

# The Palaearctic *Dermestes undulatus* Brahm 1790 (Coleoptera: Dermestidae: Dermestinae) species complex: descriptions of neotype and three new species

Graham J. Holloway<sup>1\*</sup>, Andreas Herrmann<sup>2</sup>

**Abstract** - Many species of Dermestidae have not been adequately described to facilitate current taxonomic studies. According to the World Catalogue of Dermestidae, the whereabouts of the holotype of *Dermestes undulatus* is not known. In the current study, a neotype is raised for taxonomic stability. In addition to the nominate species, three new species are described, one from North Africa and a further two from Kazakhstan. Species are identified by the structure of the male genitalia. The distributions of all four species are provided.

**Key words:** *algeriensis*, genitalia, identification, *kazakhstanicus*, *smithi*.

**Riassunto** - Il complesso di specie paleartiche *Dermestes undulatus* Brahm 1790 (Coleoptera: Dermestidae: Dermestinae): descrizioni del neotipo e di tre nuove specie.

Molte specie di Dermestidae non sono state descritte in modo tale da facilitare gli attuali studi tassonomici. Secondo il World Catalogue of Dermestidae, non è nota l'ubicazione dell'olotipo di *Dermestes undulatus*. Nel presente studio, viene proposto un neotipo per assicurare la stabilità tassonomica. Oltre alla specie nominale, vengono descritte tre nuove specie, una proveniente dal Nord Africa e altre due dal Kazakistan. Le specie sono identificate in base alla struttura dei genitali maschili. Sono fornite le distribuzioni di tutte e quattro le specie.

**Parole chiave:** *algeriensis*, genitalia, identification, *kazakhstanicus*, *smithi*.

## INTRODUCTION

The current estimate is that there are just over 1900 species of Dermestidae (Háva, 2024). The number of species continues to rise rapidly (Háva, 2024) partly because

of an appreciation of the need to examine genitalia to be certain of the species under study, and partly because of the redescription of poorly or inadequately described species (Hermann & Holloway, 2020; Armstrong *et al.*, 2023; Holloway & Sparks, 2023; Holloway & Herrmann, 2024). Sometimes, a good description of a single species [*Anthrenus pimpinellae* (Fabricius 1775), Holloway & Bakaloudis, 2020] can open the door to the discovery of similar species, for example *A. chikatunovi* Holloway 2020 (Holloway, 2020), *A. isabellinus* Küster 1848 (Holloway *et al.*, 2020), and *A. quernerii* Holloway 2024 (Holloway, 2024), and a better understanding of distributions (Holloway *et al.*, 2021; Holloway *et al.*, 2023).

The higher taxonomy of the subfamily Dermestinae is relatively well understood (Háva, 2024). Five genera sit within Dermestinae, four extant and one fossil (*Paradermestes* Deng, Ślipiński, Ren & Pang 2017). The extant genera include *Dermalius* Háva 2001 with one species, *Mariouta* Pic 1889 with two species, *Rhopalisilpha* Arrow 1929 with one species, and the large genus *Dermestes* Linnaeus 1758. *Dermestes* is split into three subgenera, *Derbyana* Lawrence & Ślipiński 2005 with one species, *Dermestes* with 37 species and split on the basis of pronotal structure from *Dermestinus* Zhantiev 1967 with 48 species (Háva, 2024; Herrmann, 2024). *Dermestes undulatus* Brahm 1790 sits with the subgenus *Dermestinus*.

*Dermestes undulatus* is considered well-known and widely distributed across the entire Holarctic region (Mroczkowski, 1968; Háva, 2024). A lot of life-history work has been carried out courtesy of its significance in forensic biology (Charabidze *et al.*, 2014; Magni *et al.*, 2015; Bonacci *et al.*, 2017; Gunn, 2018). Along with distribution, much is known about the morphology of larvae (Lambiase *et al.*, 2024) and development periods under different conditions (Martin-Vega *et al.*, 2017; Lambiase *et al.*, 2018). Given the importance of *D. undulatus* in forensic science, it is surprising that the species has not been thoroughly and accurately described. Brahm's (1790) description of *D. undulatus* (translated from old German, so the precise meaning of some of the words might be vague) is brief:

Wetted Lardbeetle.

Very rare. In meadows. Black, the thoracic shield covered with long rust-coloured and black hairs, the elytra greyish-wetted appearance, the abdomen white-grey, and the thighs of the penultimate and last pair of legs white-grey ringed.

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Brahm's (1790) description was adequate to differentiate among the few *Dermestes* species known at the time, but requires more detail to function appropriately amongst the 90 species currently known (Háva, 2024). According to the World Catalogue of Dermestidae (Háva, 2024), the whereabouts of the holotype of *D. undulatus* is not known. Moreover, Bernd Jaeger (pers. comm.) confirmed that it is not in the Museum für Naturkunde, Berlin, where many of Brahm's specimens can be found. All this considered, there is a need to nominate a neotype specimen.

In the current study, the genital structure of 72 specimens from across Europe, North Africa, and Asia is examined. A neotype is described (from Germany, where Brahm's *D. undulatus* were almost certainly collected) and the distribution of *D. undulatus* is indicated. Three new species on the periphery of this distribution are diagnosed and described, establishing that *D. undulatus* is a species complex.

## MATERIALS AND METHODS

The material examined was borrowed from the following collections:

AHEC = Andreas Herrmann's Private Collection

NHMUK = Natural History Museum, London

OUMNH = Oxford Natural History Museum

Dissection was carried out under a Brunel BMSL zoom stereo LED microscope. The abdomen was removed, the ventrites peeled away, and the male genitalia or female sternite VIII removed. Habitus images were captured at  $\times 10$  magnification using a Canon EOS 2000D camera mounted on the BMSL microscope. Images of median lobe, parameres, and female sternite VIII were captured at  $\times 50$  magnification using a Canon EOS 1300D camera mounted on a Brunel monocular SP28 microscope. After dissection, for each specimen, all body parts were mounted on a card. The antennae were teased out, and images were taken at  $\times 50$  magnification. All images were fed through Helicon Focus Pro version 8.2.2 focus-stacking software. Measurements were made using DsCap.Ink software version 3.90. Measurements taken:

- body length (BL): distance from the anterior margin of the pronotum to the apex of the elytra.
- median lobe length (ML): from posterior to anterior tips.

Scale bars were added using ImageJ 1.53M (Schneider *et al.*, 2012). The distribution map was generated using SimpleMappr (Shorthouse, 2010)

## Taxonomy

Class Insecta Linnaeus 1758

Order Coleoptera 1758

Family Dermestidae Latreille 1804

Subfamily Dermestinae Latreille 1804

Tribe Dermestini Latreille 1804

Genus *Dermestes* Linnaeus 1758

Subgenus *Dermestinus* Zhantiev 1967

## *Dermestes undulatus* Brahm 1790

Figs. 1 and 2.

## Material examined

AHEC: Dagestan, Laksy district, 17-22 v 2015, leg. S.V. Pushkin (2♀♀); Germany, Hamburg, 12 vi 1997, leg. A.

Herrmann (5♀♀, 3♂♂); Romania, Bacău/Moldovia 10-15 v 2011, leg. A Pintilioaie (2♀♀, 5♂♂); Crimea, Sevastopol, 21 vii 2001, unknown collector (5♀♀, 1♂); Greece, Peloponnes, Menalo, 11 vi 2001, leg. J. Louda, (3♀♀, 1♂); The Netherlands, Scheveningen, 13 ix 2002, leg. R. Westerduijn (1♀, 1♂); Georgia, Abhazia, 2 vi 2014, leg. D. Lundvshev (2♀♀); Menorca, NW Es Canutells, 7 ix 2012, leg. M. Lillig & Ch. Lauer (1♂); Greece, Crete, Thripti, 14 iii 2018 leg. I. Brachat & Meybohm (1♀, 3♂♂); Croatia, Dubrovnik, vi 2011, leg. A. Herrmann (5♀♀, 3♂♂). **NHMUK:** Paris, Dejean collection (1♀); Germany, Ruthe, (1♀); Spain, Adalucia, Huelva, Doñana, v-vi 1917, leg. G.M. Matfort (1♀); S. Syria, Umm es Charatite, 2 iv 1945, Middle East Biological Studies Scheme (1♀); Croatia (Dalmatia), Dejean collection (1♀); France (Gallia), Fry collection (1♂); Austria, Dejean collection (1♂); Constantinople (Istanbul), v 1902, leg. Camera (1♂); Alderney, 1925, leg. W.R. Thompson (1♂); Crimea, 1916, N.L. Sacharov (1♂); E. Austria, Neusiedl-am-See, 11 ix 1964, leg. C.C. Vardy (1♂); Lusitan (Portugal), 1905, Fry collection (1♂); Malta, Wied Baba, 4 iv 1956, leg. G.V.P. Sewell (2♂♂); Spain, Dejean collection (1♂). **OUMNH:** France, Brassac, 8 ix 1991, leg. C. Rayden (1♀); Hungary, Győr, 7 viii 1991, leg. C. Rayden (1♀); Crete, Plakias, 16 7 1990, leg. C. Rayden (2♀ 1♂); Greece, Peloponnes, 26 vi 2003, D.J. Mann (2♀♀ 2♂♂). Mean ♂ BL = 6.47±0.56 [standard deviation] mm, mean ♀ BL = 6.88±0.64 mm, Females are significantly larger than males (Fig. 1A) ( $F_{1,66} = 7.55$ ,  $p = 0.008$ ).

## Diagnosis neotype: external features

BL neotype (Fig. 1A) = 7.46 mm. Integument black throughout. Heavily punctate head without ocellus (typical of most Dermestidae), vertex down to and including temples covered in short, fine dark orange hairs. Face down to and including clypeus covered in longer dark orange hairs. Labrum dark orange, fringed with long orange hairs. Eyes bulging. Pronotum densely punctured, distance between punctures less than width of punctures. Pronotum covered in long, narrow black, dark orange, pale yellow and white hairs, orange and yellow hairs randomly distributed across anterior half of pronotum but arranged in two sinuous, parallel bands across posterior half of pronotum (NB hairs wavy is if under flowing water or soaked, hence old German word "gewässerter" used by Brahm (1790) in original description). Posterior margin of pronotum and outer corners of pronotum carrying fringes of orange hairs. Heavily punctured scutellum carrying long orange hairs. Elytra heavily punctured and covered in black, recumbent hairs with sparse patches of white hairs across entire elytral surface. Basal elytral margins carrying orange hairs.

Pro- and mesosterna black. Anterior coxae black with orange hairs at tip, middle coxae with more extensive covering of orange hairs. Metasternum covered with dense coating of white to slightly creamy hairs apart from anterior outer corners which are covered in black hairs. Ventrite (Fig. 1B) integument black apart from reddish brown posterior margins on each ventrite. Ventrite 1 covered in creamy white hairs across middle third, outer third on each side covered in black hairs. Ventrites 2–4 covered in creamy white hairs apart from patches of black hairs on outer anterior corners at margin. Ventrite 5 covered in black hairs apart from two

patches of sub-lateral marginal creamy white hairs against anterior margin.

Eleven-segmented antenna (Fig. 1C) reddish-brown. Antennomere 1 larger than antennomeres 2-7. Antennomere 8 shallow, disc-shaped, tight up against antennomere 9. Large club consisting of terminal three, loosely connected antennomeres. All components of legs black to very dark brown. White ring of hairs around middle and hind femora.

**Diagnosis neotype: internal features (male)**

Median lobe (Fig. 2A, ML=1.259 mm), knife-like, evenly curved with attachment peg emerging from dorsal surface at anterior end at 90°. Median lobe mid-brown on concave dorsal surface, becoming paler to very pale yellow along convex ventral surface. Ventral margin narrowly bordered with membranous material. Parameres (Fig. 2B) stout, peg-like, and dark brown, parallel to each other for first ¾ of length and clasping either side of laterally very thin median lobe. Along final ¼ parameres diverge and terminate in rounded posterior tips, each adorned with tufts of yellow hair. Sternite IX (Fig. 2C) with posterior lobe nearly 1/3 length of entire sternite. Posterior tip flat to very slightly convex, and lateral margins diverge from each other only slightly producing rectangular appearance. Posterior lobe pale brown apart from yellowish margins. Posterior lobe covered in recumbent, fine black hairs all pointing posterior and extending beyond posterior margin. No hairs along lateral margins. At base of posterior lobe, lateral margins form right angles with flanges that attach to tergites. Anterior to flanges, lateral margins straight and convergent towards sharp attachment point.

**Diagnosis: internal features (female)**

Bursa copulatrix contains six well-developed, circular sclerites, sometimes eight with addition of two small sclerites towards entrance of bursa copulatrix. Sternite VIII (Fig. 2D) umbrella-shaped with long, pale brown (sclerotized) anterior stem that bifurcates at posterior end. Thin, delicate, yellow parasol-shaped cap on top of stem. Margins of cap not evenly rounded but straight along each lateral margin and flat to slightly convex across posterior margin. Cap disc white carrying a few short setae. Yellow marginal regions carry many long black setae, especially along posterior sections of lateral margins and across posterior margin.

**Type material**

*Neotype*

GERMANY • ♂ (in good condition) Hamburg (53.571, 9.997); 12 vi 1997; collector A. Herrmann; NHMUK.

*Other material examined*

GERMANY • 2♂♂, 5♀♀ (in good condition) Hamburg (53.571, 9.997); 12 vi 1997; collector A. Herrmann; (1♂ 3♀♀ AHEC, 1♂ 1♀ NHMUK, 1♀ OUMNH).

***Dermestes Algeriensis* sp. nov.**

Figs. 3-6

urn:lsid:zoobank.org:act:B2B8B8A1-8141-4766-B7A4-75365AE208EF

**Material examined**

Two specimens, both NHMUK

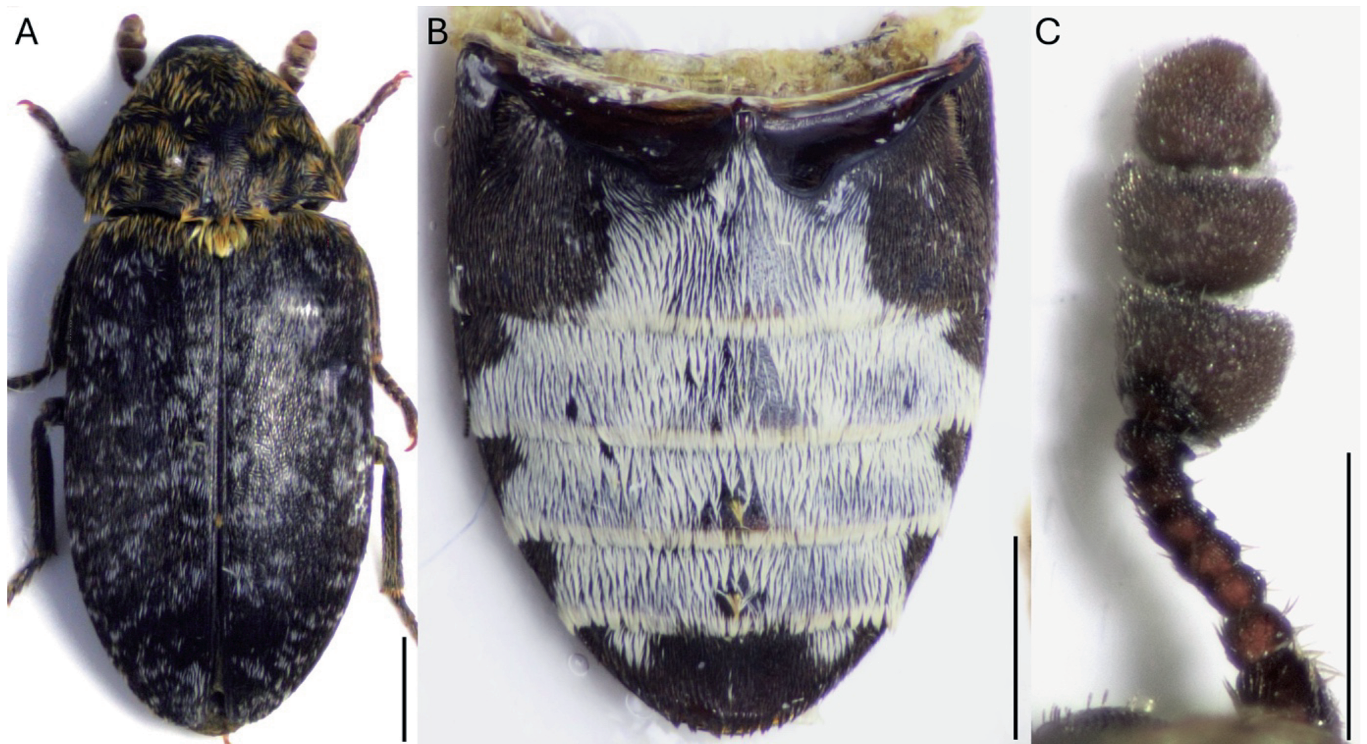


Fig. 1 – *Dermestes undulatus* from Hamburg, Germany. A) Habitus (scale bar = 1 mm); B) ventrites (scale bar = 1 mm); C) antenna (scale bar = 0.5 mm). / *Dermestes undulatus* proveniente da Amburgo, Germania. A) Habitus (barra di scala = 1 mm); B) ventriti (barra di scala = 1 mm); C) antenna (barra di scala = 0,5 mm).

**Diagnosis: external features**

BL (holotype) = 6.29 mm, (paratype) 6.05 mm. No definitive external differences found between *D. algeriensis* (Figs. 3A, 4A) and *D. undulatus*. Paratype shows fewer white hair tufts on dorsal surface than holotype (Fig. 3A).

**Diagnosis: internal features**

Median lobe (Fig. 5A) long (ML=1.512 mm), narrow, mid-brown, darker along dorsal concave margin, paler along convex ventral margin. Membranous along ventral margin, particularly towards posterior end.



Fig. 2 – *Dermestes undulatus* from Hamburg, Germany. A) Median lobe; B) parameres; C) sternite IX; D) sternite VIII (female). Scale bar = 0.5 mm in all cases. / *Dermestes undulatus* proveniente da Amburgo, Germania. A) Lobo mediano; B) parameri; C) sternite IX; D) sternite VIII (femmina). Barre di scala = 0,5 mm in tutti i casi.

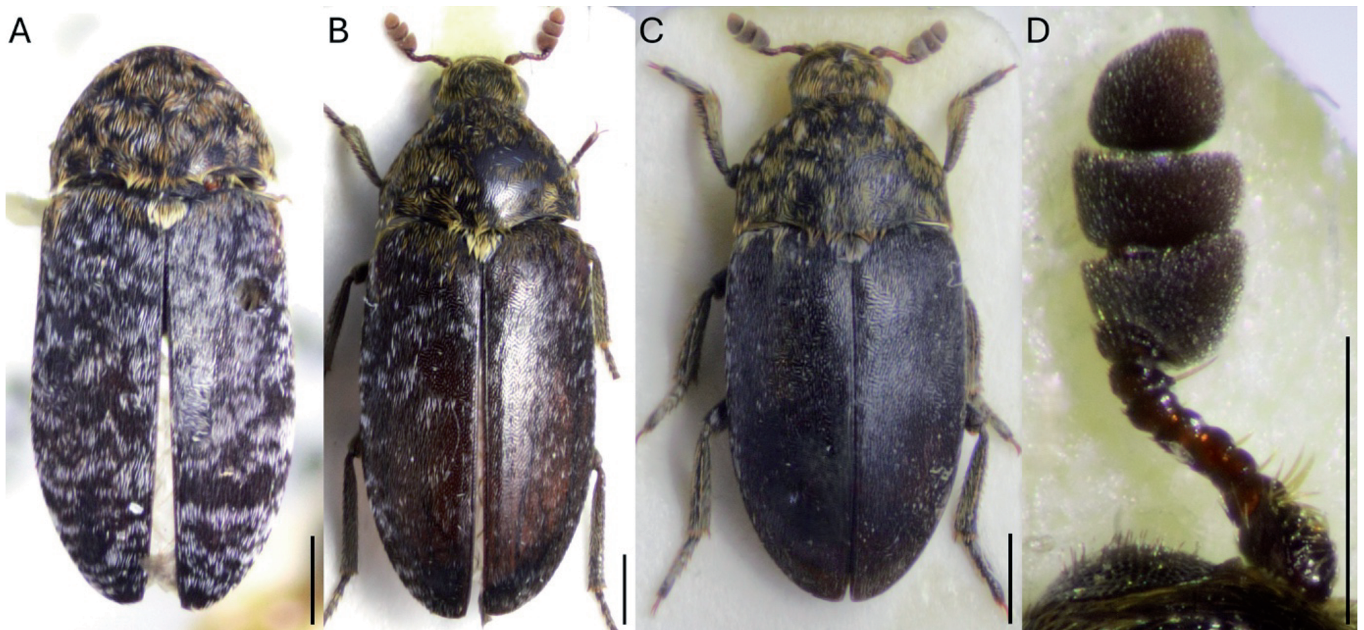


Fig. 3 – A) *Dermestes algeriensis* sp. nov. (scale bar = 1 mm); B) *Dermestes smithi* sp. nov. (scale bar = 1 mm), *Dermestes kazakhstanicus* sp. nov.; C) habitus (scale bar = 1 mm); D) antenna (scale bar = 0.5 mm). / A) *Dermestes algeriensis* sp. nov. (barra di scala = 1 mm); B) *Dermestes smithi* sp. nov. (barra di scala = 1 mm), *Dermestes kazakhstanicus* sp. nov.; C) habitus (barra di scala = 1 mm); D) antenna (barra di scala = 0,5 mm).

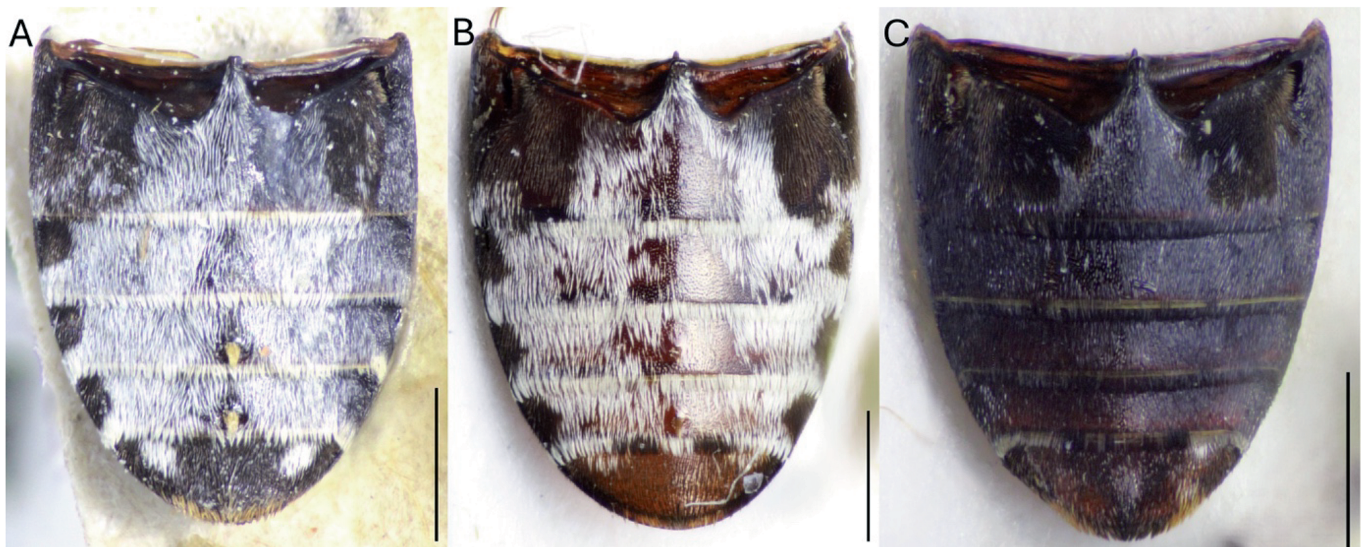


Fig. 4 – Ventrites. A) *Dermestes algeriensis* sp. nov.; B) *Dermestes smithi* sp. nov.; C) *Dermestes kazakhstanicus* sp. nov. Scale bars = 1 mm in all cases. / Ventriti. A) *Dermestes algeriensis* sp. nov.; B) *Dermestes smithi* sp. nov.; C) *Dermestes kazakhstanicus* sp. nov. Barra di scala = 1 mm in tutti i casi.

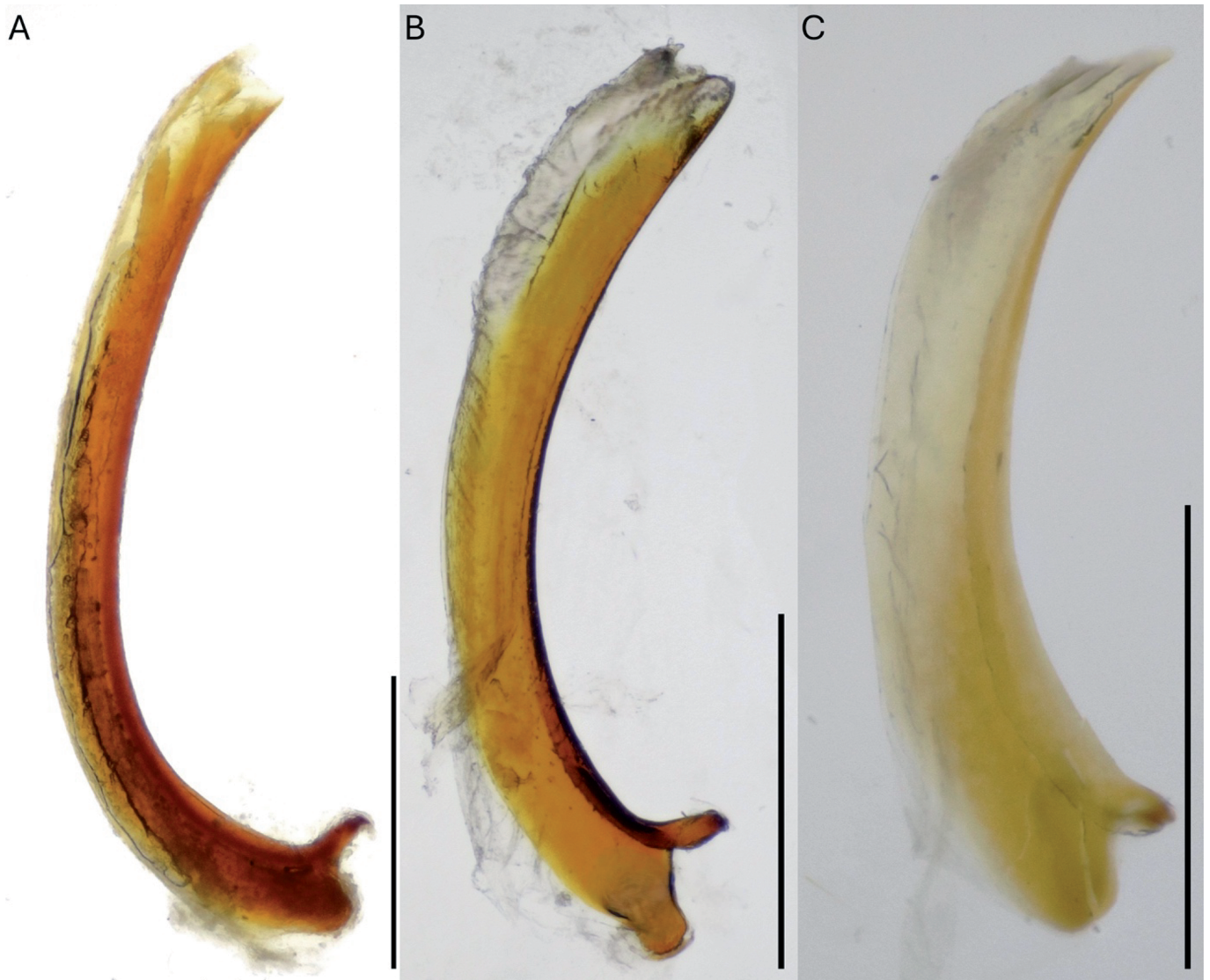


Fig. 5 – Median lobe. A) *Dermestes algeriensis* sp. nov.; B) *Dermestes smithi* sp. nov.; C) *Dermestes kazakhstanicus* sp. nov.. Scale bars = 0.5 mm in all cases. / Lobo mediano. A) *Dermestes algeriensis* sp. nov.; B) *Dermestes smithi* sp. nov.; C) *Dermestes kazakhstanicus* sp. nov.. Barre di scala = 0,5 mm in tutti i casi.

Attachment peg at anterior end on dorsal margin shorter than *D. undulatus* (Fig. 2A). Median lobe unevenly curved with greater curvature in anterior half than posterior half. Sternite IX (Fig. 6A) with posterior lobe approximately  $\frac{1}{4}$  length of entire sternite. Posterior tip is flat possibly with small central notch, lateral margins diverge from each other only slightly producing rectangular appearance. Posterior lobe pale brown apart from whitish margins. Posterior lobe covered in recumbent, fine black hairs all pointing posterior and extending beyond posterior margin where longer hairs curve inwards. Hairs overlapping lateral margins towards posterior end. Anterior to marginal flanges below posterior lobe, lateral margins straight and convergent towards long narrow tail.

#### *Etymology*

The species epithet refers to the type location, Algeria.

#### *Type material*

##### *Holotype*

ALGERIA • ♂ (in good condition) Chiffa Gorge (36.401, 2.767); August 1980; collector P. Lambley; NHMUK.

##### *Paratype*

MOROCCO • ♂ (in good condition) Tetouán (35.581, -5.376); no date; collector J.J. Walker; NHMUK

#### *Dermestes smithi* sp. nov.

Figs. 3-6

urn:lsid:zoobank.org:act:3F1E0EAE-45B3-42D4-9E1F-90106B46451C

One specimen (AHEC)

#### *Diagnosis: external features*

BL (holotype Fig. 3B)=7.35 mm. Integument dark chestnut

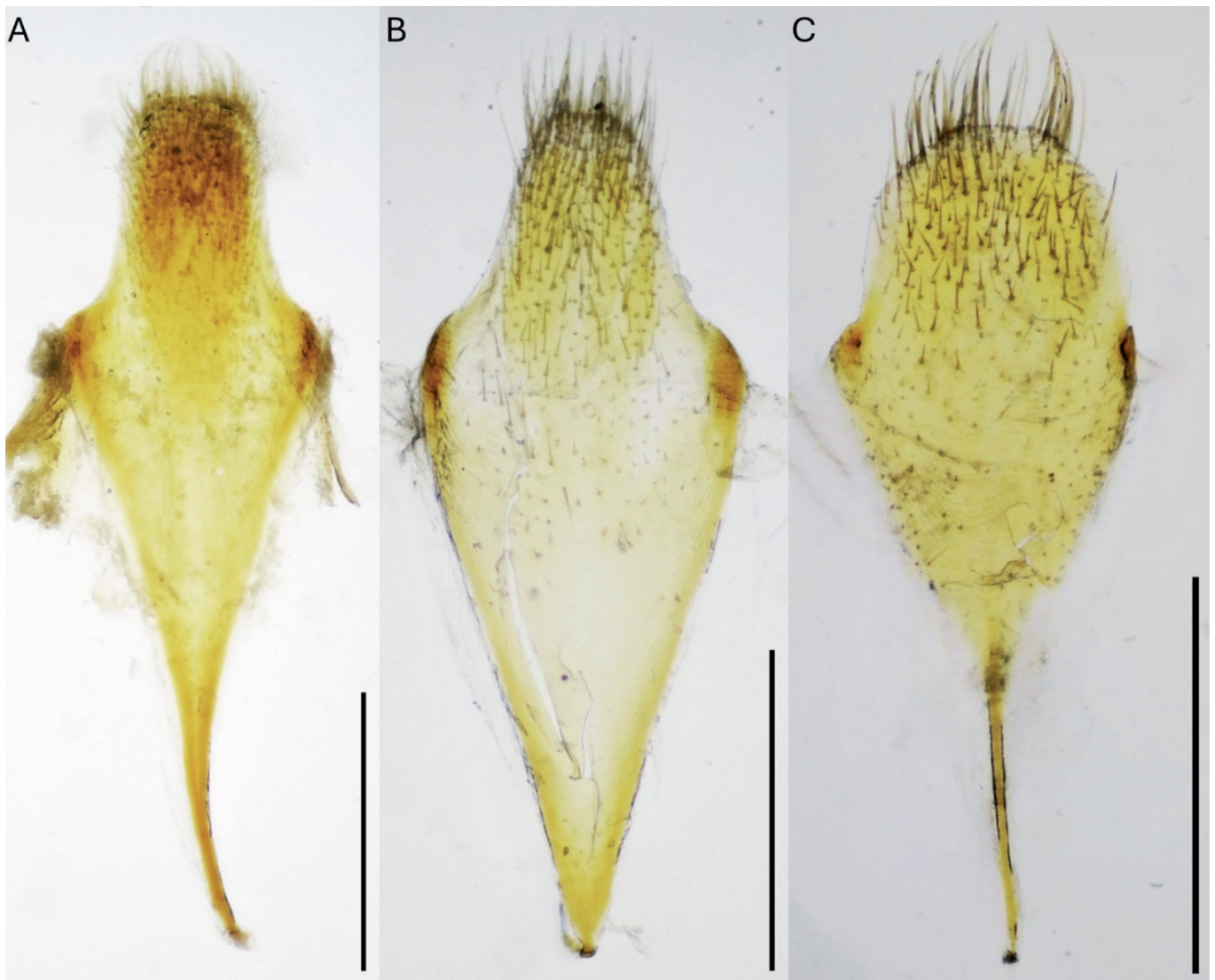


Fig. 6 – Sternite IX. A) *Dermestes algeriensis* sp. nov.; B) *Dermestes smithi* sp. nov.; C) *Dermestes kazakhstanicus* sp. nov.. Scale bars = 0.5 mm in all cases. / Sternite IX. A) *Dermestes algeriensis* sp. nov.; B) *Dermestes smithi* sp. nov.; C) *Dermestes kazakhstanicus* sp. nov.. Barre di scala = 0,5 mm in tutti i casi.

brown rather than black, otherwise similar to *D. undulatus* especially on dorsal surface. Large spots of black hairs at margins of ventrites 3 and 4 (Fig. 4B) below anterior margins so that white hairs encircle black spots (apart from at margin). Large spots of black hairs on margin of ventrite 2 are surrounded by white hairs (not the case in *D. undulatus*). White hairs across anterior margin of ventrite 5 and some on ventrite disc.

#### **Diagnosis: internal features**

Median lobe (Fig. 5B, ML=1.288 mm) evenly curved, mostly pale brown and sclerotized apart from broad section of membrane along ventral margin for final 1/3 to rounded tip. Dorsal margin narrowly edged darker brown for most of length including attachment peg at anterior end. Attachment peg shorter than *D. undulatus* and not forming right angle with dorsal margin, dorsal margin forms smooth curve into peg. Sternite IX (Fig. 6B) posterior lobe short, less than 1/4 of entire length of sternite. Posterior margin evenly curved and down lateral margins that diverge away from each other. Posterior lobe not rectangular as in *D. undulatus*. Posterior lobe pale brown apart from white margins. Posterior lobe covered in black hairs, longest straight hairs extending beyond posterior margin. Lateral margins of posterior lobe continue in anterior direction onto lateral flanges (appearing as brown shoulders) rather than right angles as in *D. undulatus* (Fig. 2C). Below flanges, lateral margins straight and joining at a sharp tip. Sternite IX whitish between flanges and anterior tip with some small black hairs, although lateral margins pale brown.

#### **Etymology**

The species is named after Professor Robert H. Smith, an expert in rodent control and forensic entomology, who guided one of us (GJH) with great patience through his post-graduate and postdoctoral years.

#### **Type material**

##### *Holotype*

KAZAKHSTAN • ♂ (in good condition) S Kazakhstan, Dzhabagly, W. Ugam mountains 1800m (42.298, 70.674); 26 iv 2000; collector unknown; AHEC.

##### *Paratypes*

None.

#### ***Dermestes kazakhstanicus* sp. nov.**

Figs. 3-6

urn:lsid:zoobank.org:act:9C66060B-FC81-453E-8EB1-E0D3178DFB76

One specimen (AHEC)

#### **Diagnosis: external features**

BL (holotype Fig. 3C) =5.63 mm. Similar to *D. undulatus*. There are more patches of white hairs on pronotum and head (but only one specimen so could be phenotypic variation). Ventrite (Fig. 4C) patterning not clear but two patches of ginger hairs present extending inwards towards ventrite disc from posterior margin of ventrite 5. Small patches of white hairs on anterior margin of ventrite 5 extend laterally to lateral margins where they extend a short way posterior. Terminal antennal segment more asymmetrical than *D.*

*undulatus* with a stout spine on anterior surface of antennomere 7 (Fig. 3D).

#### **Diagnosis: internal features**

Median lobe (Fig. 5C) short (ML=0.962 mm) broad and evenly curved along dorsal margin. Sclerotized section of median lobe (pale brown) spans width of lobe at anterior end but narrows to slither along dorsal margin at posterior end. Median lobe (apart from the anterior end) consists mostly of membranous material. Median lobe ends in sharp point at dorsal margin. Short, stubby attachment peg at anterior end angled backwards towards anterior (*D. undulatus* peg longer and at right angles to margin). Sternite IX (Fig. 6C) posterior lobe very broad and evenly rounded, occupying nearly 1/2 the length of membranous part of sternite. Posterior lobe densely hirsute with longest hairs extending beyond posterior margin. Below lateral flanges, a few small, scattered setae. Below flanges, margins converge to point that extends into well-defined, narrow tail.

#### **Etymology**

The species epithet refers to the type location, Kazakhstan.

#### **Type material**

##### *Holotype*

KAZAKHSTAN • ♂ (in good condition) NW Kazakhstan, Aktjubinsk region, Mugodzhar'y (50.283, 57.223); 11 May 1999; collector unknown; AHEC.

##### *Paratypes*

None.

## **DISTRIBUTIONS**

The specimens of *D. undulatus* studied here (Fig. 7) are distributed across the Palaearctic from Iberia in the southwest, north into Germany, east into Crimea and Georgia, south into Turkey. The new species are all peripheral to the distribution of *D. undulatus*, with *D. algeriensis* found in north Africa, *D. smithi* in southern Kazakhstan, and *D. kazakhstanicus* in northwestern Kazakhstan.

## **DISCUSSION AND CONCLUSIONS**

*Dermestes undulatus* has been considered easy to recognise and widely distributed, negating the incentive to examine the species more closely. Presumably, it has never been felt that any further description of the species is required than that provided by Brahm (1790). This is a surprise given the importance of *Dermestes* in forensic science. The community of insects infesting a cadaver is used to estimate the timeline of events, and a great deal of work has been carried out examining the development period of *D. undulatus* under different conditions. It is possible that specimens derived from North Africa or Kazakhstan and which to date have been assumed to be *D. undulatus* (Háva, 2024), have not been studied under various conditions to establish development rates. Since we now know that these peripheral populations are not *D. undulatus*, it is important that these species are also studied to establish their value in forensic science.

The purpose of the current study was to raise and describe a neotype for *D. undulatus* and to establish the *D. un-*

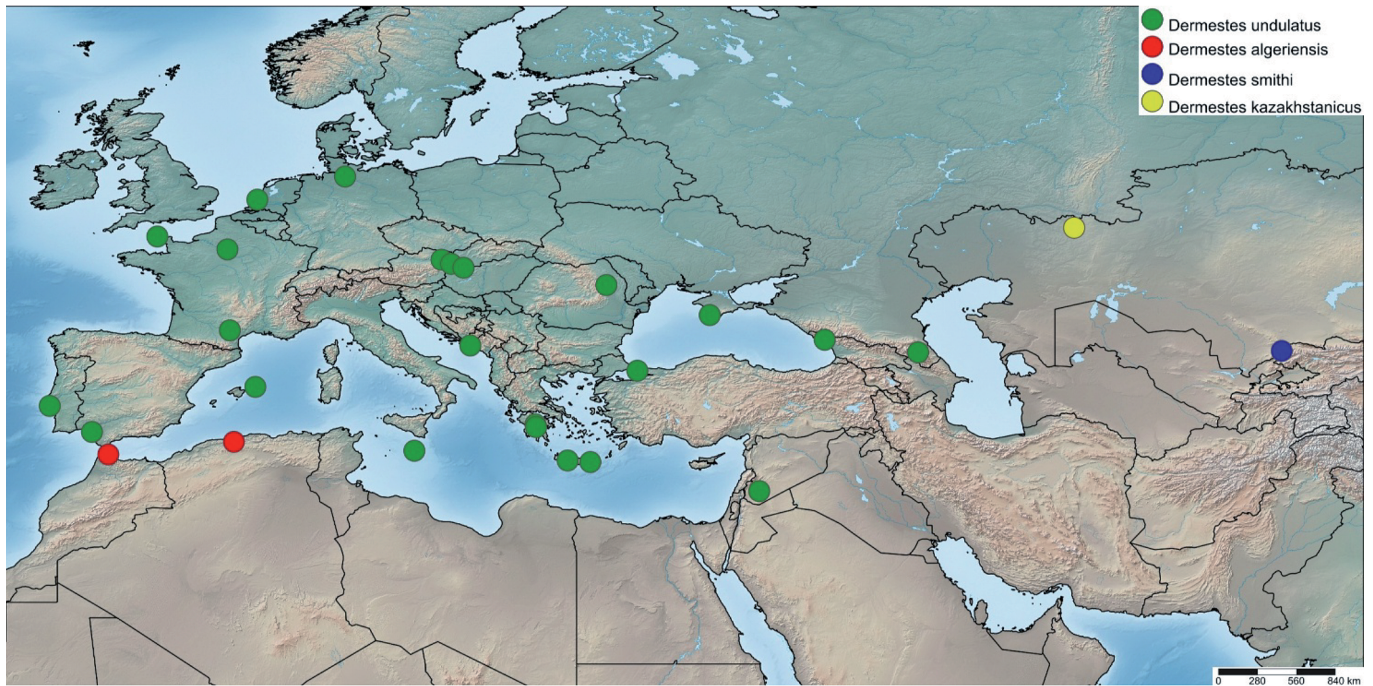


Fig. 7 – Distributions of the points of collection of the specimens of *Dermestes undulatus*, *D. algeriensis*, *D. smithi*, and *D. kazakhstanicus* from the current study. / Distribuzione dei punti di raccolta dei campioni di *Dermestes undulatus*, *D. algeriensis*, *D. smithi* e *D. kazakhstanicus* nell'ambito del presente studio.

*dulatus* range. The whereabouts of the holotype *D. undulatus* is unknown (Háva, 2024), if indeed there ever was one. Brahm lived in Mainz and all his work appears to have been within the Rhineland-Palatinate region of western Germany (Niehuis, 2011). Furthermore, all his discoveries were of species that can be found in Rhineland-Palatinate (Brahm, 1790; Niehuis, 2011), so it is reasonable to assume that the holotype *D. undulatus* was found there as well. The neotype specimen described here and associated paratypes were collected in Germany.

The current study establishes that *D. undulatus* is a species complex. Háva (2024) describes the distribution of *D. undulatus* as across North Africa, the whole of Europe, and very large parts of Asia. The current study casts doubt on the accuracy of parts of this distribution, although *D. undulatus* is certainly widely distributed (Fig. 7). Háva (2024) states that *D. undulatus* is found in all north African countries from Morocco to Egypt; results from the current study would suggest that this is the likely distribution of *D. algeriensis* (Fig. 7). Two new species from Asia, *D. smithi* and *D. kazakhstanicus* suggests that Asian *D. undulatus* require more attention to establish how far the distribution of *D. undulatus* extends in Asia and whether more Asian species within the *D. undulatus* complex exist.

Theoreticians have speculated for many years on the various mechanisms through which speciation could occur (Ridley, 2004; Futuyama, 2005), but all agree that allopatric (isolated geographical populations) is the most common route, at least in animals (Mayr, 1963; Coyne & Orr, 2004). Isolation is considered likely to occur at the edge of ranges, providing conditions for allopatric speciation to occur. Fig. 7 shows that all three new species described here lie on the periphery of the *D. undulatus* distribution.

## ACKNOWLEDGEMENTS

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