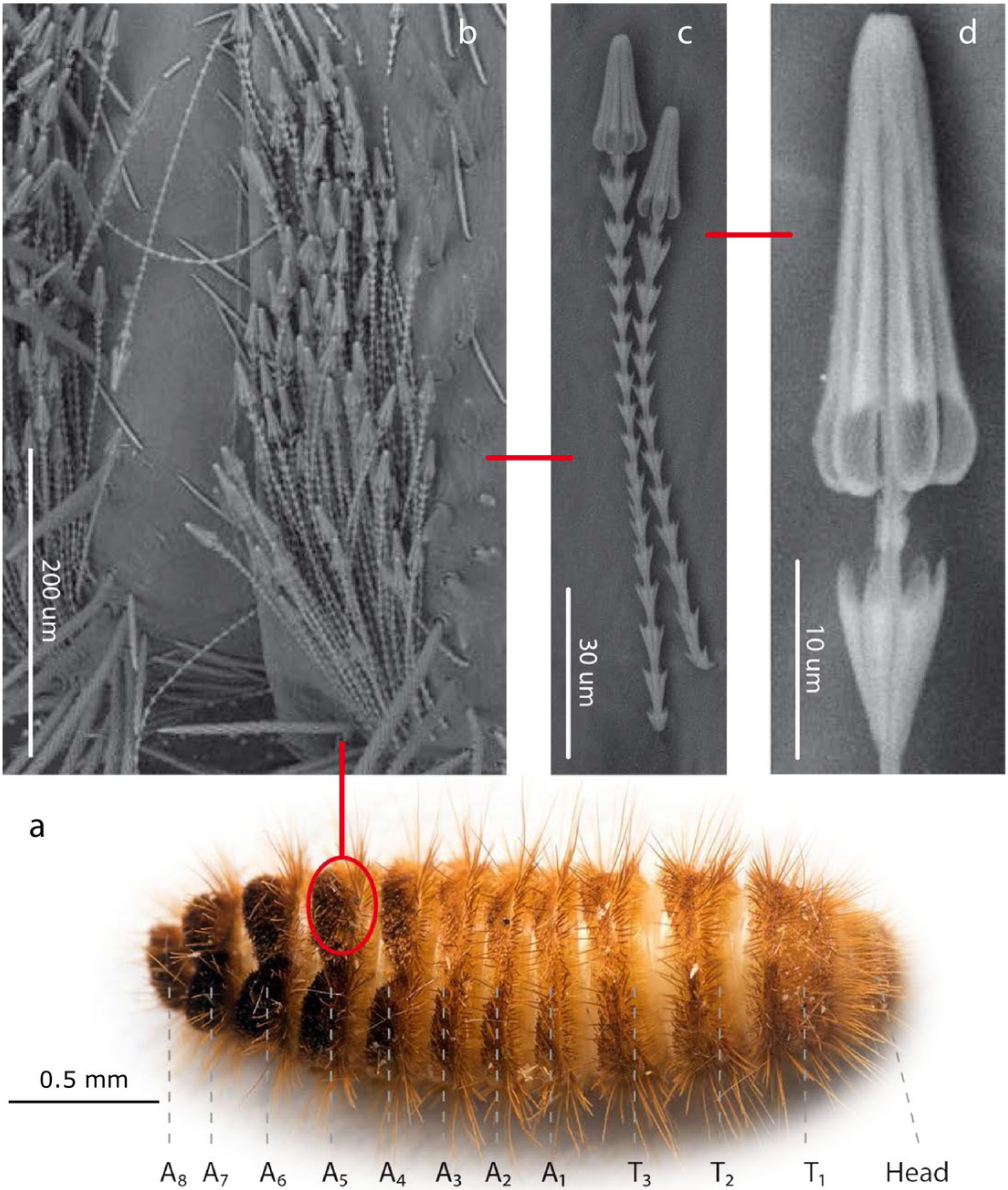
b
200 um
c
30 um
d
10 um
a
0.5 mm
A8 A7 A6 A5 A4 A3 A2 A1 T3 T2 T1 Head

Figure 2

Schematic representation of Dermestidae phylogeny (based on Kiselyova and McHugh, 2006), with an indication of feeding habits of the adult beetles, duration of larval lifespan, and larval-pupal defensive structures.

The size of the colored bands in each subfamily is an approximated representation of the number of species. Image credit: Paolo Paolucci.