

Occurrence, ecological function and medical importance of dermestid beetle hastisetae

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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 serious threat for public 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.

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Abstract

Hastisetæ are a specific group of detachable setæ characterizing the larvae of Megatominae (Coleoptera: Dermestidae), commonly known as carpet and khapra beetles. These setæ 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 hastisetæ is to work as a mechanical obstacle, but they are also capable to block and kill a predator. Hastisetæ, 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 hastisetæ may affect vertebrates as well. Although information on the impacts of vertebrate predators of the beetles is lacking, hastisetæ have been shown to be a serious threat for public 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 hastisetæ 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 (Steinbrecht, 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), Erebidiae, 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. Although information on the impacts of vertebrate predators of the beetles is lacking, hastisetae have been shown to be a serious threat to public health (Gorgojo *et al.*, 2015). 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

implications in the public health. Finally, future perspectives on the study of the hastisetæ with special emphasis on Dermestidae are envisaged.

Survey methodology

In order to compile and then review the most exhaustive literature on hastisetæ we performed a careful and reiterated research in Google Scholar and Scopus through the use of keywords such as “hastisetæ”, “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

Hastisetæ, structure and function

Hastisetæ (or hastate setæ) 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 hastisetæ vary substantially not only among genera and species but also among tergites of the same species. The hastisetæ 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 hastisetæ 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 through 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 increase 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 (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’ nests: 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. Based on amber fossils, it is possible affirmation that hastisetae morphology is highly conserved and it remains 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 hastisetæ in the dermestids is, in the necrophagous clade, the transition from scavenger habits of adults to anthophily or aphagy (Zhantiev, 2009) (Fig. 2).

Hastisetæ and public health

Dermestidae are commonly treated as pest insects, causing considerable loss and damage to stored goods (of both animal and plant materials) (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, Stengaard Hansen *et al.*, 2012; Quarner, 2015). However, their presence in dwellings, public spaces and contamination of foodstuffs with their remains have important implications for public health (Gorham, 1979; 1989; Gorgojo *et al.*, 2015). Although it is believed that the hastisetæ primarily play a defensive function purely against other invertebrates, it is now widely recognized that these hairs have important and unpleasant effects on humans. The exposure to the hastisetæ manifests itself with inflammatory symptoms. Food contamination and hastisetæ ingestion cause inflammation of the digestive system (Krause *et al.*, 1998; Hirao, 2000); contamination of the working (Loir and Legagneux 1922; Siegel *et al.* 1991; Brito *et al.*, 2002, Renaudin, 2010) or living environment (Ayres and Mihan, 1967; Pauli and Bessot, 2009; Gorgojo *et al.*, 2015) cause rhinoconjunctivitis (Feo Brito *et al.*, 2002) and asthma (Cuesta-Herranz *et al.*, 1997; Brito *et al.*, 2002; Bernstein *et al.*, 2009), and the direct exposure of hastisetæ to the skin causes severe dermatitis (Sheldon and Johnston, 1941; Cormia *et al.*, 1945; Okamura, 1967; Ahmed *et al.*, 1981; Alexander, 1984; Southcott, 1989; Horster *et al.*, 2002; Zanca *et al.*, 2012; Hoverson *et al.*, 2015; McArthur *et al.*, 2016). Unusual, and apparently asymptomatic findings of hastisetæ have been done on sputum (Johnson and Batchelor, 1989) and cervical specimens (Bechtold *et al.*, 1985; Bryant and Maslan, 1994; Williamson *et al.*, 2005). It is still unclear whether the inflammatory effect of the hastisetæ is attributable to the mechanical action of the seta or if it is associated to the presence of specific molecules.

Conclusions

The scant information about the fine morphology and the ecological roles of hastisetæ, and its important implications in human health opens a whole horizon of research possibilities. Hastisetæ morphology is undoubtedly the starting point for any future study. The characterization of hastisetæ 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 hastisetæ will help to solve Megatominae systematics, highlighting the evolution of these structures in relation to phylogeny and biology. A detailed knowledge of hastisetæ morphology will allow us to understand the defensive mechanism and if it acts similarly in all Megatominae. Comparing reactions of different predators to hastisetæ 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 hastisetæ, and if so what are the causes of the unpleasant side-effects in humans? Is it the penetration of these setæ through 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. Hastisetæ 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 hastisetæ content can aid in developing tools to detect insect fragments in contaminated stored products, especially food.

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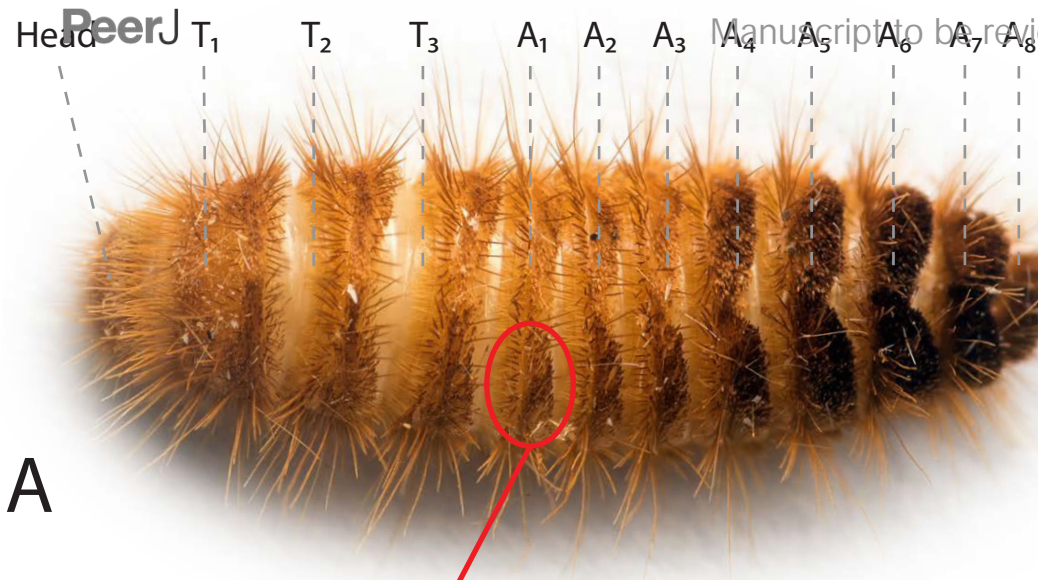
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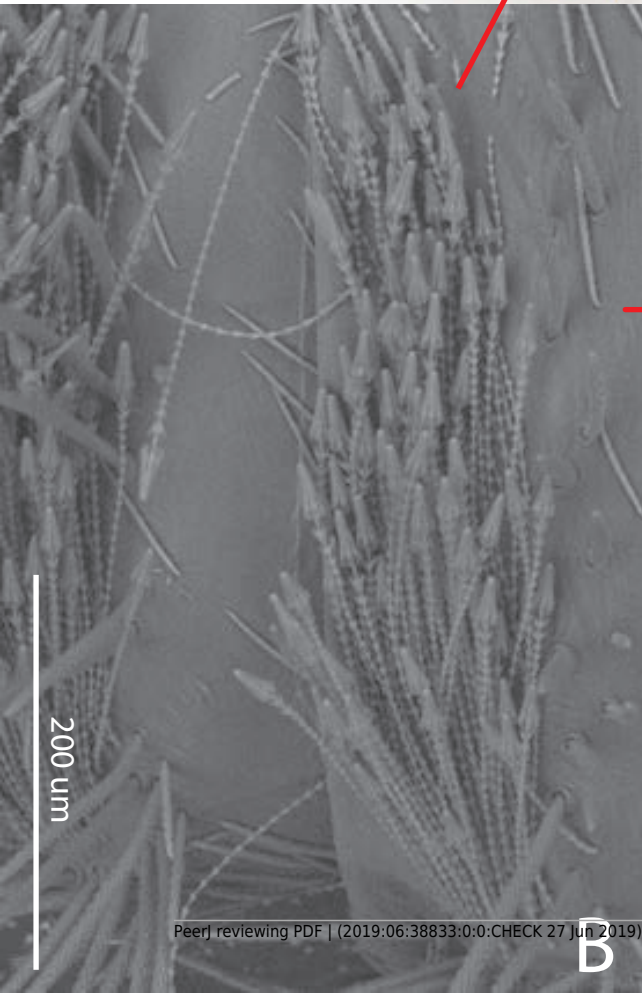
Figure 1(on next page)

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

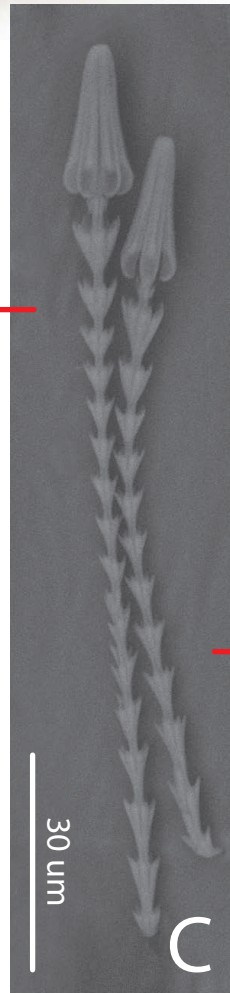
(A). Example of Megatominae larva, dorsal view. T1-T3: thoracic segments; A1-A8: abdominal segments. (B). Tuft of hastisetæ on abdominal segments. (C). Hastisetæ, lateral view. (D). Head of the hastiseta (subconical anchor-like, spear-shaped head).



A



B



C



D

Figure 2 (on next page)

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.

