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Research Article

From cabinets to collectomics: discovering females and primary larvae of Strepsiptera in a historical collection

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Abstract

Natural history collections house material from centuries of collecting efforts. In the Phyletisches Museum Jena (PMJ), ca. 1 Mio specimens are deposited, some of them dating back as far as the 17th century. Modern imaging techniques have the potential to gain new insights from this historical material. However, a large part of the PMJ insect collection has not been revised by scientists in recent times. We screened the entire Auchenorrhyncha collection and found several specimens parasitized by two different species of the genus *Halictophagus* (Halictophagidae, Strepsiptera) that had previously been overlooked. These historical findings represent the only evidence to date of the occurrence of these two species in Germany and therefore suggest, at least historically, a larger distribution area than was previously known. In addition, hitherto unknown females and primary larvae were morphologically documented using state-of-the-art techniques such as synchrotron-radiation-based X-ray μCT and scanning electron microscopy. The data generated in this study cover the field of collectomics and can be seamlessly used as a basis for the emerging discipline of museomics. In taxonomic and systematic research and in the context of environmental change, pinned insects may play an outstanding role in the near future, as their DNA is not damaged by formalin fixation and thus can yield remarkable results even after more than 100 years. Our results underpin the value of historical material for modern research questions, especially for species that are difficult to find in nature.

Key words: Collectomics, insect, museum, natural history collections, parasite, provenance, Strepsiptera, synchrotron μCT

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Introduction

Natural history collections (NHC) play a crucial role in biodiversity research. They provide information about where a species occurred at a certain point in time (Lane 1996; Ward 2012), give new insights into evolutionary changes (Holmes et al. 2016), and enable phylogenetic interpretations. These collections are also increasingly important for research in the context of human-driven climate change, deforestation, invasive species, and intensive agriculture. Therefore, insect collections take a prominent role, as they not only comprise many millions of specimens but are well represented in almost all NHCs. Moreover,

insects are the most diverse group of organisms on the planet (Kharouba et al. 2019). An essential point is that NHCs form the backbone of taxonomy, as they contain crucial type specimens and potentially specimens still unknown to science. Some of these specimens may already be extinct in nature and are only preserved in collections (Zimmer 2023). However, it is important to note that their importance does not end with the naming of new species; they can also be used to test taxonomic, phylogenetic, or evolutionary hypotheses.

The Phyletisches Museum Jena (PMJ) collection houses historically and scientifically valuable specimens, such as the Goethe-Auerochs (the type specimen of *Bos primigenius* Bojanus, 1825) (von Knorre and Beutel 2018) or a series of type specimens described by the famous but controversial museum founder Ernst Haeckel (1834–1919). Besides this, the museum has an important insect collection of both local faunistic samples and specimens from all over the world, e.g., from the Kerguelen Islands, Sri Lanka, and China. Moreover, the collection contains valuable insects from a historically rare private collection of Chalcidoidea by Ferdinand Rudow (Krogmann et al. 2007) or, as published in current studies, type material of Psocodea, Coleoptera, and Formicidae (Boudinot et al. 2024; Weingardt et al. 2025). Additionally, a highlight of the PMJ insect material is valuable species of Strepsiptera, including all postembryonic stages and also stem group fossils (Pohl et al. 2005, 2021; Pohl and Beutel 2016).

The historical Auchenorrhyncha (Hemiptera) collections of Adolf Frank and Ernst Schmidt contain more than 4,000 pinned specimens. For the first time, they were systematically screened for parasitism by twisted-wing parasites (Strepsiptera). This small order of holometabolous insects contains around 650 species worldwide (Cook 2019; Millena et al. 2025). It displays a specialized lifestyle with minute and free-living primary larvae, subsequent endoparasitic larval stages, endoparasitic females (except for Mengenillidae) that exhibit paedomorphic features, and extremely short-lived males (Pohl and Beutel 2005, 2008; Kathirithamby 2018, 2025a; Millena et al. 2025).

The evaluation revealed parasitism of female individuals of two different species of the genus *Halictophagus* Curtis, 1832 (Strepsiptera, Halictophagidae). This genus currently contains six valid species in Europe, which are parasites of different species of Auchenorrhyncha (Kinzelbach 1978; Cook 2019). Two species are currently described from Germany: *Halictophagus silwoodensis* Waloff, 1981 and *Halictophagus agalliae* Abdul-Nour, 1970 (Melber 1989; Pohl and Melber 1996; Rösch 2023).

We found a female of *Halictophagus tettigometrae* Silvestri, 1934 stylopizing (i.e. a strepsipteran parasitizing its host) *Tettigometra impressopunctata* Dufour, 1846 (Auchenorrhyncha, Tettigometridae), and four previously undescribed females stylopizing *Eupelix cuspidata* Fabricius, 1775 (Auchenorrhyncha, Cicadellidae). Furthermore, we discovered minute primary larvae of both species inside the respective females. *H. tettigometrae* was not previously known from Germany and has only been found at a few historical localities (Silvestri 1934, 1941; Kinzelbach 1978; Cook 2019; GBIF 2025b; Kathirithamby 2025b). We documented the parasitized specimens using microphotography, scanning electron microscopy (SEM), and synchrotron-radiation micro-computed tomography (SR-µCT). Our findings highlight the importance of museum collections, not only with respect to taxonomic issues but also in a broader

context of evolution and climate change. Furthermore, we provide a complete checklist (Suppl. material 1) of the Auchenorrhyncha collection of the PMJ contained in the so-called “Hauptsammlung” (main collection).

Material and methods

Abbreviations of collections

PMJ Phyletisches Museum Jena, Germany
SMF Senckenberg Museum Frankfurt a. M., Germany

Material

Examined material

Halictophagus sp.

GERMANY – Thuringia • 1 ♀; Erfurt; 7 Apr. 1891; A. Frank leg.; collected in host *E. cuspidata*; glued onto cardboard, in host; original label: Erfurt; Thymus; 7.4.1891; Frank; *feroducta*; Gen. [handwritten label]; PMJ Hex 998 • 2 ♀, 23 primary larvae; Erfurt; 11 Oct. 1891; A. Frank leg.; collected in host *E. cuspidata*; glued onto cardboard, in host; original label: Erfurt; Rasen; 11.10.1891; Frank. [handwritten label]; PMJ Hex 998 • 1 ♀; Braunsdorf; 8 Aug. 1892; A. Frank leg.; collected in host *E. cuspidata*, glued onto cardboard, in host; original label: Braunsdorf, Wiesengras; 8.8.1892; Frank; *spathulata*; coll. Frank 1930. [handwritten label]; PMJ Hex 998.

Halictophagus tettigometrae

GERMANY • 1 ♀, 5 primary larvae; Thuringia, Arnstadt, Angelhausen-Oberndorf; 24 Jun. 1936; E. Schmidt leg.; collected in host *T. impressopunctata*; glued onto cardboard, in host; original label: E. Schmidt; 24.6.36; Oberndorf; Arnst.; *Tettigometra impressopunctata*. Duf.; det. E. Schmidt; ♂. [handwritten label]; PMJ Hex 989.

Material used for comparison

Halictophagus tettigometrae

HUNGARY • 1 ♀; Fejér, Soponya; 23 Sep. 1923; G. Horváth leg.; collected in host *T. impressopunctata* Dufour, 1846 (Auchenorrhyncha, Tettigometridae); cephalothorax on slide; original labels: *Halictophagus*; ♀; SMFS53; Kartei-Nr. 0981; R. KINZELBACH; det. 1973; Nagyláng (Ung.); 23. IX. 1923; ex: *Tettigometra impressopunctata* Duf.; det. HORVÁTH; leg. HORVÁTH. [handwritten label]; SMFS53.

ITALY • 4 ♀; Caserta, Piedimonte d’Alife; F. Silvestri leg.; collected in host *Tettigometra impressifrons* Mulsant et Rey, 1855 (Auchenorrhyncha, Tettigometridae); on slide; original labels: *Halictophagus tettigometrae* SILV.; L1; SMFS54/2; Kartei-Nr. 0305; R. KINZELBACH; det.; Piedimonte d’Alife; ex: *Tettigometra impressifrons* Muls & Ray; det. F. SILVESTRI; leg. F. SILVESTRI. [handwritten label]; SMFS54/2.

Methods

Screening

The insects from 22 drawers were manually counted, and a checklist was compiled (Suppl. material 1). For the visual identification of infestation by strepsipteran parasites, we used a Zeiss Stemi SV 11 (Carl Zeiss, Oberkochen, Germany) and a Leica MS 5 (Leica, Wetzlar, Germany), with a maximum magnification of 40×.

Provenance of specimens

Collection of Adolf Frank

A well-known private collection in the stock of the museum fundus is that of Adolf Frank (1849–1921). It was purchased by the museum using financial resources from the collector Otto Wohlberedt (1870–1945) in 1930. The collection is mostly known for its more than 8,000 dipteran specimens, accompanied by a five-volume catalogue handwritten by Adolf Frank. This catalogue contains information on locality, ecology, and faunistics, as well as literature references related to collected species (Bährmann 2004) (Fig. 1C). This underlines that the collection is an outstanding source of scientific information (Jentzsch 2016). In addition to his well-known Diptera collection, Frank published a comprehensive work on the Hemiptera of Thuringia (Frank 1913). He collected approximately 6,000 hemipteran specimens, with the majority belonging to Heteroptera, and only those are treated in his publications. Within this collection, slightly more than 1,000 specimens belong to Auchenorrhyncha, including 49 individuals of *Eupelix cuspidata* (Cicadellidae), mostly from the region of Erfurt (Thuringia). The Frank collection was integrated into the "Hauptsammlung" of the Phyletisches Museum but remains distinguishable from other parts of the collection by its labels stating "Adolf Frank 1930."

Collection of Ernst Schmidt

The well-documented private collection of Ernst Wilhelm Schmidt (1884–1962, Arnstadt, Thuringia, Germany) was added to the collection of the Phyletisches Museum in 1966 through a donation by his son Joachim Schmidt (1913–1999). Very little is known about Ernst Schmidt, except for what is mentioned by von Knorre and Thiele (2016) in "Forscher- und Erfindergeist aus Arnstadt". Schmidt had profound knowledge of Heteroptera (true bugs) and Auchenorrhyncha and assembled a remarkably comprehensive and well-documented collection. It consisted of around 9,000 heteropteran specimens and ca. 2,500 specimens of the clade Auchenorrhyncha. As in the case of the Frank collection, specimens from the Schmidt collection can be identified by labels stating "E. Schmidt Arnstadt." Within this collection, we found 32 specimens of *T. impressopunctata*, one of which was stylopized by *H. tettigometrae*. Most individuals from Schmidt's collection were collected by himself, including the stylopized planthoppers. Today, the Schmidt collection is split, with parts stored at the Naturkundemuseum Stuttgart (Baden-Württemberg, Germany) and at the Senckenberg Deutsches Entomologisches Institut (SDEI) in Müncheberg (Brandenburg, Germany) (Schawaller 2016).

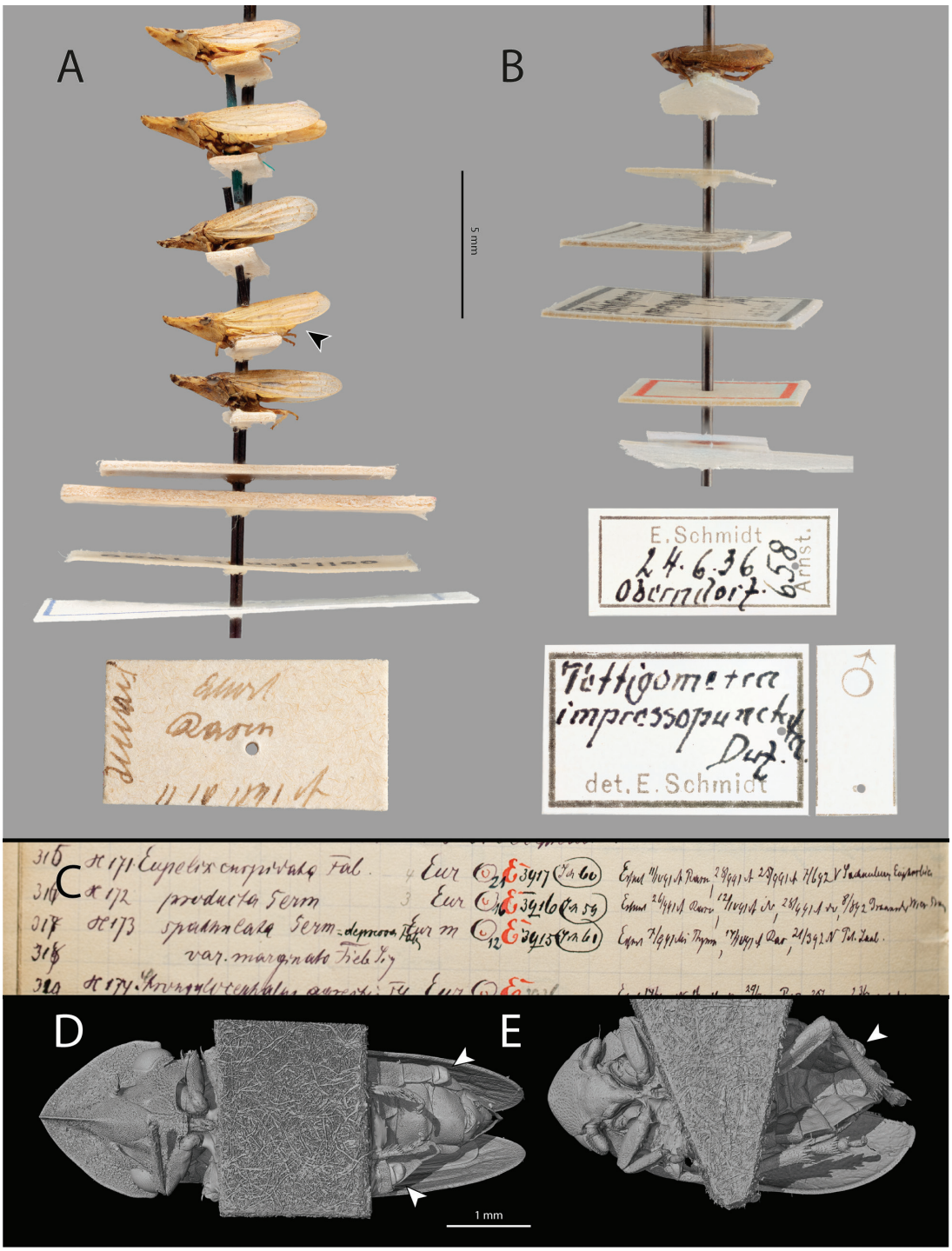

Figure 1. A. Photographs of *Eupelix cuspidata* specimens from Adolf Frank's collection in the PMJ, showing the delicate "stacking" of several individuals typical for his collection; the arrow indicates the stylopized individual that was SR-µCT-scanned at DESY; the original label with Adolf Frank's handwriting states "Frank," "Erfurt" (Thuringia, Germany), "Rasen" (on lawn), and "11.10.1891 A" (A = his short signature); **B.** Photograph of a stylopized *Tettigometra impressopunctata* specimen from Ernst Schmidt's collection in PMJ; the original label from Schmidt states "E. Schmidt," "Arnst." (Arnstadt, Thuringia, Germany), "24.6.36" (1936), and "Oberndorf" (Oberndorf, near Arnstadt, Thuringia, Germany); **C.** Photograph of Adolf Frank's collection ledger containing catalogue numbers of collected specimens, locality, host plant, and date; **D.** 3D reconstruction of *Eupelix cuspidata* with two female *Halictophagus* sp., ventral view; arrows indicate female cephalothoraces (interactive version of this model available on Sketchfab: https://skfb.ly/pFMzF); **E.** 3D reconstruction of a *Tettigometra impressopunctata* specimen with one female *Halictophagus tettigometrae*, ventral view; the arrow indicates the female cephalothorax (interactive version of this model available on Sketchfab: https://skfb.ly/pFMzI).

Sample preparation for micro-computed tomography (µCT)

The insects in the drawers were glued onto cardboard. The pins fixing the pieces of cardboard were replaced by a self-made Poly(methyl methacrylate) needle. This ensured stable mechanical fixation and safe handling of the specimens. The Poly-needle was fixed on the sample holder with hot glue (Fig. 2). Poly(methyl methacrylate) was chosen as it does not yield artifacts and remained stable during scanning (authors' personal observations in previous scans). The same sample preparation was applied to all scanned specimens.

µCT

Desktop µCT scan

The abdomen of a specimen of *Eupelix cuspidata* containing two strepsipteran females of *Halictophagus* sp. was scanned with a SkyScan 1272 (Bruker, Billerica, USA) at the Max Planck Institute for Chemical Ecology, with a pixel size of 1.00 µm, to check for the presence of strepsipteran primary larvae.

The specimen of *T. impressopunctata* containing a female of *H. tettigometrae* was scanned with an Easytom XL CT scanner (RX Solutions, Chavanod, France) at the Helmholtz-Zentrum Hereon. A helical tomography profile was applied, reaching a pixel size of 1.94 µm at a voltage of 80 kV.

SR-µCT scan

The same *E. cuspidata* specimen was scanned in its entirety (fsu_303_PMJ_hal_a & b, ID: 11020683) using synchrotron radiation at Beamline P05 (IBL) (Haibel et al. 2010; Greving et al. 2014; Wilde et al. 2016), operated by the Helmholtz-Zentrum Hereon at the storage ring PETRA III (Deutsches Elektronen Synchrotron—DESY, Hamburg, Germany). A detector distance of 80 mm and a photon energy of 20 keV were used. Projections were recorded using a custom-developed 20 MP CMOS camera system (Lytaev et al. 2014) with an effective pixel size of 0.64 µm. A total of 3,501 projections were recorded for each tomographic scan, with an exposure time of 250 ms. Raw projections were binned two times, resulting in an effective pixel size of 1.28 µm in the reconstructed volume. Tomographic reconstruction was performed by applying transport-of-intensity phase retrieval and using the filtered back-projection algorithm (FBP) implemented in a custom reconstruction pipeline (Moosmann et al. 2014) using MATLAB (MathWorks, Natick, MA, USA) and the Astra Toolbox (Palenstijn et al. 2011; Van Aarle et al. 2015, 2016). The scan was conducted as a two-section scan along the z-axis to avoid artifacts during the scanning process (Giantsoudi et al. 2017).

Data segmentation and rendering

The SR-µCT-generated image stack of *E. cuspidata* and the µCT-generated image stack of *T. impressopunctata* were segmented and 3D-reconstructed in Amira 6.0.1 (Thermo Fisher Scientific, Waltham, MA, USA). TIFF image stacks

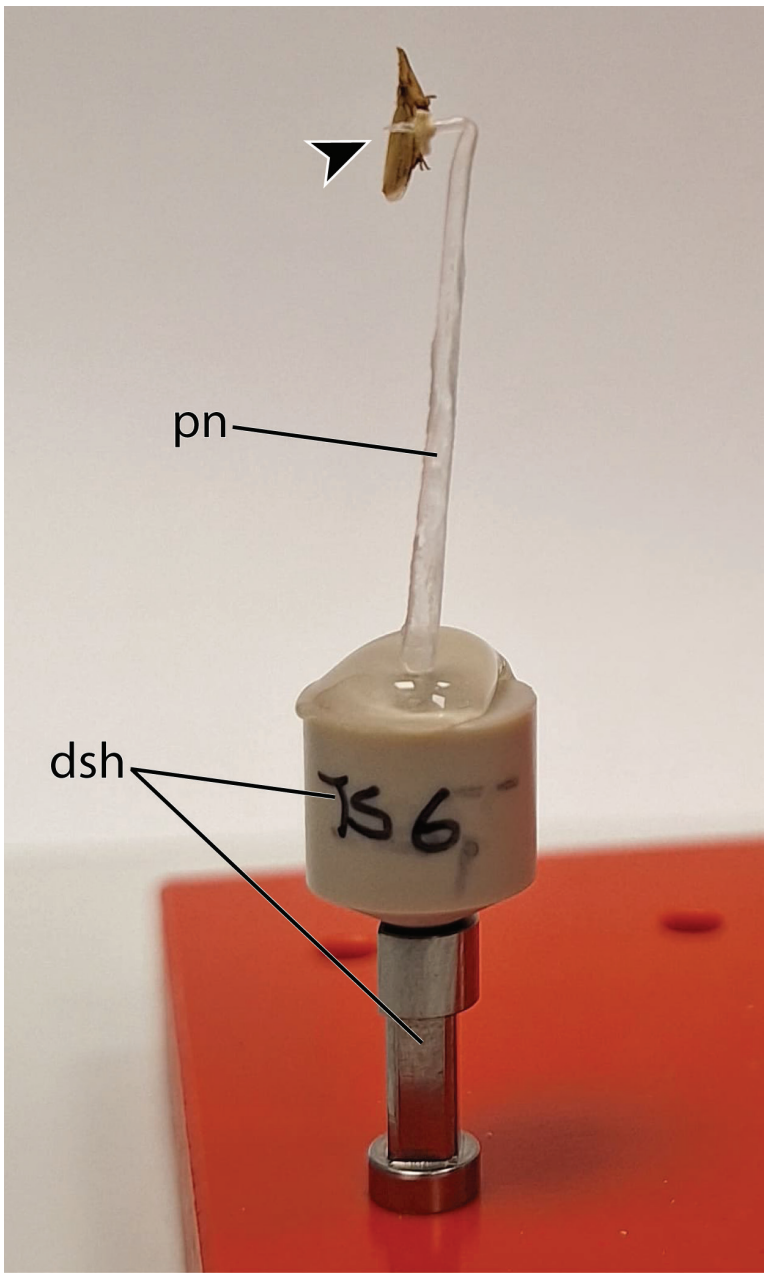

Figure 2. A scan setup for a historical specimen of *Eupelix cuspidata*. The arrow indicates the specimen. dsh, DESY sample holder; pn, Poly-needle (the Poly-needle was heated and bent at the tip for improved specimen adjustment to the scan setup).

and isosurfaces were exported (Amira macro "Multi-Export"; Engelkes et al. 2018), and the isosurfaces were reduced and smoothed (parameters: itTotal = 5; smooth: iteration = 4, lambda = 0.6; reduction = 0.6). Surface renders were further simplified (modifier: decimate) and smoothed (modifier: smooth), and 3D models were created using Blender (Blender Foundation, Amsterdam, Netherlands; version 4.3.2). The 3D models were subsequently uploaded to Sketchfab (https://sketchfab.com) via the free Blender plugin Sketchfab for Blender 1.5.0 (https://github.com/sketchfab/blender-plugin/releases/tag/1.5.0). TIFF image stacks were imported into VGStudio Max 2.0 (Volume Graphics, Heidelberg, Germany), and the Phong reflection model option was used for volume rendering.

Sample preparation for microphotography and SEM

One dried *E. cuspidata* specimen containing two female *Halictophagus* sp. and one *T. impressopunctata* specimen containing one female of *H. tettigometrae* (both with primary larvae as observed in the µCT scans) were rehydrated under a glass dome using hot water vapor. Females and primary larvae were dissected from the host and transferred into 70% ethanol. Primary larvae were placed inside a microporous chamber (Electron Microscopy Sciences, Hatfield, Pennsylvania). In a descending ethanol series, both were brought down to 10% ethanol (70%, 10 min; 50%, 10 min; 40%, 10 min; 20%, 10 min; 10%, 10 min) and rinsed twice with aqua dest. Females and primary larvae were then cleaned with Proteinase K (5 mg/ml) (recombinant, PCR grade; buffer: 30 mM Tris-HCl) (Roche Diagnostics, Rotkreuz, Switzerland) (Schneeberg et al. 2017) for approximately 2 days at 37 °C. Additionally, the females were cleaned of sugary excretions from their hosts using 100% chloroform for 2 days at 40 °C (Ammar et al. 2015). Afterwards, both were transferred through an ascending ethanol series and finally placed in absolute ethanol (aqua dest., 10%, 10 min; 20%, 10 min; 40%, 10 min; 50%, 10 min; 70%, 10 min; 80%, 10 min; 90%, 10 min; 4x eth. abs., 10 min).

Microphotography

Overview images of the stylopized *E. cuspidata* and *T. impressopunctata* specimens were taken with a Canon EOS 6D (Canon, Krefeld, Germany) mounted on a StackShot macro rail (Cognisys, Traverse City, MI, USA) and equipped with a Canon MP-E 65 mm f/2.8 1–5× macro photo lens (Canon, Krefeld, Germany). Single focused images were stacked using Zerene Stacker 1.04 (Zerene Systems, Richland, WA, USA). For even illumination, a white plastic dome (Rayher, Laupheim, Germany) was ground with abrasive paper (Starcke, Melle, Germany), colored with white (RAL 9010) spray paint (Maston, Veikkola, Finland), and placed over the specimen. The scene was illuminated by two flash units (Phottix Juno Li60 Flash, New York, USA) controlled with two Yongnuo RF603C II wireless triggers (Yongnuo, Shenzhen, China). The insects glued on cardboard were pinned onto a piece of white foam. For detailed images of the dissected female cephalothoraces of *Halictophagus* sp. and *H. tettigometrae*, the same setup was used, except that the Canon MP-E lens was replaced with a Mitutoyo M Plan Apo 10× (Mitutoyo, Kawasaki, Japan). Specimens were transferred from absolute ethanol into Balea hand sanitizer gel (dm Drogeriemarkt, Karlsruhe, Germany) in a Petri dish, and a coverslip was placed over the sample. All images were developed using Adobe Lightroom Classic (version 11.5), and editing and image plates were prepared using Adobe Photoshop 2024 and Adobe Illustrator 2024 (Adobe, San Jose, USA). The photograph of the DESY sample setup (Fig. 2) was taken using a Samsung Galaxy A54 5G (Samsung, Suwon, South Korea) with standard settings.

SEM

The specimens were dehydrated at the critical point using an EM CPD300 critical point dryer (Leica, Wetzlar, Germany) at the Max Planck Institute for

Chemical Ecology, applying the "super slow" option. Primary larvae of *Halictophagus* sp. were subsequently mounted on a conductive tab (Plano GmbH, Wetzlar, Germany) using a fine hair. Too few primary larvae were found inside the female of *H. tettigometrae* (n = 5) for SEM examination. They were stored inside the microporous chamber and will be documented using a less invasive technique in an upcoming project. One female of *Halictophagus* sp. and the female of *H. tettigometrae* were glued to a micro-needle and mounted on a rotatable specimen holder (Pohl 2010). All samples were subsequently coated with gold using an Emitech K 500 (Quorum Technologies, Ashford, Great Britain). SEM micrographs were taken with a Philips ESEM XL30 (Philips, Amsterdam, Netherlands). Overview images were acquired at a high voltage of 10 kV. For detailed images, a high voltage of 19 kV was used. In both cases, a working distance of 5 mm was chosen.

Line drawings

Drawings of the legs and sternal plates of the primary larva of *Halictophagus* sp. were produced using Adobe Fresco (v. 4.8.0) (Adobe Systems Incorporated, San Jose, USA) and were based on SEM micrographs.

Measurements

The female cephalothoraces and primary larvae were measured based on SEM micrographs and microphotographs using the "ruler" tool in Adobe Photoshop 2024 (Adobe, San Jose, USA). The cephalothorax length was measured from the apex of the frontoclypeal region to the constriction of abdominal segment I. The width of the cephalothorax was defined as the maximum distance between its lateral margins. The length of the head region was measured from the tip of the cephalothorax to the anterior margin of the birth opening. The total length of the primary larvae was measured from the apex of the head to the tip of abdominal segment XI, excluding the caudal setae. Width was measured at the maximum distance between the lateral margins of the larval body, usually at abdominal segment II. The total length of the caudal setae was also measured.

Terminology

The terminology of the female cephalothoraces was adopted from Benda et al. (2022). It was originally established for females of Xenidae (Strepsiptera) and was adapted for the family Halictophagidae in some cases in this study. The terminology for primary larvae was adopted from Pohl (2000). The nomenclature for the chaetotaxy of the primary larvae was also adopted from Pohl (2000), in which various older terms used in the literature were standardized. The color of the female cephalothoraces likely faded during decades of storage and therefore probably does not correspond to the coloration of fresh specimens. Consequently, only darker and lighter shades are referred to. The female cephalothorax is morphologically described in the anatomically correct orientation, although its functional orientation in the host's body is inverted.

Results

Morphological description of examined life stages

Halictophagus sp.

Female (Figs 3, 4)

Diagnosis of female cephalothorax. The female of *Halictophagus* sp. is identifiable among all other *Halictophagus* described from Europe by the following combination of morphological features: Cephalothorax bell-shaped (Figs 3A, 4A), birth opening with slightly arcuate anterior margin but strongly bent posteriorly on both sides, nearly reaching posterior margin of cephalothorax in front of the spiracle (Figs 3A, 4A), mandible with one pronounced subapical bulge and one acute apical tooth (Fig. 4E), area of ventral pigmentation of abdominal segment I drop shaped (Fig. 3A). It differs from *Halictophagus kuehnelti* Hofeneder, 1949, *H. silwoodensis,* and *H. tettigometrae* in the presence of one mandibular tooth and a pronounced subapical bulge instead of two mandibular teeth and the shape of the birth opening, which is triangular in *H. kuehnelti*, bent posteriorly and reaches the edge of the cephalothorax in a semicircle in *H. silwoodensis,* and kidney-shaped in *H. tettigometrae* (Fig. 9A) (Silvestri 1941; Hofeneder 1949; Kinzelbach 1978; Waloff 1981). From *H. agalliae* it differs in the shape of the cephalothorax, which is quadratic in that species (Abdul-Nour 1970). The corner behind the spiracles is bent at an angle of 150° in *Halictophagus languedoci* Abdul-Nour, 1969, in contrast to an angle of 90° in *Halictophagus* sp. (Abdul-Nour 1969).

Position in host. *E. cuspidata* (♀): ♀ underneath tergite VI, ventrolateral, left side; *E. cuspidata* (♂): ♀ underneath tergite VI, ventrolateral, left side; *E. cuspidata* (♂): ♀1 underneath tergite V, ventrolateral, left side; ♀2 underneath abdominal segment VII, ventrolateral, right side (Figs 1D, 3C).

Measurements: (in µm): length of cephalothoraces: 262, 259; width of cephalothoraces: 250, 275; length of head region (tip of cephalothorax to birth opening): 153, 152.

Description of cephalothorax. *Coloration and shape*: mostly with uniform dark coloration, but regions around mandibular capsule, mouth opening, and spiracles darker, clypeal lobe and pigmentation of abdominal segment I with lighter shade (Fig. 3A, B); bell-shaped, as long as wide, anteriorly tapering, and slightly arcuate; corner below spiracles rounded, bent with angle of almost 90°; cephalothorax abruptly narrowing below spiracles (Figs 3A, 4A); multiple longitudinal strengthening ridges present dorsolaterally (Fig. 4D), cuticle of entire dorsal side smooth (Fig. 4B, D, F); drop-shaped area of abdominal segment I with darker pigmentation (Fig. 3A).

Cephalic area*:** anterior clypeal area forming blunt clypeal lobe, protruding rostrally, with circular pits distributed evenly over entire dorsal area; ventral area smooth (Fig. 4C); borders between clypeal, frontal and labral area indistinct; labral area rectangular, with groups of small circular pits distributed over posterior side; mouth opening present as transverse cleft, arcuate on each side (Fig. 4A, B); cuticle of anteroventral side smooth; lateral side of cephalic region slightly bulging (Fig. 4A, B, F), with cuticle with small circular pits distributed over entire area; head region distinctly separated posteroventrally from remaining cephalothorax by birth opening (Fig. 4A), but border indistinct dorsally; ***an-

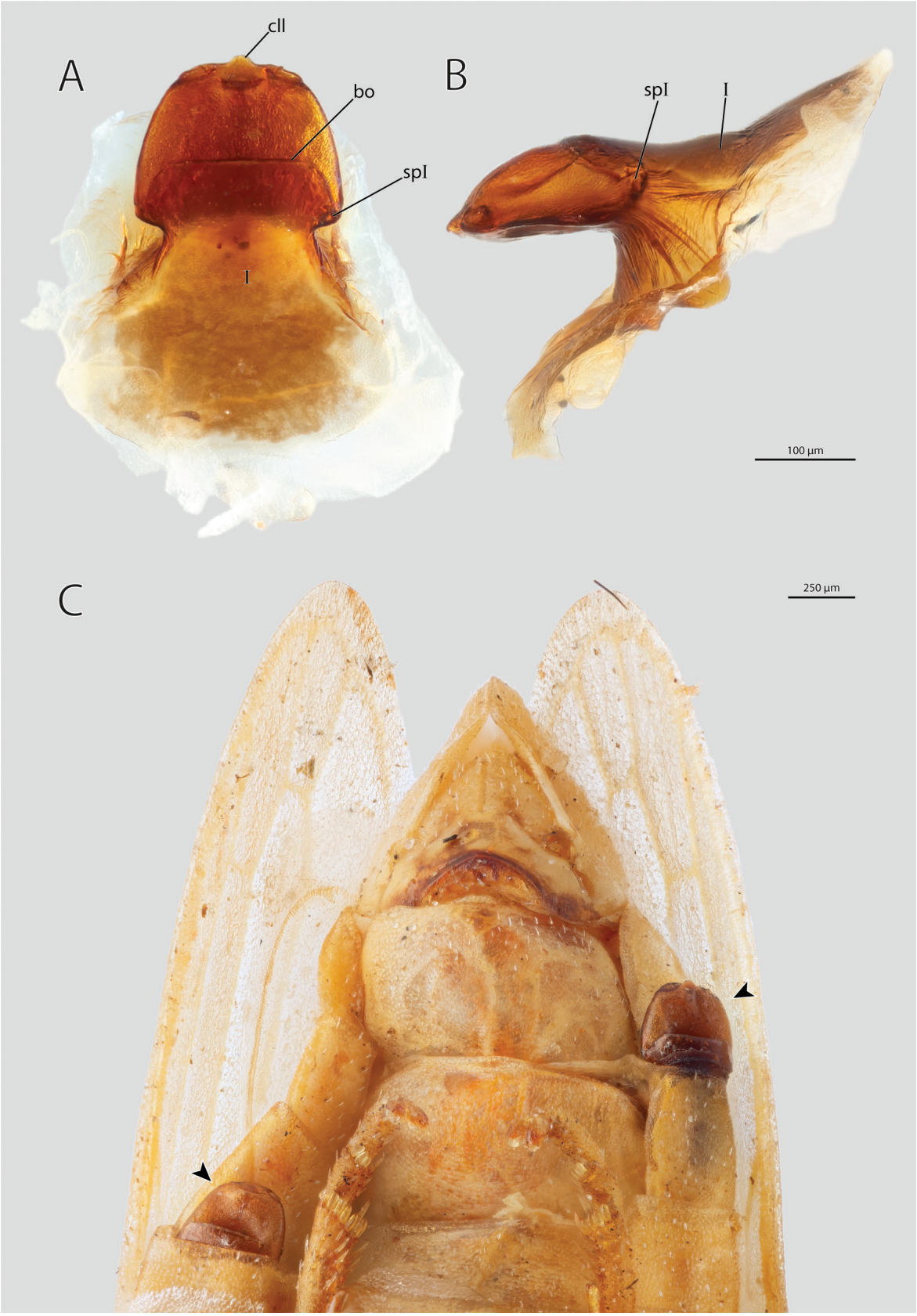

Figure 3. Female cephalothoraces of *Halictophagus* sp. from Adolf Frank's collection in PMJ, photomicrographs; **A.** Cephalothorax of *Halictophagus* sp. in ventral view; **B.** Cephalothorax of *Halictophagus* sp. in lateral view; **C.** Two female cephalothoraces endoparasitic within the abdomen of *Eupelix cuspidata*. Arrows indicate the two female cephalothoraces. bo, birth opening; cll, clypeal lobe; spI, spiracle of abdominal segment I; I, abdominal segment I.

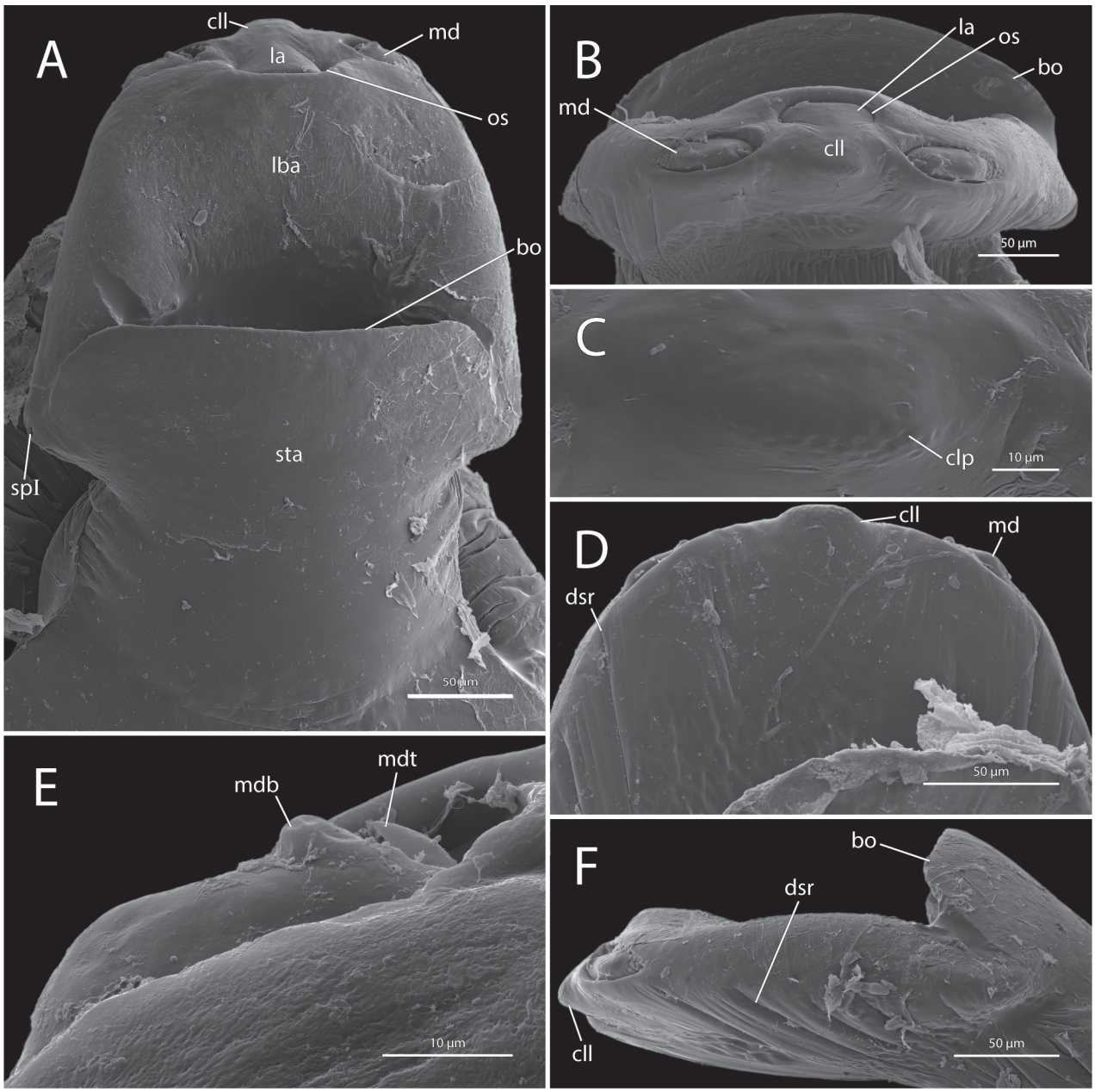

Figure 4. Female cephalothorax of *Halictophagus* sp. from Adolf Frank's collection in PMJ, SEM micrographs; **A.** Ventral view; **B.** Frontal view; **C.** Clypeal area in fontal view; **D.** Dorsal view; **E.** Mandible in ventral view; **F.** Lateral view; bo, birth opening; cll, clypeal lobe; clp, clypeal pits; la, labral area; lba, labial area; dsr, dorsal strengthening ridge; md, mandible; mdb, mandibular bulge; mdt, mandibular tooth; os, mouth opening; spI, spiracle of abdominal segment I; sta, sternal area.

***tennae*:** not visible; ***mandible*:** anteromedially directed at an angle of 10°; mandibular body enclosed in mandibular capsule, slender, with pronounced bulge subapically, and pointed tooth apically (Fig. 4E); ***maxillae*:** not developed as distinct structure; ***labium*:** not developed as distinct structure, convex labial area delimited anteriorly by mouth opening and posteriorly by birth opening (Figs 3B, 4A), as long as wide, cuticle covered with small pores (Fig. 4A).

***Birth opening*:** opens rostrally with a slightly curved anterior margin that curves strongly posteriorly on both sides, almost reaching the posterior margin of the cephalothorax in front of the spiracle (Figs 3A, 4A, B).

***Thorax and abdominal segment I*:** segmental borders between thoracic segments and abdomen indistinct; cuticle mostly smooth (Figs 3A, 4A), but dorsally strongly wrinkled (Fig. 3B); area surrounding spiracle of abdominal segment I slightly elevated (Fig. 4A, F).

Primary larvae (Figs 5, 6, 7)

Diagnosis of primary larvae. The primary larva of *Halictophagus* sp. is identifiable among all other known primary larvae of species of the genus from Europe by the following combination of morphological features: body shape cylindrical, maxillary seta short (Fig. 6A), labial palp seta long (Fig. 6A), outer ocular seta short (Fig. 6B), seta of anterior head margin absent, median coxal tooth shorter than adjacent ones (Figs 6F, 7), trochanterofemoral tooth not furcated (Figs 6F–I, 7), lateral abdominal seta present on abdominal segments VII–X (Fig. 5B, C), lateral caudal seta absent. In *H. silwoodensis* the trochanterofemoral tooth is bifurcated in contrast to *Halictophagus* sp., and abdominal segments VII and VIII lack lateral abdominal setae (Pohl 2000). In *H. agalliae* a seta is present on the anterior margin anterolaterally on the ventral side of the head, the maxillary seta is longer, and lateral abdominal setae are present on abdominal segments II–X (Pohl 2000). The body shape of the primary larvae of *H. tettigometrae* is fusiform and the outer ocular seta is shorter (Silvestri 1941). *H. languedoci* lacks lateral abdominal setae on abdominal segments VII and VIII. Note that the examination of the primary larva of *H. tettigometrae* and *H. languedoci* was not yet carried out with SEM; therefore, crucial morphological details remain unclear. The primary larva of *H. kuehnelti* is not known.

Measurements (minimum, maximum, mean values of all measured specimens in parentheses, number of measured specimens in brackets, in µm): total length (without caudal setae): 132–168, avg. 151 (20); breath at abdominal segment II: 33–48, avg. 41 (16); length of caudal setae: 53–91, avg. 69 (20).

Description of primary larva. *Head capsule*: *stemmata*: five equal sized stemmata, three ventral and two dorsal (Fig. 6A, B); ***dorsal side*:** four pairs of dorsal cephalic setae: outer ocular seta inserted submedially above stemmata, seta of posterior margin inserted laterally below stemmata, very short anterior frontal sensillum and long anterior frontal seta placed submedially close to anterior head margin (Fig. 6B); ***ventral side*:** anterolateral seta of anterior margin placed on the ventral side of the head is absent (Fig. 6A); ***apical preoral cavity*:** fissure-shaped opening serrated, with four ventral and two small dorsal cuticular teeth (Fig. 6A); ***mandible*:** plate-like, placed inside apical preoral cavity, with apical cuticular tooth and short subapical sensillum (Fig. 6N); ***maxilla*:** broad and horseshoe-shaped, without median suture, posterior margin ending with elongated tip; short maxillary seta inserted submedially close to posterior margin; maxillary palp inserted laterally on anterior margin, with long maxillary palp seta (Fig. 6A); ***labium*:** broadly trapezoid, nearly as long as wide; anterior margin with variable number (ca. 20) of long spinulae; labial palp long and narrow, with long seta inserted at posterior margin (Fig. 6A); ***cervix*:** narrow (Fig. 6A).

***Thorax*: *terga*:** with transverse line; pronotum with three, meso- and metanotum with two pairs of setae, one pair inserted anterosubmedially, two pairs posterosubmedially; meso- and metanotum without setae anterosubmedially

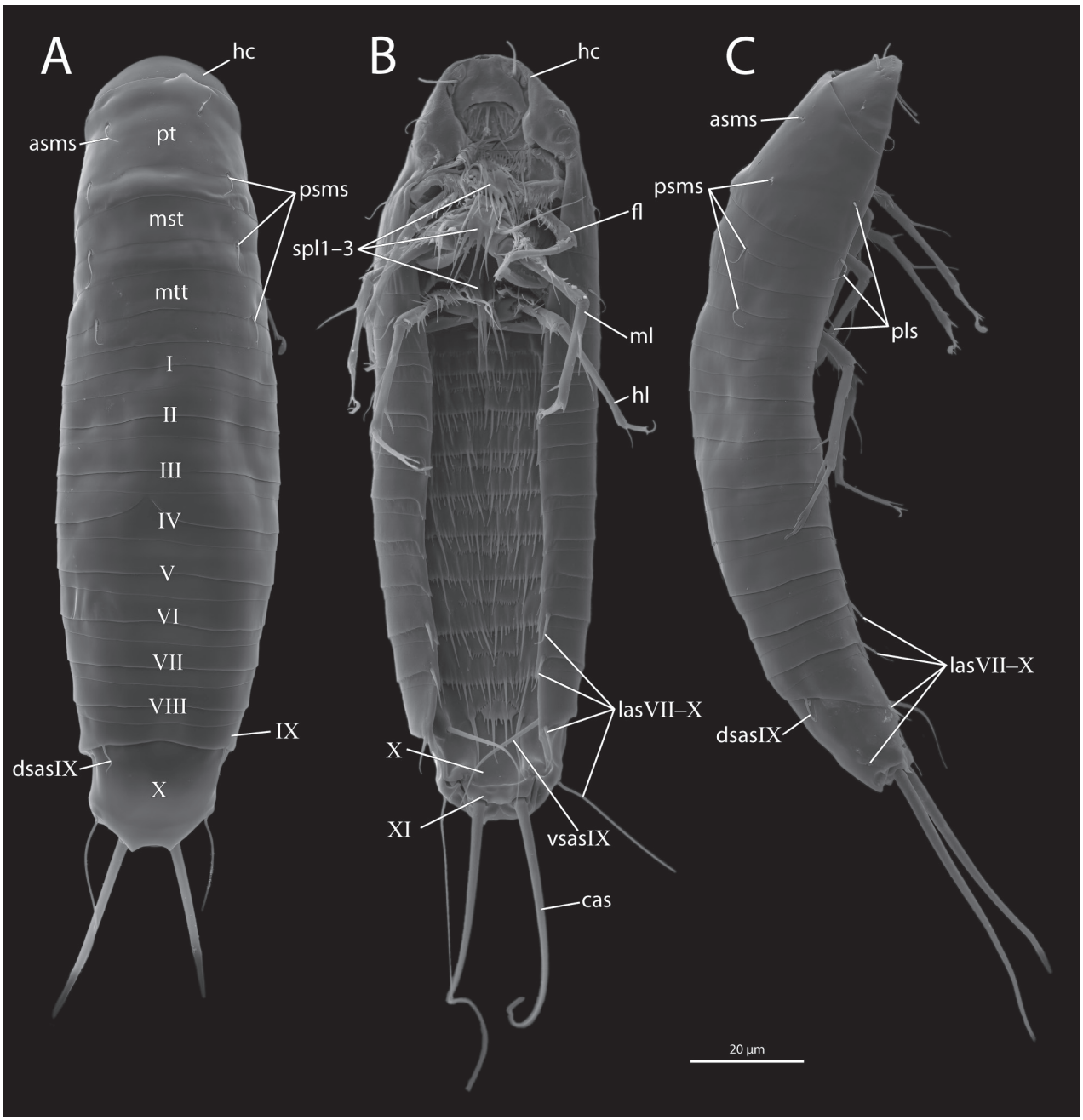

Figure 5. Primary larvae of *Halictophagus* sp. from Adolf Frank's collection in the PMJ. Larvae show shrinking artifacts due to the dried condition, SEM micrographs; **A.** Habitus in dorsal view; **B.** Habitus in ventral view; **C.** Habitus in lateral view. asms, anterior submedian seta; cas, caudal seta; dsasIX, dorsal submedian abdominal seta IX; fl, foreleg; hc, head capsule; hl, hindleg; lasVII–X, lateral abdominal setae VII–X; ml, middle leg; mst, mesothorax; mtt, metathorax; pls, posterior lateral seta; psms, posterior submedian seta; pt, prothorax; spl1–3, sternal plate 1–3; vsasIX, ventral submedian abdominal seta IX; I–XI, abdominal segment I–XI.

and posterolaterally on level of transverse line (Fig. 5A, C); ***sterna*:** anterior margin of each sternum with rows of 50–60 short spinulae and one pair of long spinulae with multifurcated apical part (Fig. 5B); ***sternal plates*:** prosternal plate with three rows of 40–50 short and four long spinulae at anterior margin; meso- and metasternal plates with two rows of ca. five short and four long spinulae; posterior margin of all three extended as three pairs of long spinulae (Figs 6C–E, 7).

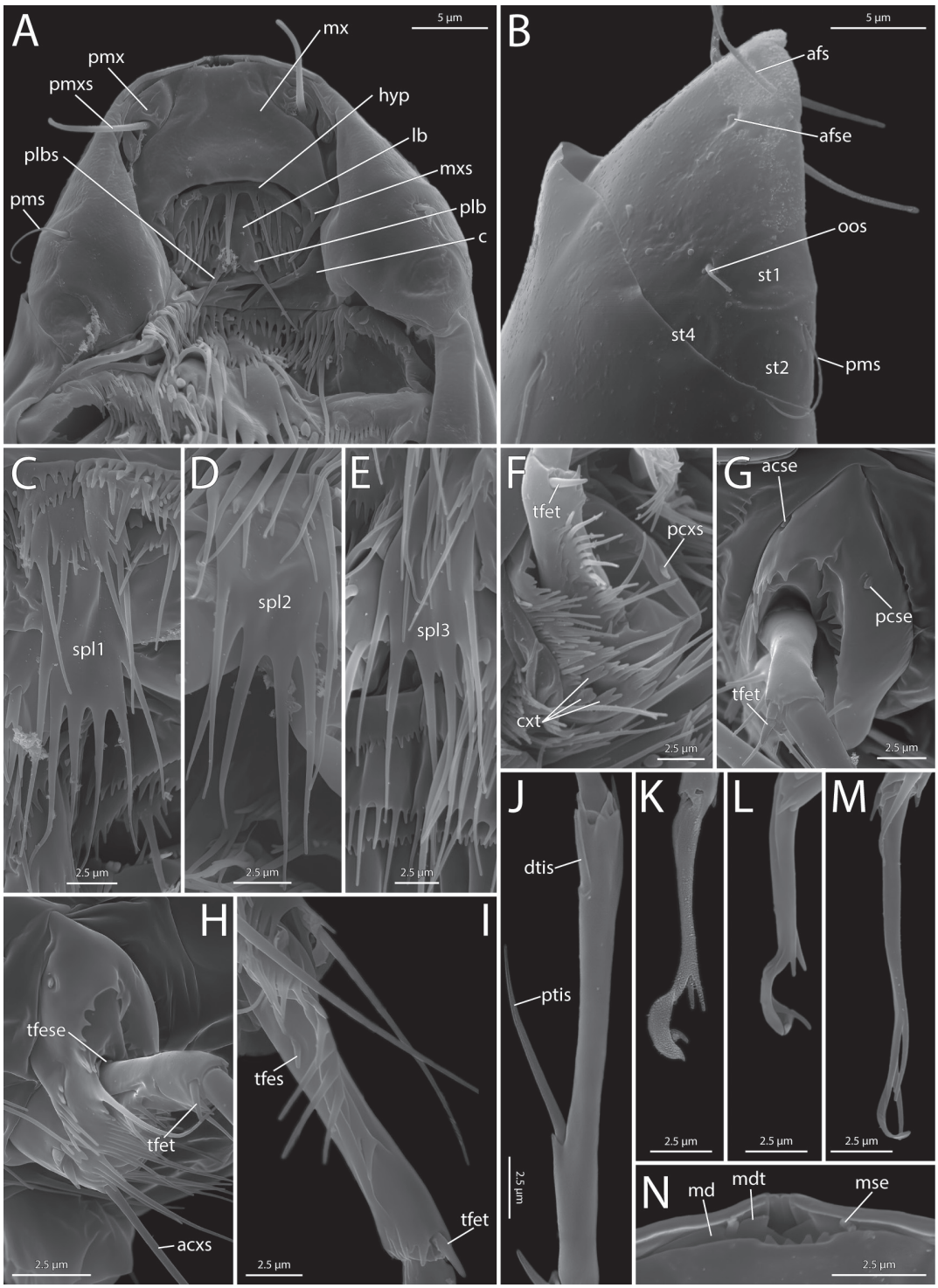

Figure 6. Primary larvae of *Halictophagus* sp. from Adolf Frank's collection in PMJ, SEM micrographs; **A.** Head in ventral view; **B.** Head in lateral view; **C.** Prosternal plate in ventral view; **D.** Mesosternal plate in ventral view; **E.** Metasternal plate in ventral view; **F.** Procoxa in ventral view; **G.** Mesocoxa in ventral view; **H.** Metacoxa in ventral view; **I.** Mesotrochanterofemur in ventral view; **J.** Mesotibia in dorsal view; **K.** Protarsus in lateral view; **L.** Mesotarsus in lateral view; **M.** Metatarsus in lateral view; **N.** Anterior head capsule with visible mandibles in ventral view. acse, anterior coxal sensillum; acxs, anterior coxal seta; afs, anterior frontal seta; afse, anterior frontal sensilla; c, cervix; cxt, coxal teeth; dtis, distal tibial seta; hyp, hypopharynx; lb, labium; md, mandible; mdt, mandibular tooth; mse, mandibular sensillum; mx, maxilla; mxs, maxillary seta; oos, outer ocular seta; pcse, posterior coxal sensillum; pcxs, posterior coxal seta; plb, labial palpus; plbs, labial palpus seta; pms, posterior margin seta; pmx, maxillary palp; pmxs, maxillary palp seta; ptis, proximal tibial seta; spl1–3, sternal plate 1–3; st1, 2, 4, stemma 1, 2, 4; tfes, trochanterofemoral seta; tfese, trochanterofemoral sensillum; tfet, trochanterofemoral tooth.

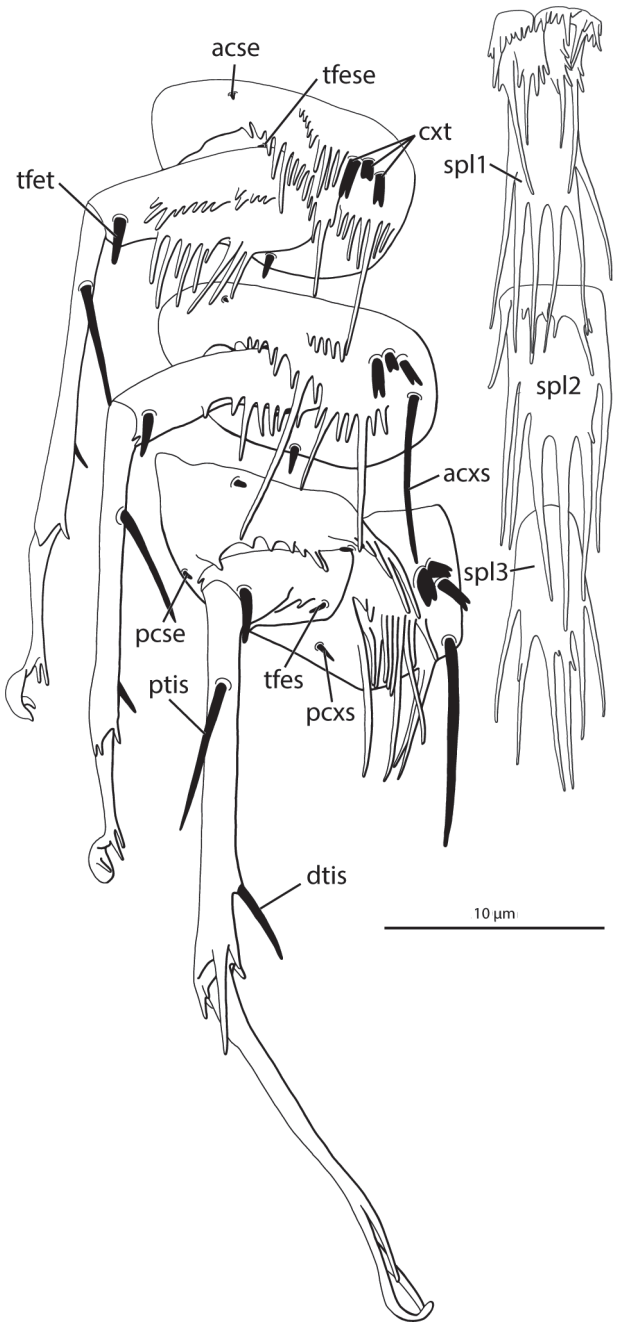

Figure 7. Legs and sternal plates of primary larvae of *Halictophagus* sp. from Adolf Frank's collection in the PMJ, line drawings. acse, anterior coxal sensillum; acxs, anterior coxal seta; cxt, coxal teeth; dtis, distal tibial seta; pcse, posterior coxal sensillum; pcxs, posterior coxal seta; ptis, proximal tibial seta; spl1–3, sternal plate 1–3; tfes, trochanterofemoral seta; tfese, trochanterofemoral sensillum; tfet, trochanterofemoral tooth.

***Legs*: *coxa*:** anterior margin with two rows of 40–50 spinulae, either short or long; anterosubmedially with three coxal teeth with bifurcate tips, the two outer ones elongated, antero- and posterolaterally with two very short sensilla; inner coxal margin with row of short spinulae and one short posterior seta, only meso- and metacoxa posterad coxal teeth with long anterior coxal seta, missing on procoxa (Figs 6F–H, 7); ***trochanterofemur*:** one very short sensillum inserted dorsoproximally; two rows of ca. 20 long or short spinulae present ventrally, one short seta ventroproximally, and ca. five short spinulae and one

single spinula at posterodistal margin (Figs 6F–I, 7); ***tibia*:** with one long proximal and one short distal seta; distal margin with row of ca. five short or long spinulae (Figs 6J, K, 7); ***tarsus*:** pro- and mesotarsus with two long and one short spinula on distal third, with shovel-like tip; one spinula inserted on ventral side of apical region; metatarsus with two long and one short spinula on distal third and with variously bent hook-shaped apical part (Figs 6K–M, 7).

***Abdomen*: *terga*:** with transverse line separating tergum in longer anterior region and half as long posterior part; anterior part of terga I–IX caudally extended as ventrolaterally directed narrow lobes with one or two spinulae at posterior tip; tergum VII–IX additionally with one pair of short lateral abdominal setae laterad of lobe; tergum IX with one pair of dorsal submedian abdominal setae, tergum X without transverse line, twice as long as preceding segments, with one pair of lateral abdominal setae (Fig. 5A, C); ***sterna*:** sterna I–VIII with one medial transverse row of 20–50 short spinulae, and posterior margin with row of 30–40 alternating short and long spinulae; small medial area of sternum IX with one medial row of ca. 20 short spinulae, extended as short lobe with alternating short and long spinulae; one pair of long spinulae inserted laterally at base of medial area; posterosubmedially with one pair of long ventral submedian setae; sternum X laterally extended, forming two short lobes; sternum XI short and trapezoid, with one pair of long caudal setae, lacking lateral caudal setae (Fig. 5B).

Halictophagus tettigometrae

For a detailed morphological description of the life stages, see Silvestri (1934, 1941). In the following we provide a revised description of the female cephalothorax based on SEM images showing details that were not covered in the original descriptions due to technical limitations.

Female (Figs 8, 9)

Diagnosis of female cephalothorax. Identifiable among all other *Halictophagus* species described from Europe by the following combination of morphological features: Cephalothorax roundish (Figs 8A, 9A), with kidney-shaped birth opening (Figs 8A, 9A, D); mandible with one apical and one subapical acute tooth (Fig. 9B); ventral pigmented area of abdominal segment I trapezoid (Fig. 8A). Differs from *H. agalliae*, *H. languedoci,* and *Halictophagus* sp. described here by the presence of two acute mandibular teeth instead of one subapical bulge and one acute apical tooth and the shape of the birth opening, which has a slightly arcuate anterior margin that strongly bends posteriorly on both sides in those species (Fig. 4A) (Abdul-Nour 1969, 1970). Differs from *H. silwoodensis* and *H. kuehnelti* in the shape of the birth opening, which is bent posteriorly and reaches the edge of the cephalothorax in a semicircle in the former but is triangular in the latter (Hofeneder 1949, Waloff 1981).

Position in host (Figs 1E, 8C): *T. impressopunctata* (♂): ♀ underneath tergite V, ventrolateral, right side.

Measurements. (in µm): length of cephalothorax: 251; breadth of the cephalothorax: 287; length of the head region (tip of cephalothorax to birth opening): 112.

Description of cephalothorax. *Shape and coloration*: cephalic region lightly colored, labial area with darker shade, thoracic region behind birth opening with

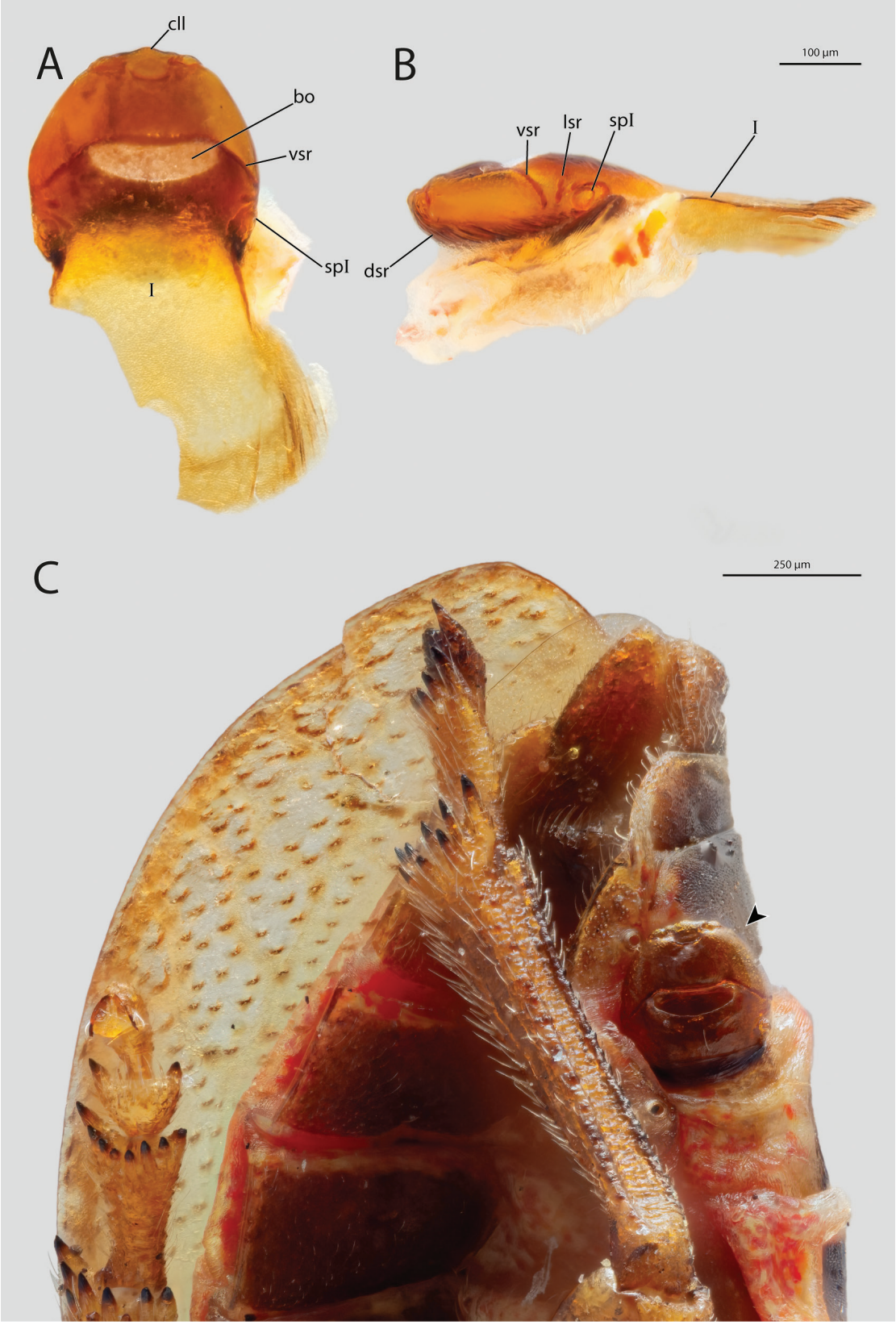

Figure 8. Female of *Halictophagus tettigometrae* from Ernst Schmidt's collection in PMJ, photomicrographs; **A.** Female cephalothorax in ventral view; ventral pigmentation of abdominal segment I damaged on the left side; **B.** Female cephalothorax in lateral view; **C.** Female endoparasitic inside the host *Tettigometra impressopunctata*; the arrow indicates the cephalothorax of the female. bo, birth opening; cll, clypeal lobe; dsr, dorsal strengthening ridge; lsr, lateral strengthening ridge; spI, spiracle of abdominal segment I; vsr, ventral strengthening ridge; I, abdominal segment I.

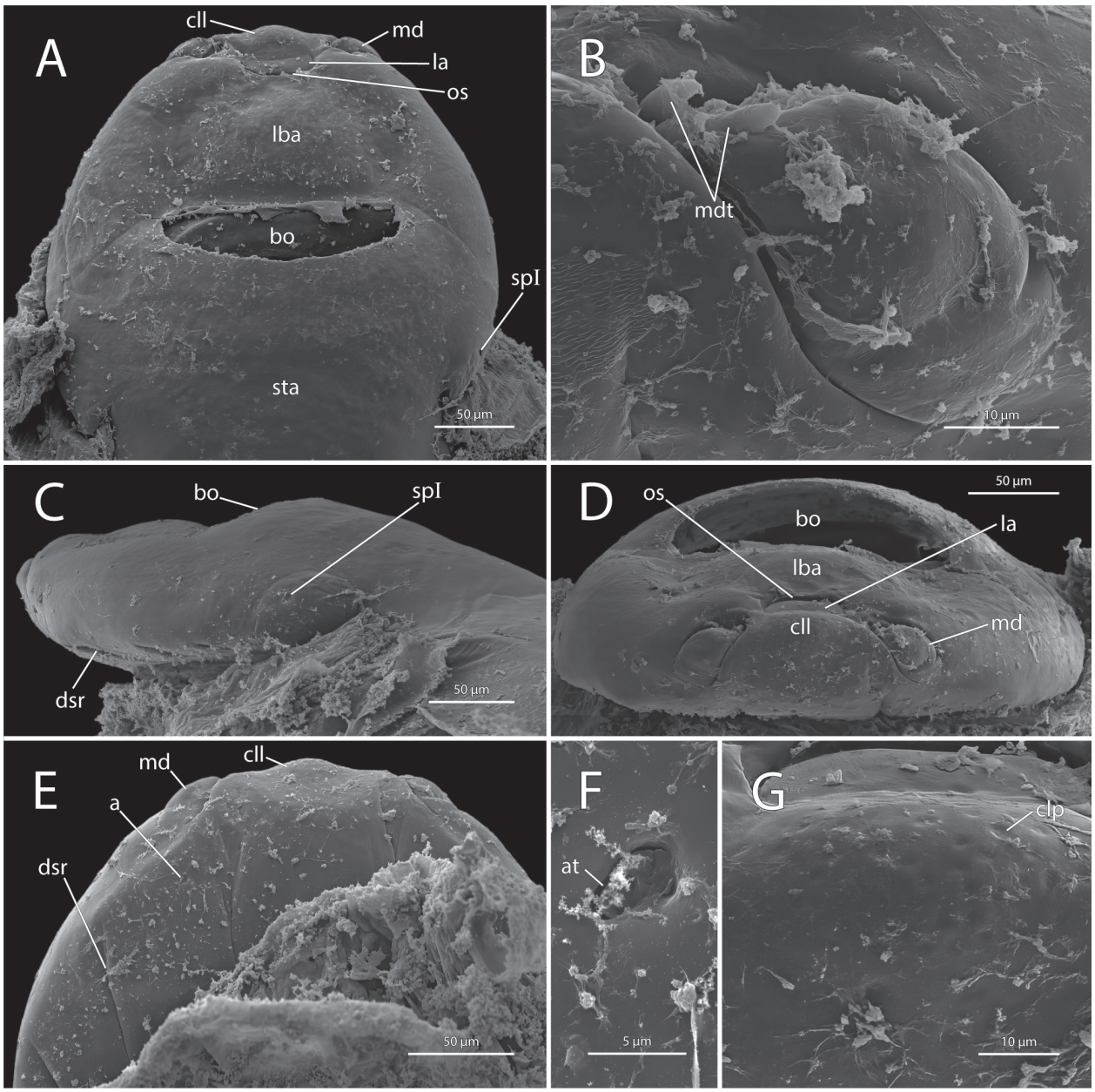

Figure 9. Female Cephalothorax of *Halictophagus tettigometrae*, SEM micrographs; **A.** Ventral view; **B.** Mandible in frontal view; **C.** Lateral view; **D.** Frontal view; **E.** Dorsal view; **F.** Left antenna in dorsal view; **G.** Clypeal region in frontal view. a, vestigial antenna; at, antennal torulus; bo, birth opening; cll, clypeal lobe; clp, clypeal pits; dsr, dorsal strengthening ridge; la, labral area; lba, labial area; md, mandible; mdt, mandibular teeth; os, mouth opening; spI, spiracle of abdominal segment I; sta, sternal area.

darker coloration, and pigmentation of abdominal segment I very light (Fig. 8A, B); shape roundish, slightly wider than long (Figs 8A, 9A), with dorsal side flat and ventral side convex; ca. six longitudinal strengthening ridges distributed on dorsolateral side, but cuticle of entire dorsal side smooth (Fig. 9E); oblique ventral strengthening ridge extends from anterior margin of birth organ to posterolateral margin of cephalothorax (Figs 8A, 9A); straight lateral strengthening ridge extends dorsoventrally in front of spiracle (Fig. 8B).

***Cephalic area*:** anterior clypeal area forming rounded clypeal lobe, protruding rostrally, with circular pits distributed evenly over entire region (Fig. 9G); borders between clypeal, frontal and labral area indistinct; labral area oval, mouth opening present as transverse cleft, arcuate on each side (Fig. 9A, D); cuticle of

anteroventral side smooth; lateral side of cephalic region slightly bulging (Fig. 9A, C), cuticle with large circular wrinkles distributed over entire area; cephalic region distinctly separated from remaining cephalothorax by birth opening and ventral strengthening ridge posteroventrally (Fig. 9A), but border on dorsal side indistinct; ***antennae*:** small, on anterolateral cephalic region; triangular antennal area distinct, incomplete antennal torulus present as furrow between antenna and surrounding area (Fig. 9E, F); ***mandible*:** anteromedially directed at an angle of 45°; mandibular body broad, drastically tapering anteriorly, with one subapical and one apical acute tooth (Fig. 9B); ***maxillae*:** not developed as distinct structure; ***labium*:** not developed as distinct structure; labial area delimited anteriorly by mouth opening and posteriorly by birth opening, slightly bulged; cuticle with large circular wrinkles distributed over entire area (Fig. 9A).

***Birth opening*:** opens rostrally, kidney-shaped (Fig. 9A, D).

***Thorax and abdominal segment I*:** segmental borders between thoracic segments and abdomen indistinct, area behind birth opening convex; cuticle with large circular wrinkles distributed over entire area (Fig. 9A); area surrounding spiracle of abdominal segment I bulging (Figs 8B, 9C), separated from surrounding area by thin chitinous ring, with multiple short setae inserted proximad bulge (Fig. 9A, C); projecting corner below spiracles rounded (Figs 8A, 9A), cephalothorax constricted behind projecting rounded corner below spiracles; darker pigmentation of ventral abdominal segment I large and trapezoid (Figs 8A, 9A).

Known host species

Tettigometra impressifrons Mulsant & Rey, 1855 (Silvestri 1934), *T. obliqua* Panzer, 1799 (Silvestri 1941), *T. picta* Fieber, 1865 (Silvestri 1941), *T. impressopunctata* Dufour, 1846 (Székessy 1959), this publication, *T. concolor* Fieber, 1865 (Székessy 1959).

Known distribution

Type locality: Italy (Silvestri 1934), Germany (this publication, see Examined material), Hungary (Székessy 1959; GBIF 2025b).

Discussion

The value of historic private collections

Natural history collections play a crucial role as one of the most important sources of biological data (e.g., Bradley et al. 2014; National Academies of Sciences and Medicine 2020; Ewers-Saucedo et al. 2021; Shultz et al. 2021). In many museums, as for instance in the case of the Phyletisches Museum, private collections form an essential basis of the entirety of the stored material (von Knorre 1983). However, their value as a source of scientific data is often underestimated (Casas-Marce et al. 2012). Here, two former private collections are revealed as valuable resources, providing important new insights in combination with modern imaging techniques. These techniques enabled a detailed morphological evaluation of the historic material. The specimens

were documented using different approaches, including photography, SEM, and µCT or synchrotron µCT. The latter two methods, in particular, are suitable for thoroughly documenting old and rare museum material, as they are minimally invasive and do not destroy it. However, µCT is not limited to documenting individual and particularly valuable specimens but can also be applied to digitize a large number of collection specimens, as demonstrated, for instance, by the open science initiative "Antscan" using high-throughput synchrotron µCT (Katzke et al. 2025). The resulting data sets can be stored and used locally to create a morphological database and can be made available in online data repositories, increasing the accessibility and transparency of the presented data (Akkari et al. 2015; Aibekova et al. 2022; Tröger et al. 2023; Boudinot et al. 2024). Moreover, µCT is also a useful method for investigating endoparasitic parasites, which can otherwise only be studied by dissecting the host. By using µCT, we were able to check the endoparasitic females for the presence of primary larvae before sacrificing valuable collection specimens. Previously undocumented morphological features on female cephalothoraces and primary larvae, such as cuticular surface structures including setae, were visualized using SEM—the optimal tool for examining fine surface details. These cuticular details can be used as diagnostic features for species delimitation in the studied genus *Halictophagus*. Additional documentation of museum material at the molecular level is also an option, as it is now possible to extract DNA sequence data from dried specimens up to 100 years old (Blaimer et al. 2016). We emphasize that the combined approach applied here to different life stages of Strepsiptera could also be used for other organisms and can be considered an example of a good-practice workflow using state-of-the-art methods. With the fully digitized specimens, we cover the field of collectomics and its multidimensional, specimen-based data (Sigwart et al. 2025), which paves the way for a future museomic approach.

Morphological evaluation of the studied life stages

Female of *Halictophagus* sp.

Although females of Strepsiptera, especially endoparasitic ones, display fewer diagnostic features than males due to their specialized endoparasitic lifestyle and simplified morphology, several new species have recently been described based on female cephalothoraces and male cephalothecae (Benda et al. 2022, 2023, 2024a, 2024b, 2025a, 2025b). This demonstrates that, by examining these life stages using appropriate techniques—in this case SEM—sufficient characters can be obtained to delimit species. In the present study, we were also able to discover new diagnostic features in females and primary larvae using SEM. The newly described females exhibit a unique combination of characteristics and use a new host species, which distinguishes them from other species described in Europe. The female cephalothoraces most closely resemble those of *H. languedoci*, which is known only from southern France (Abdul-Nour 1969; Cook 2019; Kathirithamby 2025b). The female mandibles of this species are also equipped with one apical tooth and a subapical bulge, the birth opening and ventral pigmented areas of abdominal segment I are similarly shaped, and the hosts of both species belong to the subfamily Deltocephalinae

of Cicadellidae (Abdul-Nour 1969). Moreover, the only distinguishing feature proposed here—namely the angle of the corner behind the spiracle—might not be sufficient to clearly separate the two species, as their intraspecific variability is presently insufficiently known. Therefore, we presently refrained from introducing a new species.

Primary larva of *Halictophagus* sp.

The primary larvae of Strepsiptera differ between species in terms of their chaetotaxy, the shape of their mouthparts, tarsi, and cuticle structure, among other characteristics (Pohl 2000). This also applies to the newly described primary larva of *Halictophagus* sp., which can be distinguished from the primary larvae of other species by its setae, particularly on the head, legs, and abdomen. To identify these characteristics, it is essential to examine the larvae using SEM, as these setae are often less than 5 µm long. A definitive taxonomic assessment is currently not possible, as only *H. agalliae* and *H. silwoodensis* have been documented using SEM to date (Pohl 2000).

Female of *H. tettigometrae*

Some features of the female cephalothorax were not addressed in the original description because of the technical limitations at the time (Silvestri 1941). These include details of the clypeal, labral, and labial areas, the cuticular texture of these parts, small setae near the spiracle, and the vestigial antennae. In females of Xenidae, the antenna is described either as a groove, cavity, or poorly defined area with an incomplete vestigial torulus (Benda et al. 2022). In *H. tettigometrae*, it consists of an inner plate-like area surrounded by an incomplete antennal torulus. A defined supra-antennal sensillary field, which has been described in females of Xenidae, is not visible (Benda et al. 2022). The clypeal lobe of *H. tettigometrae* is covered with circular pits. Similar pits are found on the clypeal lobe of females of Xenidae and Stylopidae and are interpreted by Benda et al. (2022, 2024a) as sensilla.

Taxonomic placement of *Halictophagus* sp. stylopizing *Eupelix cuspidata*

The initial impetus that led us to search for female *Halictophagus* stylopizing *E. cuspidata* in the Auchenorrhyncha collection of the Phyletisches Museum was a publication by Crowson (1975). The coleopterist pointed out that specimens of *Halictophagus* found inside the host *E. cuspidata* could belong to the species *Halictophagus curtisii* Dale, 1832. At that time, females, larvae, and the host were not known. *H. curtisii* is the type species of the family Halictophagidae and was described based on a single male specimen from southern England by J. CH. Dale, published in Curtis (1832). Crowson (1975) found several adult individuals of *E. cuspidata* stylopized by endoparasitic females in Morroch Bay, Great Britain, and nymphs stylopized by endoparasitic male puparia near Lydney, Great Britain. The author identified the females, which also contained primary larvae, as belonging to the genus *Halictophagus*. Therefore, Crowson

(1975) speculated that these specimens could represent the female of *H. curtisii*, assuming that it was the only species of the genus present in Great Britain and being unaware of *H. silwoodensis*, which was later described by Waloff (1981). Unfortunately, no drawings or photographs of the collected specimens were provided. Consequently, the identity of the females could not be verified.

Based on the evidence presented here, it is not possible to clearly assign the females and primary larvae treated in this study to *H. curtisii*. Although morphological features distinguish these newly described life stages from the other two species reported from Germany (*H. agalliae* and *H. silwoodensis*), and *E. cuspidata* has not yet been described as a host for any other *Halictophagus* species in Europe, it cannot be ruled out that the specimens belong to a previously undescribed species. In this context, it should be noted that *H. curtisii* has not yet been recorded from Germany. However, records from western, northern, and central Europe (Great Britain [type locality], Sweden, Belgium, and Denmark) make its occurrence in Germany plausible (Heqvist 1958; Haghebaert 1993; Nielsen and Oyre 2016; GBIF 2025a). To clearly assign the life stages to *H. curtisii*, further evidence is required showing that males found in *E. cuspidata*, preferably from the same locality as the females, are conspecific with the male holotype. This would require collecting new material, which is challenging in Strepsiptera due to the extremely short lifespan of strepsipteran males (only a few hours) and the cryptic lifestyle of the endoparasitic females (Pohl and Beutel 2005, 2008; Kathirithamby 2018, 2025a; Millena et al. 2025), or searching for overlooked specimens in other museum collections.

Distribution of *Halictophagus tettigometrae*

The careful labeling of each specimen by both collectors, with corresponding labels or separate notes providing information on locality, collecting date, and host plants (Fig. 1), represents an important source for assessing regional distribution patterns and faunal changes in auchenorrhynchan populations over long time periods. The historical specimens of *H. tettigometrae* and *Halictophagus* sp. found inside their hosts represent the first and only known records of both species from Germany. *H. tettigometrae*, described in 1934 by Silvestri as stylopizing the host *T. impressifrons*, is currently known only from Italy (type locality) and Hungary (Silvestri 1934, 1941; Székessy 1959). In addition to *T. impressifrons*, four species of *Tettigometra* are known to be parasitized by *H. tettigometrae*, including *T. impressopunctata* (Silvestri 1941; Székessy 1959; Cook 2019). Our findings suggest a wider northwestern distribution of the species than previously assumed, at least historically. The host *T. impressopunctata* occurs in southern, western, and central Europe, extending northwestward to southern England and eastward to European Russia (den Bierman and de Haas 2019). In Germany, *T. impressopunctata* is mainly found in the southern and western federal states (Kunz et al. 2011). According to Germany's Red List, this rare species is classified as critically endangered, with a sharply declining long-term population trend (Nickel et al. 2016). Evidence for the current presence of *H. tettigometrae* in Germany and northwestern Europe is still lacking.

Conclusion

The first detailed screening of the Auchenorrhyncha collection of the PMJ revealed, in addition to numerous species of this group from central Europe and other parts of the world (Africa, South America, North America, Australia, and the Malay Archipelago), only two strepsipteran parasites, represented by females and primary larvae. In both cases, the historical specimens constitute the first and only records for Germany. The life stages of both species found in the historical collection could be studied in detail using modern imaging methods, providing new diagnostic features for species delimitation. We morphologically described possibly hitherto unknown females and primary larvae for the first time. It cannot be conclusively determined whether these represent previously unknown life stages of *H. curtisii* or a species that has not yet been described. Our findings underline the value of NHCs for modern research questions. Therefore, examining existing collections for overlooked specimens and associated information is essential, particularly for taxa that are exceptionally difficult to collect, such as Strepsiptera.

There is an enormous amount of information preserved in historical museum collections that remains unexplored and can be revealed using modern techniques involving curators, researchers from other institutions, and citizen scientists. In view of the dramatic global decline in biodiversity and biomass, the preservation and thorough investigation of natural history collections should be given the highest priority.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: BLB, DT. Methodology: BLB, VG, JUH, DT. Software: JUH, VG, DT. Validation: BLB, DT. Investigation: BLB, DT. Resources: VG, JUH. Data curation: BLB, DT. Writing—original draft: BLB, DT. Writing—review and editing: BLB, RGB, VG, JUH, HP, DT. Visualization: BLB, DT. Supervision: RGB, HP. Project administration: BLB, DT, HP. Funding acquisition: DT.

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Data availability

Raw data scans of *H. tettigometrae* (Media ID: 000764655) and *Halictophagus* sp. (Media ID: 000764635) are available at Morphosource: Phyletisches Museum Jena (URL: https://www.morphosource.org/projects/000764622?locale=en) (Project ID: 000764622). 3D models of the scanned and reconstructed specimens are available on Sketchfab (https://skfb.ly/pFMzN).

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Supplementary material 1

Auchenorrhyncha collection of the Phyletisches Museum Jena

Authors: Daniel Tröger, Bernhard L. Bock

Data type: xlsx

Explanation note: Compiled list of collectors, specimens and localties of the PMJs Auchenorrhyncha collection.

Link: https://doi.org/10.3897/nhcm.3.173071.suppl1