# 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 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.

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18  **Abstract**

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20  (Coleoptera: Dermestidae), commonly known as carpet and khapra beetles. These setae are

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25  mechanism of cuticular structures (spines and hairs) and body appendages (antennae, legs and

26  mouthparts). It is believed that this defensive system evolved primarily to contrast predation by

27  invertebrates, however it has been observed that hastisetae may affect vertebrates as well.

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29  have been shown to be a possible threat for human health as an important contaminant of stored

30  products (food and fabric), work and living environment. Review of past and recent literature on

31  dermestid larvae has revealed that despite these structures indicated as one of the distinctive

32  characters in species identification, very little is known about their ultrastructure, evolution and

33  mechanism of action. In the present work, we will provide the state of knowledge on hastisetae

34  in Dermestidae and we will present and discuss future research perspectives intended to bridge

35  the existing knowledge gaps.

36

37  **Subjects** Evolutionary Biology, Morphology, Pest Management, Zoology

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

39

40

## Introduction

41
42 The cuticle plays a pivotal role in several aspects of arthropod biology, representing the interface
43 between the living tissue and the external environment (Bereiter-Hahn *et al.*, 1984). Thus, the
44 cuticle displays structural specializations such as denticles, setae, setulae and spines, all with
45 specific functions (Winterton, 2003). Correlations between structure and function are well
46 studied especially in insects (Neville, 1975) and crustaceans (Garm, 2004a, b; Garm and
47 Watling, 2013). Setae are multicellular protuberances on the cuticle, used primarily for
48 mechanoreception (Steinbrecht, 1984; Keil and Steinbrecht, 1984; Keil, 1997; Winterton,2003;
49 Barth, 2004). In all groups of arthropods, the role of setae has evolved from simple
50 mechanoreception to various other functions, including defense (Battisti *et al.*, 2011),
51 locomotion (Lebarque *et al.*, 2017), prey capture (Felgenhauer *et al.*, 1989), pheromone dispersal
52 (Stainbrecht, 1984), sexual display (Perez-Miles *et al.*, 2005), preening (Felgenhauer *et al.*,
53 1989), and camouflage (Zeledon *et al.*, 1973; Hultgren and Stachowicz, 2008; Stevens and
54 Merilaita, 2009). Detachable setae are true setae characterized by the loss of the neural
55 connection and the detachment of the base of the hair from the integument (Battisti *et al.*, 2011).
56 The proximal end of each seta is attached to an integument stalk or inserted into a socket and can
57 be easily removed with any kind of mechanical stimulation. This class of hairs has evolved as a
58 defensive structure against predation at least four times in Arthropoda. The class is subdivided in
59 two main morpho-ecological groups: urticating hairs and anchor-like setae. Urticating hairs are
60 characterized in some Lepidoptera families such as the Nodotontidae (subfamily
61 Thaumetopoeinae), Erebidae, Saturniidae and Zygenidae and the spider family Theraphosidae
62 (sub. fam. Theraphosinae) (Battisti *et al.*, 2011) and are described to protect from vertebrate
63 predators (Battisti *et al.*, 2011; Bertani and Guadanucci, 2013). Anchor-like setae are
64 characterized in some larvae of Dermestidae (Insecta: Coleoptera) and Polyxenidae (Myriapoda:
65 Polyxenida) where they work as entangling mechanism against invertebrates (Nutting and
66 Spangler, 1969; Eisner *et al.*, 1996). Dermestid detachable setae (hastisetae) are used by the
67 larvae as an active trapping system against arthropod predators (Nutting and Spangler, 1969).
68 These specialized setae are almost exclusively prerogative of Megatominae, the most species
69 rich group in the entire family (Hava, 2015). The mechanism of action of hastisetae and their
70 microstructure remains largely obscure and restricted to few case studies (Nutting and Spangler
71 1969; Mills and Partida, 1976); furthermore, how the evolution of hastisetae is related to the

72  biological success of the Megatominae remains unresolved. Although information on the impacts
73  of hastisetae on vertebrate predators is lacking, dermestid larvae and Megatominae in particular
74  have been documented as possible source of allergens in human (Mullen and Durden, 2009).
75  Hastisetae and integument fragments carrying them can be contaminants of stored commodities
76  and are present in working and living environments (Hinton, 1945). Hastisetae seem to be
77  involved in allergic reactions through skin contact, ingestion or inhalation; symptoms can vary
78  accordingly to exposition and consist of skin rushes, asthma, conjunctivitis and digestive system
79  inflammation (Gorgojo *et al.*, 2015; MacArthur et al. 2016). Correlation between the presence of
80  hastisetae and the incidence of allergies in humans exists but the scarce and incomplete
81  information available do not allow to consider hastisetae as a major hazard in living and working
82  places. The aim of this review is to synthesize the knowledge on the hastisetae of dermestid
83  beetles, to evaluate their occurrence in the group and their ecological importance, and to assess
84  their possible implications in the human health. Finally, future perspectives on the study of the
85  hastisetae with special emphasis on Megatominae are envisaged.
86

87  **Survey methodology**
88  In order to compile and then review the most exhaustive literature on hastisetae we performed a
89  careful and reiterated research in Google Scholar and Scopus through the use of keywords such
90  as "hastisetae", "Dermestidae", "defense", "larva", integrated by the usage the Boolean operators
91  AND, OR, NOT and the use of " " for specific word combinations. The literature not available
92  online has been recovered thanks to Network Inter-Library Document Exchange (NILDE), a
93  web-based software for the service of Document Supply and Inter-Library Loan, managed by the
94  Italian National Research Council. Our research has enabled the collection of more than a
95  hundred publications, of which ninety were considered in the realization of this review. The
96  library created was comprehensive of literature in English, German and French.
97

98  **Results**
99  **Hastisetae, structure and function**
100 Hastisetae (or hastate setae) have been cited in several papers dealing with Dermestidae
101 systematics (Rees, 1943; Kiselyova and McHugh, 2006), species identification (Booth *et al.*
102 1990; Peacock, 1993), and product contamination (Bousquet, 1990). However, the amount of

103    information available concerning their microstructure (Elbert, 1976; 1978), function (Nutting and

104    Spangler, 1969; Mills and Partida, 1976) and evolution (Zhantiev, 2000; Kiselyova and McHugh,

105    2006) is quite scarce. These hairs, located on the dorso-lateral surface of the tergites of larvae

106    and pupae (Fig. 1) (Rees, 1943; Beal, 1960; Kiselyova and McHugh, 2006; Kadej, 2012a, Kadej,

107    2012b; Kadej and Jaroszewicz 2013, Kadej, *et al*. 2013; Kadej and Guziak 2017; Kadej 2017;

108    2018a, b), are generally quite small with an estimated length, according to the literature, between

109    150 and 900 μm. Density and distribution of the hastisetae vary substantially not only among

110    genera and species but also among tergites of the same species. The hastisetae of the thoracic

111    segments are generally scattered and in low numbers in respect to the other parts of the body.

112    While the abdominal tergites present a wider distribution pattern, from hastisetae covering the

113    major part the tergal disc up to proper setae fields located at the posterior corners of tergites (i.e.

114    *Reesa*, *Trogoderma*). In some larvae, the hastisetae give origin to real tufts of hairs located on

115    the posterior corners of the terga IV-VII (i.e. *Ctesias*) or V-VII (i.e. *Anthrenus*) (Mroczkowski,

116    1975; Kadej *et al*. 2013; Kadej 2017; 2018a, b). The hastisetae are inserted in setal sockets on the

117    integument and are connected to the tormogen cell trough the pedicel (Elbert, 1978). The pedicel

118    is the breaking point of the shaft which allows the detachment of the hastiseta (Elbert, 1978).

119    Hastisetae microstructure consists of two main parts: the shaft and the apical head (Fig. 1). The

120    shaft is long and filiform, subcylindrical in section. It is made by repeated modules, from 5 to 77,

121    each of them constituted by one cylindrical segment provided with one wreath of spines/scales in

122    the distal part (Elbert, 1978). These spines/scales are postero-laterally oriented and can vary in

123    number from five to seven (Elbert, 1978). The last module of the shaft is generally bigger and

124    thicker than the previous and can slightly vary in general shape to the others; this structure,

125    however, has not been characterized yet. The head of the seta is a subconical anchor-like, spear-

126    shaped structure subdivided longitudinally in sections; the apex of the head is blunt (Elbert,

127    1976; 1978) (Fig. 1). The head consists of five to seven longitudinal, circularly arranged,

128    elements separated from each other by one deep groove, connected to the stem in the upper half

129    by cross-bracing and free in the lower part. The "anchor-like head", set against the thorns of the

130    last shaft module, is involved in entangling invertebrate body parts (Nutting and Spangler, 1969),

131    functioning as trap for antennae, legs, mouthparts, setae and spines (Mills and Partida, 1976).

132    This structure is apparently species specific, varying in shape and length between taxa (Elbert,

133    1976; Kiselyova and McHugh, 2006; Kadej *et al*. 2013; Kadej 2017; 2018a). The shaft allows

134    setae to cluster together amplifying the "trapping" effect and the spines increases friction and

135    entangling among hastisetae and between setae and body parts. The combined action of several

136    hastisetae affects small predators (Nutting and Spangler, 1969) and possibly food competitors

137    (Kokubu and Mills, 1980). These setae are hollow (Elbert, 1976; 1978) and could potentially

138    contain proteins or other chemicals involved in the defense, as it has been shown in Lepidoptera

139    (Battisti *et al*., 2011). Hastisetae morphology and distribution, combined together with other

140    characters, constitute a useful tool for species identification (Rees, 1943; Beal, 1960; Peacock,

141    1993, Kadej, 2012a, b; Kadej and Jaroszewicz 2013, Kadej, *et al.,* 2013; Kadej and Guziak 2017;

142    Kadej 2017; 2018a, b).

143

144    **Hastisetae in the systematic and ecology of Dermestidae**

145    Dermestidae is a cosmopolitan, comparatively small family of Coleoptera, regarded as 'a well-

146    defined, monophyletic group' (Lawrence and Newton, 1982), consisting of six subfamilies:

147    Orphilinae, Thorictinae, Dermestinae, Attageninae, Trinodinae and Megatominae (Hava, 2015)

148    (Fig. 2). Dermestids are homogeneous only in general appearance, hiding a complex and rich

149    diversity in term of morphological, ecological and ethological aspects. Specific traits and

150    evolutionary tendencies could be observed in several lineages, associated to ecological groups

151    and niches (Zhantiev, 2009); these traits can be observed at adult (Zhantiev, 2000) and larval

152    stage (Kiselyova and McHugh, 2006). Orphilinae are mycetophagous, with sclerotized

153    burrowing larvae (Lenoir *et al*., 2013). Thorictinae are myrmecophilous and larvae protection is

154    provided by the associated ant species (Lenoir *et al*., 2013). Dermestinae, the basal group of the

155    "necrophagous clade" (*sensu* Zhantiev, 2009), have larvae feeding on fresh or relatively humid

156    animal remains (over 15% in water content) (Zhantiev, 2009). Since Dermestinae food resource

157    is highly perishable, the larvae develop rapidly and persist only for short periods. The oblong,

158    sub-cylindrical and sclerotized larvae of this subfamily can dig through the feeding substrate and

159    live in butyric fermentation condition, under animal remains. It's is plausible that the absence of

160    hastisetae on larval tergites is directly attributable to their burrowing lifestyle. Anchor-like

161    detachable setae could be disadvantageous to move within the substrate. Hastisetae would in fact

162    create friction and would be systematically lost, requiring an important energy expenditure

163    necessary for their replacement. The defensive strategy in Dermestinae is based on the fast

164    escape behavior and the sclerotized integuments of the body. The larvae specifically require the

165 pupation chamber to molt and they are capable to dig into soil and/or substrate in case of lacking

166 suitable places where to hide. The pupae of this subfamily present gin-traps on the integuments,

167 as a defensive system against predators (Hinton, 1946; Kiselyova and McHugh, 2006) (Fig. 2).

168 Attageninae have burrowing larvae associated to wood dust, fissures of rocks and sandy

169 environments and feed off of insects and other arthropods remains; the larvae are oblong-

170 fusiform with integuments covered of three different kind of hairs (Zhantiev, 2000; Kiselyova

171 and McHugh, 2006). The larvae show a fast escape behavior, similar to Dermestinae.

172 Attageninae prefer to pupate in hidden niches and the pupae bear gin-traps in most of the cases

173 (Zhantiev, 2000). Trinodinae are inquiline of animals' nets: rodent borrows with larvae phoretic

174 on mammal (Zhantiev, 2009) or larvae associated to spider nests (Beal, 1959; Kadej, 2011). The

175 hastisetae, with the single exception of the genus *Trinodes* (Trinodinae), in which modified

176 hastisetae are described (Kiselyova and McHugh, 2006), are prerogative of the Megatominae

177 larvae and they are strictly associated to larval and pupal morphology and behavior (Kiselyova

178 and McHugh, 2006; Zhantiev, 2009) (Fig. 2). Megatominae is the richest in species subfamily

179 within Dermestidae and its biological success is most probably attributable to the hastisetae

180 occurrence. Amber fossils indicate that hastisetae morphology is highly conserved and remained

181 virtually unchanged since late Cretaceous (Poinar and Poinar, 2016). This group shows a

182 remarked investment on hastisetae as a defensive tool (Nutting and Spangler 1969; Mills and

183 Partida, 1976), exploiting their resistance and durability over time to protect both larvae and

184 pupae (Kiselyova and McHugh, 2006; Zhantiev, 2009). Megatominae is the clade within the

185 xerophilous necrophagous dermestids (*sensu* Zhantiev, 2009), which can survive on low-water

186 food resources, especially chitinous and keratinous remains (Armes, 1990; Beal, 1998; Zhantiev,

187 2009). These substrates are capable to stand in the environment for a long time but the poor

188 nutrients prolong the duration of larval development, with major implications on morphology,

189 ethology and defensive behavior. Lengthening of the larval phase and its persistence in the

190 environment for a long time has promoted the evolution of morphological and ethological

191 features in Megatominae that otherwise would have been disadvantageous in a different lifestyle.

192 The inability of the larvae to delve into the living substrate (Zhantiev, 2009) favored the

193 evolution of defensive structures (hastisetae) with low energy investment for their synthesis and

194 to remain functional even after being dispersed in the environment. Over time, energetic

195 investment in cuticularized integuments in larvae and gin-traps in pupae shifted to the

196    morphology of hastisetae and its defense mechanisms. Hastisetae provide protection in both

197    larvae and pupae, favoring a positive energy trade-off in larval development. All the larvae of

198    this subfamily are stout, feebly sclerotized, slow moving and present an aggressive, non-escaping

199    defensive behavior (Kiselyova and MchHugh, 2006). In a disturbance, the larva stops moving,

200    arches its body and spread the hastisetae, frequently from the posterior part of the body where it

201    is densely packed with hastisetae towards the stimulus (Kiselyova and MchHugh, 2006). In

202    general, Megatominae do not make pupation chambers or hide, but simply pupate where they

203    have been feeding. Pupae completely lack gin-traps and remain protected inside the last larval

204    exuvia, completely covered in hastisetae (synapomorphy of Trinodinae + Megatominae)

205    (Kiselyova and McHugh, 2006) (Fig. 2). Megatominae have been able to adapt against

206    interspecific and intraspecific competition for food resources. A common trait associated with

207    the evolution of the hastisetae in the dermestids is, in the necrophagous clade, the transition from

208    scavenger habits of adults to anthophily or aphagy (Zhantiev, 2009) (Fig. 2).

209

210    **Hastisetae and human health**

211    The capability to feed on a wide range of food resources scarce in water content and to resist to

212    prolonged starvation makes Megatominae larvae the perfect candidate to inhabit working and

213    living spaces. In addiction, due to their slow movements and cryptic behavior these larvae result

214    difficult to detect and remove. For this reason, some species are now synanthropic and

215    cosmopolitan (Bouchet *et al.,* 1996; Gamarra *et al.,* 2009), having been spread all over the world

216    with trade. These species became serious pests, causing considerable loss and damage to stored

217    goods of both animal and plant origin (Hinton, 1945; Burges, 1959; Kantack and Staples, 1969;

218    Mroczkowski, 1975; Beal, 1991; Veer *et al*., 1991a, b; Veer and Rao, 1995; Veer *et al*., 1996;

219    Imura, 2003; Rajendran and Hajira Parveen, 2003; Lawrence and Slipinski, 2010) and to objects

220    of organic origin in museums of cultural and natural history (Jurecka, 1987; Zaitseva, 1987;

221    Armes, 1988; Bousquet, 1990, Pinniger and Harmon, 1999; Stengaard Hansen *et al*., 2012;

222    Quarner, 2015). The hastisetae released by the larva throughout its entire development and

223    abandoned in the environment in association to the exuviae are an important contaminant in

224    dwelling, public spaces as well as food stuff (Gorham, 1979; 1989; Burgess, 1993) and can

225    contribute as allergens in humans (Wiseman *et al*., 1959; Johansson *et al.,* 1985; Baldo and

226    Panzani, 1988; Burgess, 1993; Gorgojo *et al*., 2015; McArthur *et al*., 2016): chitin, likely the

227 main constituent of the hastisetae, is in fact a powerful and widely recognized allergen, and its

228 interaction with Th2 lymphocytes and human chitinases enhances the inflammation process

229 (Brinchmann *et al.,* 2011; Bucolo *et al.,* 2011; Mack *et al.,* 2015). However, it is still unclear

230 whether the inflammatory effect of the hastisetae is attributable to the mechanical action of the

231 seta and its penetration through the epithelia or if it is associated to the presence of specific

232 molecules capable to start an immunological reaction. Hastisetae have been directly linked to

233 occupational diseases in working environments (Loir and Legagneux 1922; Renaudin, 2010),

234 especially when processing organic materials such flour, wool, silk and other commodities (Veer

235 *et al.*, 1996; Brito *et al.*, 2002), or stored objects of organic origin in museums and art galleries

236 (Siegel *et al.* 1991). The exposure to and inhalation of hastisetae, even in the form of dust, are

237 reported to cause rhinoconjunctivitis (Brito *et al.*, 2002) and asthma (Cuesta-Herranz *et al.*,

238 1997; Brito *et al.*, 2002; Bernstein *et al.*, 2009). Megatominae are also one of the arthropod

239 groups most commonly recorded inside houses (Gamarra *et al.,* 2009; Bertone *et al.*, 2016;

240 Madden *et al.* 2016); the larvae persist in these environments for months, even for years, feeding

241 on food (Gorham, 1979; 1989; Hirao, 2000), pet food (Rudolph *et al.,* 1981), dust, insect

242 remains and clothes, especially wool fabric (Bouchet *et al.,* 1996). This prolonged presence

243 inside houses together with the persistence of the hastisetae in the environment greatly increase

244 the possibility for the humans to come into contact and develop a sensitization to these

245 detachable hairs (Wiseman *et al.*, 1959; Kaufman *et al.*, 1986; Burgess, 1993; Jakubas-Zawalska

246 *et al.,* 2016). The direct exposure of hastisetae to the skin, maybe due to contaminated bed or

247 clothes, causes severe dermatitis (Sheldon and Johnston, 1941; Cormia *et al.*, 1945; Okamura,

248 1967; Ahmed *et al.*, 1981; Alexander, 1984; Johansson *et al.,* 1985; Southcott, 1989; Horster *et*

249 *al.*, 2002; Zanca *et al.*, 2012; Hoverson *et al.*, 2015; McArthur *et al.*, 2016), while the repeated

250 inhalation over a longer period may cause asthma (Cuesta-Herranz *et al.*, 1997; Brito *et al.*,

251 2002; Bernstein *et al.*, 2009). Food contamination and hastisetae ingestion has been proved to

252 cause the inflammation of the digestive system, manifesting through nausea, fever, diarrhea

253 (Hirao, 2000), proctitis and perianal itching (Krause *et al.*, 1998). Unusual, and apparently

254 asymptomatic findings of hastisetae have been done on sputum (Johnson and Batchelor, 1989)

255 and cervical specimens (Bechtold *et al.*, 1985; Bryant and Maslan, 1994; Williamson *et al.*,

256 2005). The incidence of pathologies associated with Dermestidae and Megatominae in particular,

257 seems to be considerably reduced in recent decades probably due to the increased degree of

258    attention regarding the presence of contaminants in food and the marked improvement in the

259    processes of conservation and storage of raw materials; the development of adequate plans for

260    monitoring and management of pests and the general improvement in the quality of life of people

261    associated with greater healthiness of the houses have contributed further to the imitation of the

262    impact (Athanassiou and Arthur, 2018). However, there is also the possibility that many

263    domestic cases of exposure to hastisetae, especially in the case of skin rushes (erythematobullous

264    reactions) may be under-recognized and underdiagnosed, due to similar effects to attacks by

265    other arthropods (Burgess, 1993; McArthur *et al.*, 2016). Furthermore, almost all the cases

266    reported in the medical literature regard developed countries while the effect of hastisetae on

267    human health in developing countries remains almost obscure and widely understudied.

268    Undoubtedly, a better knowledge of the inflammation caused by hastisetae would allow the

269    recommendation of appropriated prevention measures and the formation of medical personnel

270    able to provide early diagnosis and administration of appropriate therapies. Moreover, a close

271    collaboration between occupational physicians, entomologists and immunologists could be of

272    great help for the development of new surveillance programs and new health and safety

273    guidelines for workers and people most at risk.

274

275    **Conclusions**

276    The scant information about the fine morphology and the ecological roles of hastisetae, and their

277    implications in human health opens a whole horizon of research possibilities. Hastisetae

278    morphology is undoubtedly the starting point for any future study. The characterization of

279    hastisetae through electron microscopy and micro-CT is the basic and fundamental step to

280    understand their functional morphology. The identification of specific morphological traits in the

281    hastisetae will help to solve Megatominae systematics, highlighting the evolution of these

282    structures in relation to phylogeny and biology. A detailed knowledge of hastisetae morphology

283    will allow us to understand the defensive mechanism and if it acts similarly in all Megatominae.

284    Comparing reactions of different predators to hastisetae will be useful to evaluate the different

285    effects and particularly if this defensive system is primarily directed towards invertebrates and/or

286    to vertebrates. Are humans or other vertebrates possible targets of hastisetae, and if so what are

287    the causes of the unpleasant side-effects in humans? Is it the penetration of these setae trough

288    epithelia the main cause of inflammation and are there any particular substance inducing the

289      reaction, as it has been showed in Lepidoptera? Chemical analysis of secretions can identify and

290      characterize the compounds responsible of the inflammation in humans and clarify their possible

291      role as adjuvants in defense against the threats. Understanding the causes of allergic responses in

292      humans will allow the development of specific medical therapies. Hastisetae could become an

293      important addition in species identification, with relevant application in forensic entomology and

294      pest management on stored products. Furthermore, the creation of a molecular fingerprint based

295      on hastisetae content can aid in developing tools to detect insect fragments in contaminated

296      stored products, especially food.

297

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303

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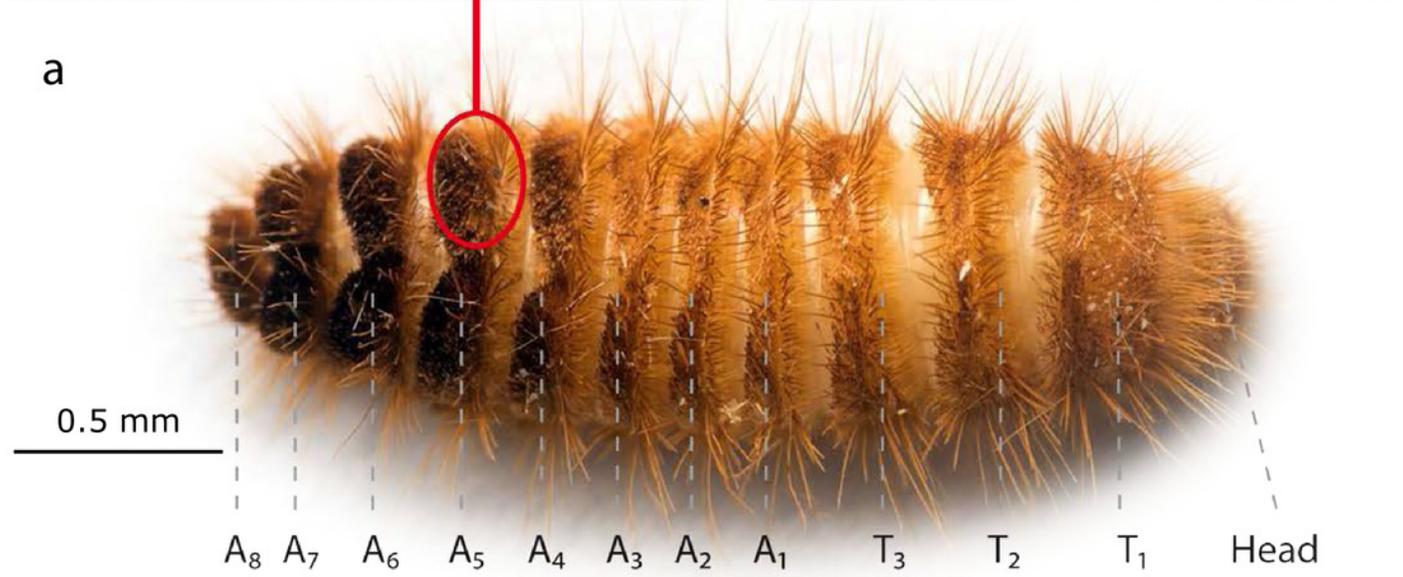
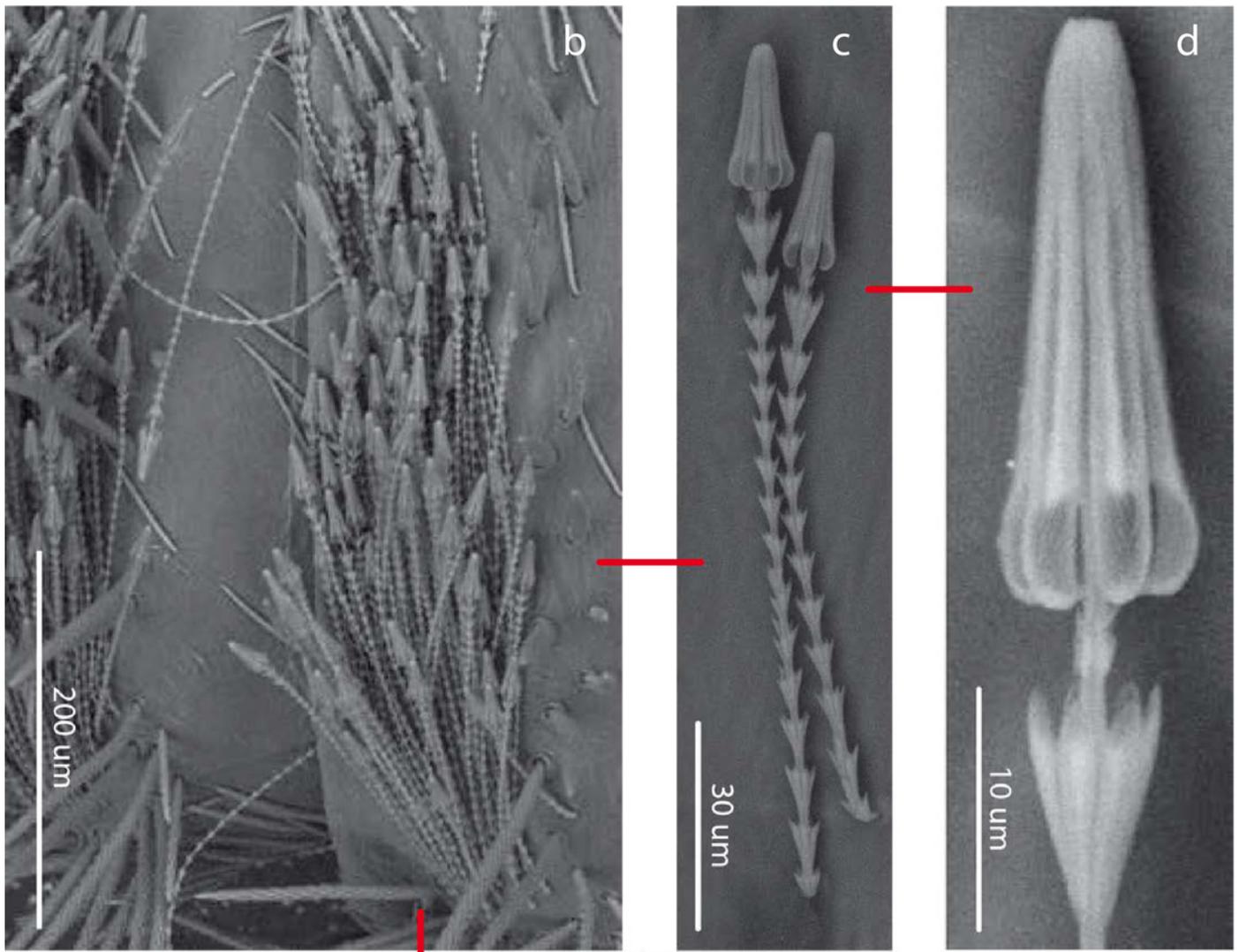
# Figure 1

*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.*

# 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.*