

Known unknowns at our doorstep: Description of 14 Western Palaearctic species within the newly defined *Aphanogmus fumipennis* species group (Hymenoptera, Ceraphronoidea, Ceraphronidae)

Tobias Salden¹, István Mikó², Arnstein Staverløkk³, Marina Moser⁴, Cristina Vasilița^{4,5}, Thomas van de Kamp^{5,6}, Jonathan Vogel¹, Lars Podsiadlowski¹, Nils Hein^{7,8}, George Japoshvili⁹, Ralph S. Peters¹

1 Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig, Bonn, Germany **2** University of New Hampshire Collection of Insects and other Arthropods, Durham, NH, USA **3** Norwegian Institute for Nature Research, Trondheim, Norway **4** State Museum of Natural History Stuttgart, Stuttgart, Germany **5** Institute for Photon Science and Synchrotron Radiation (IPS), Karlsruhe Institute of Technology (KIT), Eggenstein-Leopoldshafen, Germany **6** Laboratory for Applications of Synchrotron Radiation (LAS), Karlsruhe Institute of Technology (KIT), Karlsruhe, Germany **7** Institute of Geography Education, University of Cologne, Cologne, Germany **8** Caucasus Leibniz Biodiversity Center, Ilia State University, Tbilisi, Georgia **9** Institute of Entomology, Agricultural University of Georgia, Tbilisi, Georgia

Corresponding author: Tobias Salden (t.salden@leibniz-lib.de)

Academic editor: Tamara Spasojevic | Received 17 November 2025 | Accepted 24 February 2026 | Published 23 March 2026

<https://zoobank.org/43704005-684F-4DDA-B69B-DBCD8CAED415>

Citation: Salden T, Mikó I, Staverløkk A, Moser M, Vasilița C, van de Kamp T, Vogel J, Podsiadlowski L, Hein N, Japoshvili G, Peters RS (2026) Known unknowns at our doorstep: Description of 14 Western Palaearctic species within the newly defined *Aphanogmus fumipennis* species group (Hymenoptera, Ceraphronoidea, Ceraphronidae). Journal of Hymenoptera Research 99: 125–214. <https://doi.org/10.3897/jhr.99.178410>

Abstract

Aphanogmus fumipennis Thomson, 1858 is one of the most frequently recorded ceraphronid parasitoid wasp species, considered to have a wide geographic distribution, numerous synonyms, and a broad host spectrum. 257 specimens with a posterior mesosomal comb, a character traditionally associated with *A. fumipennis*, from eight Western Palaearctic countries were examined using an integrative taxonomic approach, combining morphological study with focus on male genitalia and analyses of DNA barcode sequences.

Among those specimens, we detected 14 new species, which are all classified in a newly diagnosed *A. fumipennis* species group and made accessible through an identification key: *Aphanogmus bispinatus* Salden, Mikó & Peters, **sp. nov.**, *A. crispy* Salden, Mikó & Peters, **sp. nov.**, *A. digitangulus* Salden, Staverløkk, Mikó & Peters, **sp. nov.**, *A. hafii* Salden, Mikó & Peters, **sp. nov.**, *A. hamatogonus* Salden, Staverløkk,

Mikó & Peters, **sp. nov.**, *A. harpagodalis* Salden, Mikó & Peters, **sp. nov.**, *A. karlazani* Salden, Mikó & Peters, **sp. nov.**, *A. kintrishi* Salden, Mikó & Peters, **sp. nov.**, *A. latiharpus* Salden & Peters, **sp. nov.**, *A. tkheliharpus* Salden, Mikó & Peters, **sp. nov.**, *A. trigoharpus* Salden, Mikó & Peters, **sp. nov.**, *A. vashlovani* Salden, Mikó & Peters, **sp. nov.**, *A. ventricoharpus* Salden, Staverløkk, Mikó & Peters, **sp. nov.**, *A. zefranki* Salden, Mikó & Peters, **sp. nov.** At least nine additional species were delimited by sequence data only, but not formally described, indicating a minimum of 23 species in the *A. fumipennis* species group in the Western Palearctic. Finally, we provide a detailed genus diagnosis for *Aphanogmus* and discuss the status of the nominal species *A. fumipennis* Thomson, 1858 as a species of uncertain identity.

This study represents the first taxonomic treatment in 66 years to describe more than a single Palearctic *Aphanogmus* species. It also provides the first Ceraphronoidea species descriptions from Georgia, where species richness has almost increased fivefold, and nearly doubles the number of ceraphronid species known from Germany. This demonstrates that even in historically well studied regions such as the Western Palearctic, many parasitoid wasp groups, and Ceraphronoidea in particular, are extremely understudied. Discovering these known unknowns paves the way for further research on ecology, evolution, application and conservation of Ceraphronoidea.

Keywords

Biodiversity discovery, dark taxa, DNA barcoding, integrative taxonomy, parasitoid wasps

Introduction

The parasitoid wasp family Ceraphronidae is a poorly studied prime example of a so-called “dark taxon” (Salden and Peters 2023; Moser et al. 2024, 2025). Approximately 410 ceraphronid species are described worldwide (Johnson and Musetti 2004; Salden and Peters 2023). A recent extrapolation suggested a global ceraphronid diversity of 6 000–10 500 species, meaning that 93–96% of the species remain undescribed (Salden and Peters 2023). The family is divided into 16 genera, with 88% of the species belonging to only two genera: *Ceraphron* Jurine, 1807 (57%) and *Aphanogmus* Thomson, 1858 (31%) (Johnson and Musetti 2004; Mikó and Deans 2009; Mikó et al. 2018). Both genera lack taxonomic revisions. Genus-level identification is not trivial and revised genus diagnoses are necessary. Male specimens are more easily distinguished than female specimens, with *Aphanogmus* males typically showing trapezoidal flagellomeres with erect sensillae, while *Ceraphron* males have cylindrical flagellomeres with sickle-shaped sensillae (Mikó and Deans 2009).

With around 130 species worldwide and more than 50 recorded from the Palearctic, *Aphanogmus* is the most diverse genus of Ceraphronidae in this region (Johnson and Musetti 2004; Evans et al. 2005; Buhl et al. 2010; Matsuo et al. 2016; Moser et al. 2023; Ranjith et al. 2023; Salden and Peters 2023; Mollaei et al. 2025). Most of the Palearctic species are known from the Western Palearctic; only four species have been recorded exclusively from the Eastern Palearctic, i.e. east of the Ural Mountains and Caucasus (Ashmead 1904; Dessart and Alekseev 1982; Alekseev 1995; Mollaei et al. 2025). Host information is available for about 30% of the described *Aphanogmus* species and spans eight insect orders: Diptera, Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Thysanoptera, and Trichoptera (Dessart and Bournier 1971; Luhman et al. 1999; Buffington and Polaszek 2009; Matsuo et al. 2016; Youssef et al. 2022; Moser et al. 2024). Recently, Debnath et al. (2025) discovered a potential

trophic interaction of unidentified *Aphanogmus* wasps within spider egg sacs. Due to the lack of clearly delimited and diagnosed species, all data on life history, including host records, require further taxonomic resolution for accurate interpretation.

Taxonomic uncertainties are particularly evident in the case of *Aphanogmus fumipennis* Thomson, 1858, a species with an unusually broad geographic and host range (Dessart 1963a, 1975a, 1981). It has been recorded across the Afrotropics, Nearctic, Neotropics, and Palaearctic, and is listed as a parasitoid of four insect orders: Diptera, Hemiptera, Hymenoptera, and Thysanoptera (Johnson and Musetti 2004; Moser et al. 2024). Originally, Thomson (1858) described the species from a female and a male specimen, collected near Lund, Sweden. Later, Ashmead (1893) designated *A. fumipennis* as the type species for the genus *Aphanogmus*. Kieffer (1907, 1914), Russo (1938), and Szelényi (1940) added brief morphological descriptions and included the species into identification keys. Parr (1960) published the most detailed redescription based on British and Swedish non-type specimens of *A. fumipennis*, nearly 100 years after the original description. Parr (1960) also highlighted morphological differences between his examined specimens and earlier morphological descriptions by Thomson (1858) and Kieffer (1914), such as the presence of a median mesoscutal sulcus, as well as a different head to mesosoma width ratio and wing venation. Three years later, Dessart (1963b) examined the Swedish syntypes, designated a female lectotype, and described and designated a male allotype from Belgium. In this study, Dessart published the first drawings of male genitalia for *A. fumipennis* and listed diagnostic characters like a weakly indicated median mesoscutal sulcus, the presence of a setose anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex, the presence of two posterior propodeal projections, the presence of a posteriodistal spine (“...minuscule dent...”) on the metacoxa, the presence of a mesosomal comb (“...palisade (ou peigne) de soies...”) along the metacoxa and metapleuron, and distinctly enlarged distal flagellomeres, especially flagellomere 8 in female specimens.

In the same year, Dessart (1963a) conducted a morphological comparison of the Swedish lectotype, a non-type specimen of Parr’s (1960) redescription and 17 Afrotropical specimens, all considered as *A. fumipennis*, including the Afrotropical type specimen of the synonymized *Allomicrops bemisiae* Ghesquière, 1935. He detected significant variation in several morphological characters, such as the curvature of the stigmal vein, the shape of the apical flagellomeres in females, and the length of the anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex. Dessart concluded that the morphology of *A. fumipennis* is intraspecifically highly variable and suspected many more synonyms, as numerous species had been described from single or few specimens, often based on only minor distinguishing characters. Until 1963, four species had been synonymized with *A. fumipennis* (Johnson and Musetti 2004). Since 1981, the number of synonyms is 13, the highest number of synonyms for any ceraphronid species (Dessart 1975a, 1981; Johnson and Musetti 2004). Even considering the sister group family Megaspilidae, only a few species have similar synonym counts. *Trichosteresis glabra* (Boheman, 1832) and *Lagynodes pallidus* (Boheman, 1832) have 13, and *Dendrocerus carpenteri* (Curtis, 1829) has 17 recorded synonyms (Johnson and Musetti 2004). Interestingly, these species also have broad geographical distributions and, in the case of *D. carpenteri*, a wide host range across

three insect orders (Diptera, Hemiptera, Hymenoptera) and an exceedingly long list of host species (Haviland 1920; Fergusson 1980; Moser et al. 2024).

Such long lists of synonyms and broad host/geographic ranges may indicate that several species are hidden behind a single species name. Especially, in the recent era of integrative taxonomy using at least morphology and DNA sequence data, there are numerous examples in Hymenoptera in which specimens described as belonging to a single species are revealed to be actually comprised of several overlooked species (e.g., Ward et al. 2020; Sheikh et al. 2022; Armstrong et al. 2024).

Dessart (1994) noted that most synonymizations and records within *A. fumipennis* were based on two main characters: the posterior mesosomal comb and the shiny and smooth head and mesosoma. The posterior mesosomal comb is distinct and easily recognizable. Although first mentioned by Box (1921) in the description of the later synonymized *Ceraphron fuliginosi* (“...dense fringe of long white hairs on each side of the metapleurae...”), it became established as a character of *A. fumipennis* not until 1960, with Parr’s redescription noting a “...fringe of...setae...”.

When Evans et al. (2005) described two new species of *Aphanogmus* from Thailand and the USA, they proposed three new species groups within the genus. One of these, the *fumipennis* group, is characterized by the presence of a median mesoscutal sulcus (“furrow”) and the presence of the basal transverse carina on the syntergite (“gastral basal carina”). However, this character combination is common for many species across the genus and it is sometimes difficult to assess, for example, whether the median mesoscutal sulcus is present, absent, or only weakly indicated. The characteristic posterior mesosomal comb was not included in the *fumipennis* group diagnosis by Evans et al. (2005).

In the present study, we provide a detailed morphological diagnosis of the genus *Aphanogmus* and expand and refine the morphological diagnosis of the *A. fumipennis* species group. Our work is based on integrative taxonomic analyses of numerous specimens equipped with a posterior mesosomal comb, collected in eight countries across the Western Palaearctic (Czech Republic, Georgia, Germany, Hungary, Norway, Slovakia, Sweden, and Switzerland). Of these, a focus was on Georgia, a country that has never been intensively studied for Ceraphronoidea, with previously only three species-level records (Japoshvili 2022). By combining morphology, specifically of the male genitalia, with DNA sequence data from the *COI* barcode region, generated with Oxford Nanopore Technologies (ONT) barcoding, we demonstrate that multiple species of the newly defined *Aphanogmus fumipennis* species group are present in the Western Palaearctic fauna.

Material and methods

Institutional abbreviations, name of institute and location

CCDB Canadian Center for DNA Barcoding, Guelph, Canada

ECAUG Entomology Collection of the Agricultural University of Georgia, Tbilisi, Georgia

LACM Natural History Museum of Los Angeles County, Los Angeles, USA

MAAS Maastricht Natural History Museum, Maastricht, Netherlands

MCSN	Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy
MNHN	Muséum National d’Histoire Naturelle, Paris, France
NHMUK	Natural History Museum, London, UK
NHMW	Natural History Museum Vienna, Vienna, Austria
NHRS	Natural History Museum of Sweden, Stockholm, Sweden
NINA	Norwegian Institute for Nature Research, Trondheim, Norway
NTNU	Norwegian University of Science and Technology, Trondheim, Norway
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
RMCA	Royal Museum for Central Africa, Tervuren, Belgium
SMNS	State Museum of Natural History Stuttgart, Stuttgart, Germany
UNHC	University of New Hampshire Collection of Insects and Other Arthropods, Durham, USA
USNM	National Museum of Natural History, Washington DC, USA
ZFMK	Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig, Bonn, Germany

Specimens and morphological examination

This study is based on 257 ethanol-preserved specimens collected in eight different countries across the Western Palaearctic and identified as members of the newly defined *Aphanogmus fumipennis* species group, based on its diagnostic characters, e.g., the posterior mesosomal comb. The majority of specimens (123) were collected between 2018 and 2022 in Georgia, as part of the Caucasus Barcode of Life (CaBOL) project. For a full list of all examined specimens see the Suppl. material 1.

All specimens were examined, dissected, described and measured under a Leica M205C stereomicroscope with a Leica Planapo 1.0× objective (M-series, WD 61.5 mm) and Leica PI 10×/23 oculars. Measurements were taken only from holotypes, using a calibrated Leica scale ocular.

Genitalia preparation

Male genitalia were dissected by transferring specimens into droplets of 100% glycerol on concave microscope slides. In a few cases, male genitalia were not dissected because they were clearly visible through the metasomal segments or distinctly exerted (e.g., ZFMK-HYM-00042504). Dissections were performed using Dumont Style 5 Inox 02 forceps and a 100 µm diameter pin. During examination, both male genitalia and corresponding specimens were kept submerged in glycerol droplets on concave microscope slides.

For long-term storage, the male genitalia were placed in a small droplet of glycerol on the interior of a micro vial stopper (Ecology Supplies: 6 mm outer diameter, 4 mm inner diameter plastic genitalia vials with white silicone stoppers), which was then closed and pinned. In some cases, the genitalia and specimen were stored together in the same glycerol droplet; alternatively, the specimen was card mounted on the same pin as the genitalia vial, depending on the condition of the specimen. Female specimens were either stored in glycerol droplets in genitalia vials or card mounted.

All studied specimens are deposited in the ECAUG, NHRS, NINA, SMNS, UNHC or ZFMK, see Suppl. material 1 for a full list.

Terminology for body morphology, female and male genitalia follows the Hymenoptera Anatomy Ontology (HAO) (Yoder et al. 2010), Mikó et al. (2013), Ernst et al. (2013), and Salden and Peters (2023). The abbreviations used in the diagnostic species descriptions are as follows: F1 = flagellomere 1, F8 = flagellomere 8, POL = posterior ocellar line, and Gvc = gonostyle/volsella complex. In the illustrations, blue dashed lines are used to highlight boundaries of genital structures that are difficult to discern but are of diagnostic importance.

Imaging and microscopy

Brightfield images of specimens, including male genitalia, from NHMW, NHRS, SMNS, and ZFMK were taken using a Keyence VHX-7100 digital microscope (Keyence Corporation, Japan). Specimens from NINA were photographed using a Nikon D850 camera mounted on a StackShot rail, featuring a bellows system and a 20X Mitutoyo lens. Microscopic images were acquired separately using an Olympus BX43 Microscope controlled by the CellSense software. All images were then depth-stacked and processed using the Zerene Stacker program. Specimens from UNHC were imaged using an Olympus CX41 compound microscope equipped with a Canon EOS Rebel 16i SLR camera. Images were post-processed and assembled into figure plates with Inkscape v.1.3 (Inkscape project).

For reconstructing the 3D models of the specimens high-throughput synchrotron X-ray microtomography (SR- μ CT) was performed of ethanol-preserved specimens at the Imaging Cluster of the KIT Light Source. The system used a parallel polychromatic X-ray beam produced by a 1.5 T bending magnet spectrally filtered by 0.5 mm aluminum to obtain a peak at about 15 keV and a fast indirect detector system. The detector included a 12 μ m LSO:Tb scintillator (Cecilia et al. 2011) and a diffraction-limited optical microscope (Douissard et al. 2012) equipped with a 12-bit pco.dimax high-speed camera with 2016 \times 2016 pixels. For each scan, 200 dark field images, 200 flat field images, and 3000 equiangular spaced radiographic projections were taken in a range of 180° with 70 frames per second, completing the scan in about 43 s each. The magnification of the optical system was adjusted to 10 \times , resulting in an effective X-ray pixel size of 1.22 μ m (Dos Santos Rolo et al. 2014). The control system concert (Vogelgesang et al. 2016) was applied for automated data collection. The tomograms were reconstructed with tofuo (Faragó et al. 2022). We trimmed the resulting TIFF image sequences in Fiji and segmented them using the thresholding and scissor tools in the image segmentation module of 3D Slicer. We generated .stl models using the same software.

Male genitalia of some specimens were imaged in a glycerol droplet on #1.5 coverslips with a Nikon A1R-HD CLSM at the University of New Hampshire Instrumentation Center using three excitation wavelengths, 409, 487, and 560 nm, and three emission ranges of 435–470, 500–540, and 570–645 nm. We used FIJI for creating volume rendered image files and animated GIF micrographs.

DNA sequencing and molecular species delimitation

Specimens were processed at the LIB-Museum Koenig Bonn (ZFMK). DNA was extracted via HotSHOT extraction by adding 15 µl alkaline lysis buffer and adding the full body specimen (non-destructive). The specimens were incubated at 65 °C for 18 minutes, followed by 98 °C for 2 minutes. Subsequently, 15 µl of neutralization reagent was added, and 2 µl of the resulting extract was used for PCR. The *COI* gene of the mitochondrial DNA barcode region was amplified using the forward primer Cer_COI_F (Vasilița et al. 2022) and the reverse primer HCO2198_JJ (Astrin and Stüben 2008), following the PCR protocol described by Müller et al. (2024). Sequencing was performed using Oxford Nanopore's MinION flowcells, as described by Sternberg et al. (2025). *COI* sequences were 619 bp in length and were excluded from the analysis if they contained ten or more ambiguous bases.

This resulted in 115 sequences generated by the LIB which are tagged with “ZFMK-HYM-...” and of which all specimens originate from Georgia. Additionally, 24 *COI* sequences of *Aphanogmus* spp. from Norway tagged with “NOCER-...”, and 37 from Germany tagged with “SMNS_Hym_...” were included. The DNA barcodes from the Norwegian and German specimens were amplified using the same primers as mentioned above. Amplicons of the specimens from Norway were sequenced by Sanger sequencing at the CCDB and of the ones from Germany by MinION sequencing as described in Vasilița et al. (2024). All sequences were uploaded to BOLD: <http://doi.org/10.5883/DS-APHFUMI> (Ratnasingham and Hebert 2007). The complete dataset of 176 sequences was aligned with MUSCLE (Edgar 2004) with default parameters (16 iterations) in AliView v1.28 (Larsson 2014).

We reconstructed a maximum likelihood tree using IQ-TREE v2.4 (Minh et al. 2020) and assessed branch support with 1000 ultrafast bootstrap replicates (Hoang et al. 2018). Based on our alignment, species delimitation was performed using the ASAP algorithm (default settings; Puillandre et al. 2021) and objective clustering with SpeciesIdentifier (spID) v1.6.2 (Meier et al. 2006) applying a 3% threshold. In addition, the tree was rooted in Figtree v1.4.4 (Rambaut 2018) using an outgroup sequence (NOCER-637 *Lagynodes* sp.) obtained from BOLD. We further applied the multi-rate Poisson Tree Processes (mPTP) species delimitation algorithm (Kapli et al. 2017) via the web server (<https://mptp.h-its.org/#/tree>, default settings, accessed 29th October 2025). The results of the species delimitation analyses were integrated into the maximum likelihood tree using Inkscape v1.3 (Inkscape project).

Consensus sequences of 619 bp length were generated for twelve newly described species (exceptions *Aphanogmus harpagodalis* sp. nov. and *A. karlazani* sp. nov. for which no verified *COI* sequence was available) in GENEIOUS Prime v.2023.1.2. The DNA barcode consensus sequence only summarizes the available sequence information and can be a helpful tool for comparing DNA barcodes. It does not reflect the true or complete intraspecific sequence variation. From the resulting alignment, we extracted a distance matrix that provided maximum intraspecific and minimum interspecific distances, with the number of sequences and the closest species given in parentheses.

Results

Molecular analyses

A total of 176 DNA barcode sequences were analysed (alignment file (.fas) available at <https://doi.org/10.17632/jpwwjyy63g.1>). Sequences include a three base pair insertion which has not been reported in Ceraphronoidea but is also present in many sequences published in GenBank and BOLD. The species delimitation analyses resulted in 24 putative species with mPTP, 25 with ASAP (first ranked partition, ASAP score: 1.5), and 27 using objective clustering in SpeciesIdentifier (spID) at a 3% distance threshold (Fig. 1). Twelve species are newly described based on the congruence between DNA barcode data and morphological characters, with focus on the male genitalia (Fig. 1). For the newly described species, *Aphanogmus harpagodalis* sp. nov. and *A. karlazani* sp. nov., no molecular sequence data are available or could be assigned and they are therefore not part of the maximum likelihood tree, but they are clearly delimited and characterized by morphological characters. The remaining undescribed putative species are represented by female specimens only. Of the twelve species described using also molecular sequence data, congruence among all three species-delimitation analyses as well as the morphological characters was observed in eight species (*A. latiharpus*, *A. digitangulus*, *A. hafti*, *A. hamatogonus*, *A. ventricoharpus*, *A. zefranki*, *A. tkheliharpus*, and *A. crispy*). In the remaining four species (*A. kintrishi*, *A. vashlovani*, *A. trigoharpus*, and *A. bispinatus*), incongruence was detected in one or more of the molecular species-delimitation results (Fig. 1). These incongruencies and the rationale behind the respective taxonomic decisions are discussed in the respective taxonomy sections below.

Taxonomy

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Latreille, 1810

Superfamily Ceraphronoidea Haliday, 1833

Family Ceraphronidae Haliday, 1833

Genus *Aphanogmus* Thomson, 1858

Aphanogmus Thomson, 1858: 287, 305. Type species: *Aphanogmus fumipennis* Thomson, designated by Ashmead (1893): 132.¹

Diagnosis. Posterolateral process of gena absent. Occipital depression absent. Dorsal margin of occipital carina ventral to dorsal margin of lateral ocellus in lateral view. Dorsomedian flange of occipital carina absent. Submedial flange of occipital carina

¹ see Johnson and Musetti (2004): 10, 11 for a full list.

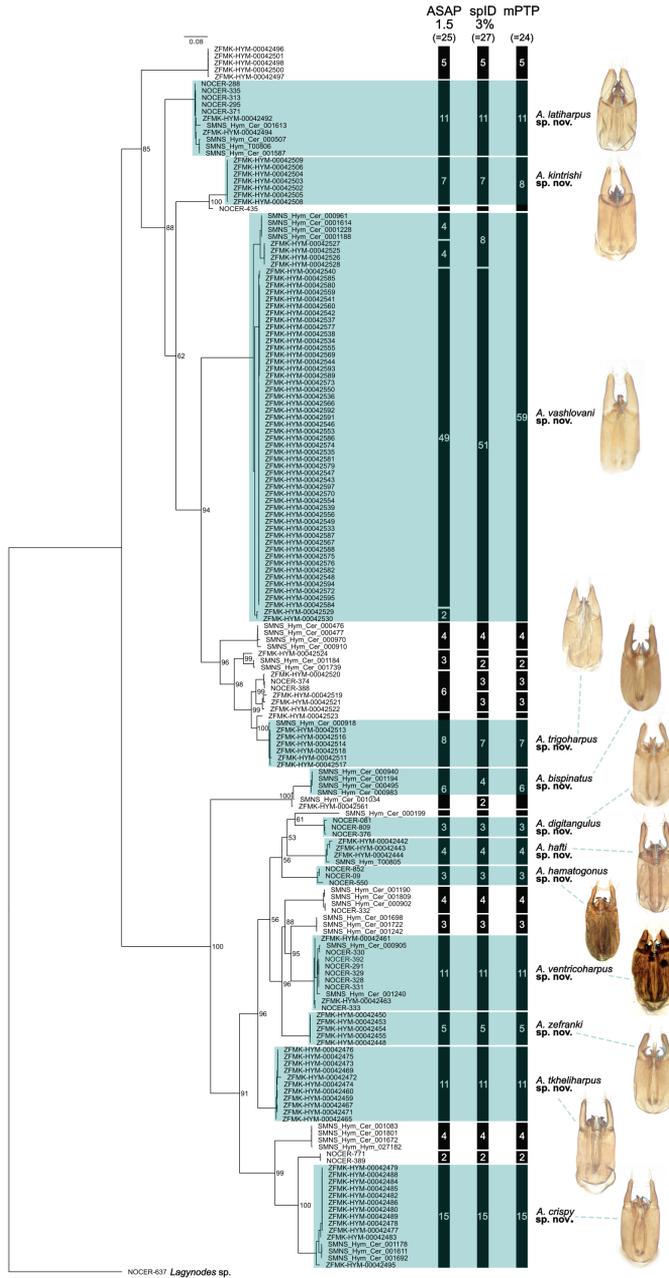


Figure 1. Maximum likelihood tree reconstructed in IQ Tree from *COI* barcode data. Species delimitation results are displayed on the right in black columns (number in the columns means number of sequences per species cluster), and sequence clusters of newly described species, according to our integrative taxonomic approach, are shaded in blue and labelled with the respective species name and male genitalia image on the right. The ASAP score of the shown result for analysis with ASAP is 1.5. Numbers in parentheses below each species delimitation method show the number of delimited species cluster by the respective method. The Ultrafast-bootstrap-support is shown on the nodes. A sequence of *Lagynodes* sp. (*Megaspilidae*) is used as outgroup.

absent. Ocular impression and postocular orbital carina absent. Postocellar carina absent. Transverse scutes on upper face absent. Frontal ledge absent. Subantennal groove absent. Intertorular carina present. Median process on intertorular carina absent. Intertorular ridge adjacent medially to epistomal ridge. Genal verricules absent. Number of mandibular teeth 2. Median conjunctiva of cardines absent. Number of maxillary palpomeres 4. Sensilla trichodea curvata on male flagellomeres absent. Erect, elongate setae on male flagellomeres present. Male specific ventral sensilla present on F5–9. Female flagellomeres 8, with few exceptions known (former *Neoceraphron*, see Dessart 1979) in which flagellomere number is 7. Female antenna widening apically. Mesosoma compressed laterally and distinctly higher than wide. Ventrolateral invagination of the pronotum present. Atrium of the anterior thoracic spiracle as wide as distal trachea. Pronope present. Posterodorsal branch of pronotal Y absent. Notaulus absent. Axillular carina absent. Posterolateral margin of mesoscutellum blunt. Sternaulus absent. Mesometapleural sulcus absent. Metapleural carina present. Anterior metapleural carina absent. Lateral propodeal carina inverted “V”: left and right lateral propodeal carinae are adjacent medially at their intersection with antecostal sulcus of the first abdominal tergum. Metapleural carina extending ventrally of propodeal spiracle. Ventral invagination of the metapleural carina absent. Median propodeal carina absent. Propodeal and metacoxal verricules absent. Mostly fully developed wings without pterostigma in fore wings, rarely with reduced wings. Ventral margin of the synsternum without anterior concave area. Single (not paired) Waterston’s evaporatorium present. Acrotergal calyx of Waterston’s evaporatorium present. Row of short setae delimiting apical cercus bearing area of male T9 present; male T10 folded medially along weakly sclerotised line. Proximal margin part of male S9 concave. Proximolateral corner of male S9 shape acute. Cupula ventromedially not extended more proximally than dorsomedially. Proximodorsal notch of cupula absent. Dorsal submedian impression of cupula present. Proximodorsal apodeme of cupula absent. Proximoventral margin of gonostyle/volsella complex shape convex and pointed proximally. Parossiculi fused with the gonostipes. Proximal region of penisvalva curved ventrally. Posterior region of female S7 not chisel-shaped, lateral concave areas absent. Intravalviferal articulation absent. Anterior flange of the first valvifer absent.

Aphanogmus fumipennis species group

Diagnosis. Randomly sized areolae on head and mesosoma absent. Median mesoscutal sulcus present, transscutal articulation present. Lateral carina on mesoscutellum absent, posterior lamella of mesoscutellum absent. Lateroventral mesopleural carina present. Posterior mesosomal comb present, scattered setae on posteriomedian metacoxa absent, setal patch on proximal metacoxa absent, posteriodistal spine on metacoxa present (Fig. 2). Transverse carina of syntergite present, submedial setiferous patches on synsternite absent. Stigmal vein longer than pterostigma marginal length.

Male genitalia. Dorsal apodeme of penisvalva present. Ventromedian apodeme of aedeagus absent. Medioventral area of gvc not folded: Parossicular seta oriented

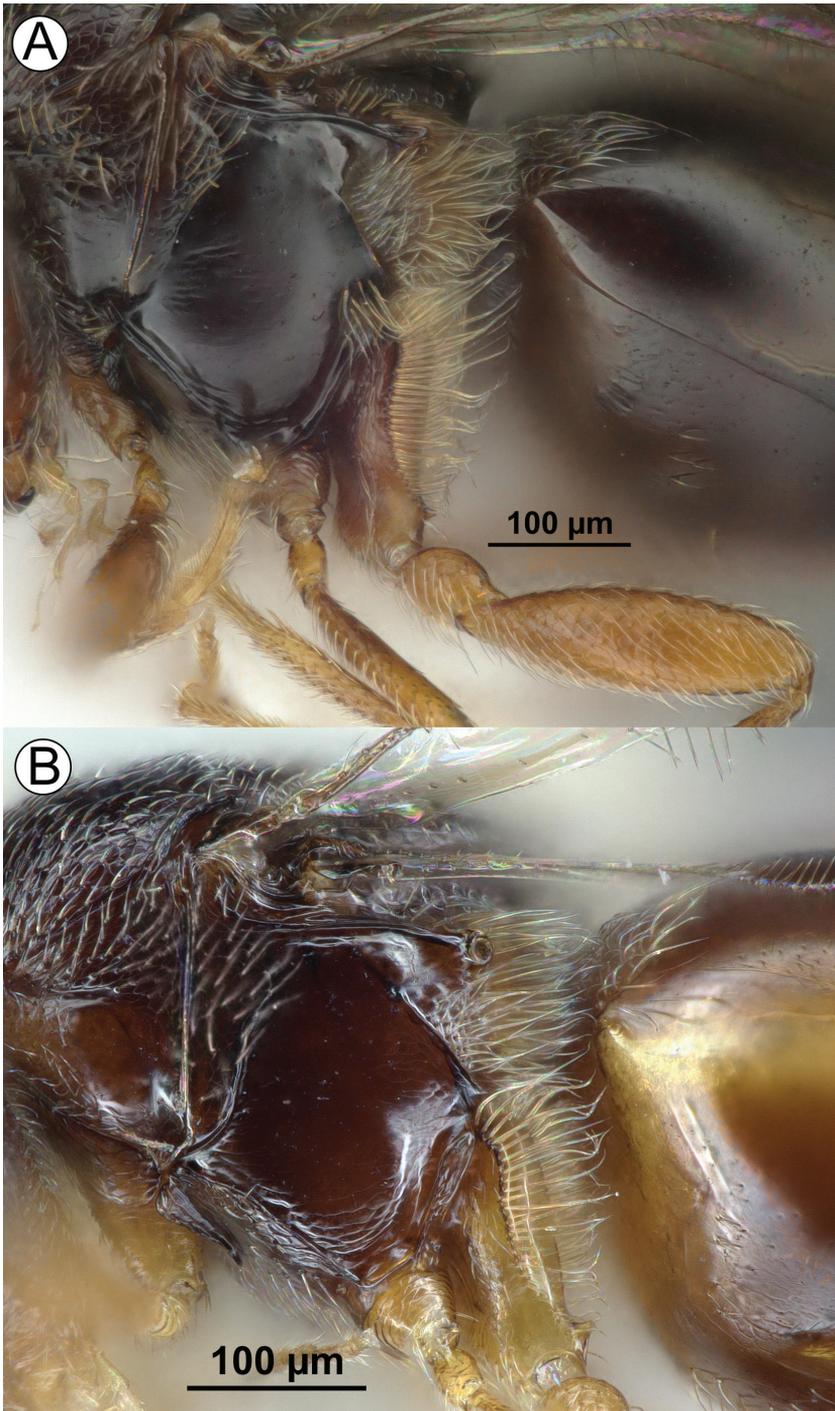


Figure 2. Posterior mesosomal comb as distinct diagnostic character of the *A. fumipennis* species group **A.** *A. kintrishi* sp. nov. (paratype: ZFMK-HYM-00042506) **B.** *A. trigoharpus* sp. nov. (paratype: ZFMK-HYM-00042517), lateral view.

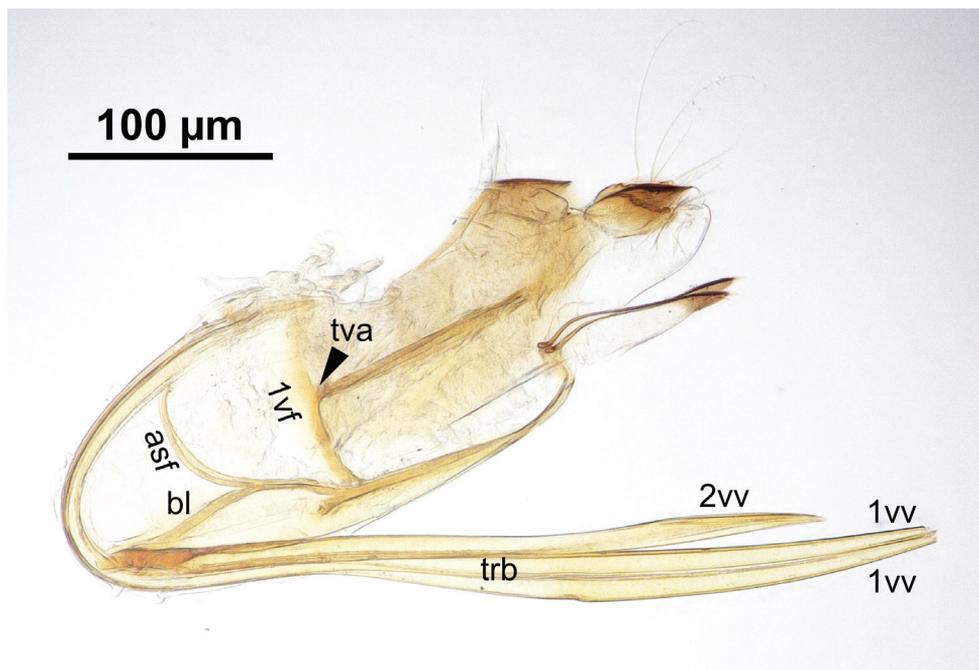


Figure 3. Female terminalia of *Aphanogmus crispy* sp. nov. (paratype: ZFMK-HYM-00042478) with anterior section of dorsal flange of the second valvifer (asf), basal line of the second valvifer (bl), tergo-valvifer articulation (tva), terebra (trb), first valvifer (1vf), first valvulae (1vv), and second valvulae (2vv), lateral view.

ventrally, visible in lateral view. Aedeagus not widened. Harpe usually finger-shaped, often with basomedian and median spine (e.g., Figs 4D, 27D) and sometimes with lamella-like extension along median margin (e.g., Figs 15D, 25D).

Female terminalia. Tergo-valviferal articulation (tva) on the posterior margin of the first valvifer (1vf) located in middle, not angled. First valvula (1vv) gradually tapering distally. Second valvula (2vv) slightly shorter than first valvula. Basal line of the second valvifer (bl) and anterior section of dorsal flange of the second valvifer (asf) distinct. Terebra (trb) slightly longer than ovipositor assembly. Ovipositor length virtually equal to mesonotum length in lateral view (Fig. 3).

Species included. *Aphanogmus bispinatus* Salden, Mikó & Peters, sp. nov., *A. crispy* Salden, Mikó & Peters, sp. nov., *A. digitangulus* Salden, Staverløkk, Mikó & Peters, sp. nov., *A. fumipennis* Thomson, 1858, sp. inq., *A. fraterculus* Salden & Peters, 2023, *A. hafti* Salden, Mikó & Peters, sp. nov., *A. hamatogonus* Salden, Staverløkk, Mikó & Peters, sp. nov., *A. harpagodalis* Salden, Mikó & Peters, sp. nov., *A. karlazani* Salden, Mikó & Peters, sp. nov., *A. kintrishi* Salden, Mikó & Peters, sp. nov., *A. latiharpus* Salden & Peters, sp. nov., *A. pilosicoxa* Salden & Peters, 2023, *A. simbai* Salden & Peters, 2023, *A. tkheliharpus* Salden, Mikó & Peters, sp. nov., *A. trigoharpus* Salden, Mikó & Peters, sp. nov., *A. vashlovani* Salden, Mikó & Peters, sp. nov., *A. ventricoharpus* Salden, Staverløkk, Mikó & Peters, sp. nov., *A. zefranki* Salden, Mikó & Peters, sp. nov.

Distribution. Afrotropics: Kenya. Palaearctic: Czech Republic, Georgia, Germany, Hungary, Norway, Slovakia, Sweden, and Switzerland.

Biology. Unknown.

Remarks. The posterior mesosomal comb is the main diagnostic character and allows quick identification of the *A. fumipennis* species group. It consists of two rows of densely packed setae interlocking at their distal parts and bordering a smooth, concave area along the posterior metacoxa. The posterodistal spine of the metacoxa marks the terminal point of the comb. On the posterolateral surface of the metanoto-propodeo-mesopecto-metapectal complex, densely packed setae continue (Fig. 2). *Aphanogmus* was previously divided into three species groups by Evans et al. (2005), based on the presence or absence of two morphological characters: the median mesoscutal sulcus (“mesoscutal median furrow” in Evans et al. (2005)) and the transverse carina of the syntergite (“gastral basal carina”). In the *clavicornis* group, both characters are absent; in the *tenuicornis* group the median mesoscutal sulcus is absent while the transverse carina of the syntergite is present; and in the *fumipennis* group both characters are present. These species groups have been adopted in recent taxonomic work (Matsuo et al. 2016; Salden and Peters 2023; Mollaei et al. 2025). The present *A. fumipennis* species group diagnosis significantly expands and refines the previous diagnosis of the *fumipennis* group by Evans et al. (2005).

Diagnostic species descriptions

Aphanogmus bispinatus Salden, Mikó & Peters, sp. nov.

<https://zoobank.org/9DD2F603-908E-432D-8649-71F75C938438>

Fig. 4; Suppl. material 2

Material examined. Holotype: SWEDEN • ♂; Gotland, Eksta socken, Stora Karlsö; 57.2846°N, 17.9718°E; ca. 30 m a.s.l.; 15 Aug. 2023; Hym inventory 2023 leg.; sweep net; NHRS; NHRS-HEVA000024898 (without DNA barcode). **Paratypes:** GERMANY • 2 ♂♂; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.1675°N, 8.7903°E; ca. 180 m a.s.l.; 16–30 Jul. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_000983, SMNS_Hym_Cer_000940 • 1 ♂; same collection data as for preceding; 27 Aug.–10 Sep. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001194 • 1 ♂; Baden-Württemberg, Tübingen, Hirschau, Oberes Tal, plot number 4244; 48.5050°N, 8.9935°E; ca. 370 m a.s.l.; 29 Aug.–12 Sep. 2014; T. Kothe, M. Engelhardt, D. Bartsch leg.; Malaise trap; SMNS; SMNS_Hym_Cer_000495 • 1 ♂; Bavaria, Landshut, Hohenthann; 48.66°N, 12.10°E; ca. 480 m a.s.l.; 01–07 Aug. 2022; NaPa Insektenmonitoring leg.; vane trap; ZFMK; ZFMK-HYM-00042662 (without DNA barcode) • 3 ♂♂; Hesse, Werra-Meißner-Kreis, Großalmerode, private garden, Siedlerweg, semi-abandoned garden with wet spot, ivy hedge and salix; 51.2591°N, 9.7871°E; ca. 380 m a.s.l.; 12–20 Jul. 2022; J. Vogel leg.; Malaise trap; ZFMK; ZFMK-HYM-00042639, ZFMK-HYM-00042643, ZFMK-



Figure 4. Male *Aphanogmus bispinatus* sp. nov. (paratype: ZFMK-HYM-00042639, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (paratype: ZFMK-HYM-00042643, in glycerol), habitus in lateral view. **B–D.** Male genitalia (holotype: NHRS-HE-VA000024898): **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine, proximodorsal notch of harpe, and median spine.

HYM-00042645 (without DNA barcodes) • 1 ♂; same collection data as for preceding; 6–12 Oct. 2023; J. Vogel leg.; Malaise trap; ZFMK; ZFMK-HYM-00042646 (without DNA barcode) • 1 ♂; North Rhine-Westphalia, ZFMK garden; 50.7216°N,

7.1141°E; ca 60 m a.s.l.; 30 Aug. 2022; T. Salden leg.; sweep net; ZFMK; ZFMK-HYM-00042657 (without DNA barcode).

Other material examined. GERMANY • 2 ♂♂; North Rhine-Westphalia, Eifel National Park, Döppeskaul; 27 Jul.–10 Aug. 2009; J. Esser leg.; Malaise trap; UNHC; PSUC_FEM 10022624, PSUC_FEM 10012532 (without DNA barcodes) • 2 ♂♂; Baden-Württemberg, Esslingen, Oberboihingen, meadow orchard; 48.6506°N, 9.3689°E; ca. 310 m a.s.l.; 12–26 Aug. 2012; T. Kothe, G. Schweizer leg.; Malaise trap; UNHC; PSUC_FEM 10022848, PSUC_FEM 10022738 (without DNA barcodes). HUNGARY • 2 ♂♂; Bács-Kiskun, Gara; 46.035°N, 19.020°E; ca. 90 m a.s.l.; 26–30 Jun. 2009; I. Mikó leg.; yellow pan trap; UNHC; UNHC_1000025, UNHC_1000049 (without DNA barcodes). SLOVAKIA • 1 ♂; Trenčín region, Hôrka nad Váhom; 12–15 Jun. 2010; E. Talamas leg.; sweep net; UNHC; PSUC_FEM 10035369 (without DNA barcode).

Diagnostic description. Male. Body length: 0.76 mm.

Colour (Fig. 4A): Body dark brown. Legs with lighter joints and tarsi.

Antenna, head (Fig. 4A): F1 with sensillae arranged in three whorled rows, F1 length slightly shorter than half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 4A): Scutoscutellar sulcus and transscutal articulation adjacent, interaxillar sulcus indicated. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex short. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, distal part virtually parallel to anterior wing margin. Three basal longitudinal carinae on syntergum.

Male genitalia (Fig. 4B–D): Gvc length one third of mesonotum length. Gvc width $0.66 \times$ gvc length; harpe/gvc index 0.45. Harpe finger-shaped, distoventrally oriented; lateral margin of harpe slightly convex in basal third, straight in apical two-thirds, and oriented distomedially; median margin of harpe concave in basal half, straight in apical half, and slightly converging distomedially. Harpe with basomedian and median spine; tip of basomedian spine slightly more proximal than tip of gonossiculus and oriented distally; median spine arising from mid-length of harpe and $2 \times$ as long as wide; tip of median spine more distal than tip of gonossiculus and oriented distomedially. Proximodorsal notch of harpe U-shaped and $0.24 \times$ as long as harpe length. Harpe width (above median spine) $0.16 \times$ gvc width, and $0.24 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, extending to apical third; harpe with at least three apical setae oriented distally; harpe with one lateral seta close to apex, oriented distolaterally. Gonossiculus length $0.64 \times$ harpe length; gonossiculus J-shaped with at least one digital tooth, tip oriented distolaterally and dorsolaterally. Aedeagus straight.

Female. Unknown.

COI barcode. Maximum intraspecific barcode distance: 0.3% (n = 4). Minimum interspecific barcode distance: 23.8% (putative species consisting of SMNS_Hym_Cer_001083, SMNS_Hym_Cer_001801, SMNS_Hym_Cer_001672, and SMNS_Hym_Hym_027182).

Consensus sequence: 5'- AGCAGGCCTCAGAATAAT'TATCCGCT-TAGAGCTTAGGTCCCCCCCCCAACAATATAATAAATAATGACCTAAT-TATAAT'TCAAT'TATTACAAATCACGCAT'TCCTCATAATCT'TTTTCCCTAGT-CATGCCTAT'TATAATAGGGGGCT'TTGGGAAT'TGGCTCCT'TCCAGTAATA-ATGGGAGCCCCAGATCTT'GCTT'TCCCCCGTATAACAATATAAGATACT-GACTCCTACCTCCT'TCTCTTACAATACTCCT'TTTAAGGATATTAACCAACAC-CGGAGTTGGAGCCGGTTGAACCC'TTACCCGCCCCTGACTT'TAGTCCCT-TACCATGATGGTGTATCAATAGATATAACAAT'TTTTTCCTTACATATCGC-GGGAATTAGT'TCAAT'TATAGGTTCTATCAAT'TTTT'TAGTAACAGCC'TTTA-AAATAAGCCTCTAAATATAGACTTAGTAAA'ACTTCCCTTATTCTGTTGAT-CAGTTATCCTCACGGCTCTCCTTCTAATCCTATCCTTACCTGTCTTAGCCG-GAGCCATCACATAAT'TTTAACTGACCGTAACATAAACACCTCCT'TTTTGA-CCCAGAAGGAGGAGGTGACCCACTTTTATACCAACACCTTTTT-3'

Variation. Body light brown in DNA-extracted specimens SMNS_Hym_Cer_000983, SMNS_Hym_Cer_000940, SMNS_Hym_Cer_001194, and SMNS_Hym_Cer_000495.

Biology. Unknown.

Distribution. Palaearctic: Germany, Hungary, Slovakia, and Sweden.

Etymology. The species name is a composition of the Latin words 'bi' and 'spina', meaning 'two' and 'spine', with reference to the distinct two spines along the median margin of the harpe.

Remarks. *A. bispinatus* can be readily distinguished from all other species of the *A. fumipennis* species group by the morphology of the male genitalia, specifically the presence of two spines on the harpe: a basomedian spine and a median spine, the latter being twice as long as wide and oriented distomedially (Fig. 4D).

In the molecular analyses, two additional specimens (SMNS_Hym_Cer_001034 and ZFMK-HYM-00042561) were assigned to the same species as the four *A. bispinatus* specimens by both ASAP and mPTP and show only comparatively small barcode distance to *A. bispinatus* (5.3%). However, the male genitalia of these specimens differ distinctly from those of *A. bispinatus*, indicating that they represent different species (see remarks under *A. karlazani*).

***Aphanogmus crispy* Salden, Mikó & Peters, sp. nov.**

<https://zoobank.org/5D756AE0-3411-4F9D-822D-552681FBFFF3>

Figs 5, 6; Suppl. materials 3, 4

Material examined. **Holotype.** GEORGIA • ♂; Kakheti, Gombori; 41.8594°N, 45.2183°E; ca. 1100 m a.s.l.; 21–28 Jul. 2021; G. Japoshvili leg.; Malaise trap; ECAUG; ZFMK-HYM-00042477. **Paratypes.** GEORGIA • 1 ♂; Kakheti, Gombori; 41.8739°N,

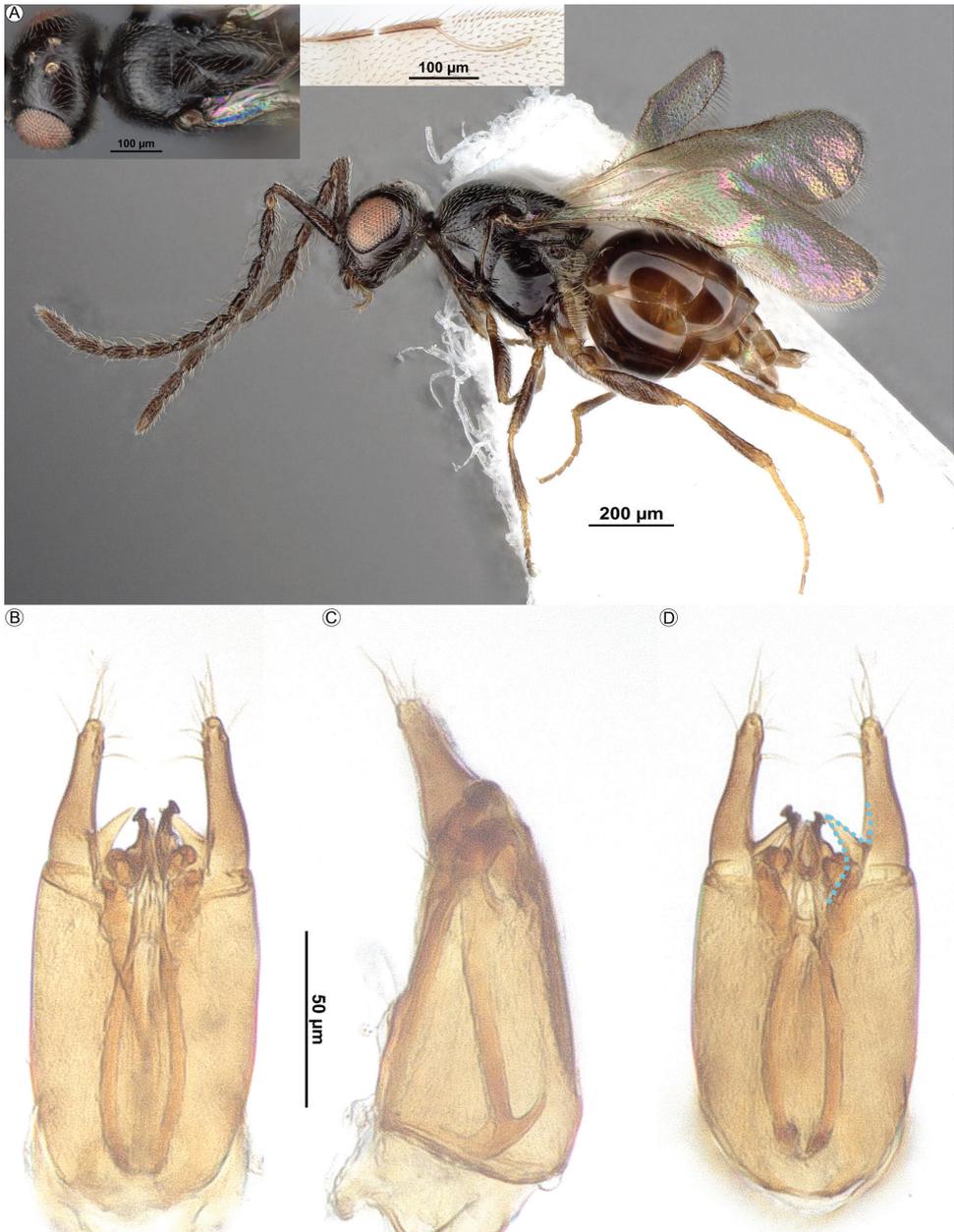


Figure 5. Male *Aphanogmus crispy* sp. nov. (paratype: ZFMK-HYM-00042490, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (paratype: ZFMK-HYM-00042478, in glycerol), habitus in lateral view. **B–D.** Male genitalia (holotype: ZFMK-HYM-00042477): **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with median spine and mediodorsal notch of harpe.

45.3553°E; ca. 1060 m a.s.l.; 20–27 Jul. 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042483 • 1 ♂; same collection data as for preceding; ZFMK; ZFMK-HYM-00042490 (without DNA barcode) • 1 ♀; Racha-Lechkhumi & Kvemo Svaneti,

Doghurashi; 42.6698°N, 42.7854°E; ca. 1070 m a.s.l.; 17–24 May 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042482 • 4 ♀♀; Racha-Lechkhumi & Kvemo Svaneti, Doghurashi; 42.6782°N, 42.8101°E; ca. 1470 m a.s.l.; 17–24 May 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042478, ZFMK-HYM-00042479, ZFMK-HYM-00042480, ZFMK-HYM-00042495 • 1 ♀; Kakheti, road to Sakisto Lake; 44.2559°N, 45.3356°E; ca. 900 m a.s.l.; 29 May 2022; R.S. Peters leg.; sweep net; ZFMK; ZFMK-HYM-00042489 • 1 ♀; Kakheti, Telavi; 41.9132°N, 45.4556°E; ca. 820 m a.s.l.; 29 May 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK; ZFMK-HYM-00042488 • 3 ♀♀; same collection data as for preceding; 30 May 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK; ZFMK-HYM-00042484, ZFMK-HYM-00042486, ZFMK-HYM-00042485. GERMANY • 1 ♀; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.16754°N, 8.7903°E; ca. 180 m a.s.l.; 9–23 Apr. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001611 • 1 ♀; same collection data as for preceding; 7–21 May 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001178 • 1 ♀; Baden-Württemberg, Enzkreis, Königsbach-Stein, NSG 2.119 Beim Steiner Mittelberg; 48.9704° N, 8.6590° E; ca. 230 m a.s.l.; 19 Jun.–3 Jul. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001692 • 1 ♂; North Rhine-Westphalia, Haltern-Borkenberge, raised bog; 51.751°N, 7.264°E; ca. 60 m a.s.l.; 19–31 Jul. 2023; K. Hannig leg.; Malaise trap; ZFMK; ZFMK-HYM-00042655 (without DNA barcode) • 1 ♂; North Rhine-Westphalia, ZFMK garden; 50.7216°N, 7.1141°E; ca. 60 m a.s.l.; 30 Aug. 2022; T. Salden leg.; sweep net; ZFMK; ZFMK-HYM-00042658 (without DNA barcode) • 2 ♂♂; Hesse, Werra-Meißner-Kreis, Großalmerode, private garden, Siedlerweg, semi-abandoned garden with wet spot, ivy hedge and salix; 51.2591°N, 9.7871°E; ca. 380 m a.s.l.; 12–20 Jul. 2022; J. Vogel leg.; Malaise trap; ZFMK; ZFMK-HYM-00042666; ZFMK-HYM-00042669 (without DNA barcodes). SWEDEN • 3 ♂♂; Gotland, Eksta socken, Stora Karlsö; 57.2841°N, 17.9700°E; ca. 30 m a.s.l.; 15 Aug.–3 Sep. 2023; Hym inventory 2023 leg.; Malaise trap; NHRS; NHRS-HEVA000023405, NHRS-HEVA000023406, NHRS-HEVA000023407 (without DNA barcodes). SWITZERLAND • 1 ♂; Aargau, Lenzburg; 47.38°N, 8.19°E; ca. 440 m a.s.l.; 24–30 Oct. 2022; NaPa Insektenmonitoring leg.; vane trap; ZFMK; ZFMK-HYM-00042668 (without DNA barcode).

Other material examined. CZECH REPUBLIC • 1 ♂; South Moravia, Lednice, riparian forest; 9 Aug. 1991; L. Masner leg.; sweep net; UNHC; UNHC_1000016 (without DNA barcode). GERMANY • 2 ♂♂; Saxony, Bautzen, Driewitz; 51.3456°N, 14.4348°E; ca. 150 m a.s.l.; 30 Jul. 2013; L. Krogmann, T. Kothe leg.; sweep net; UNHC; 10022913, 10022906 (without DNA barcodes) • 1 ♂; Saxony, Görlitz, Op-pach; 51.0619°N, 14.4922°E; ca. 330 m a.s.l.; 18–24 Aug. 2013; U. Hornig leg.; Malaise trap; UNHC; 10022925 (without DNA barcode). NORWAY • 1 ♂; Vestfold, Larvik, Bommedstad; 59.0814°N, 10.0754°E; ca. 30 m a.s.l.; 3 Oct. 2017; A. Staverløkk leg.; sweep net; NINA; MS-141 (without DNA barcode). SWEDEN • 1 ♂; Stenbrohult, Djäkabygd's bokbacke, heath with old beeches, Trap ID 24; 1–18 Aug. 2003; UNHC; IM2144 (without DNA barcode).

Diagnostic description. Male. Body length: 0.90 mm.

Colour (Fig. 5A): Body brown except metasoma and legs slightly lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 5A): F1 with sensillae arranged in three whorled rows, F1 length half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 5A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus present. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex very short. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. No basal longitudinal carinae on syntergum.

Male genitalia (Fig. 5B–D): Gvc length one third of mesonotum length. Gvc width $0.74 \times$ gvc length; harpe/gvc index 0.46. Harpe finger-shaped, distoventrally oriented, slightly narrowed along apical two-thirds; lateral margin of harpe slightly convex in basal third, slightly concave in apical two-thirds, and oriented distally; median margin of harpe slightly concave in basal third, straight in apical two-thirds, and oriented distally. Harpe with median spine; tip of median spine about as distal as tip of gonossiculus and oriented distomedially. Proximodorsal notch of harpe absent, mediodorsal notch of harpe V-shaped and $0.19 \times$ as long as harpe length. Harpe width (above median spine) $0.13 \times$ gvc width, and $0.21 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, extending to apical third; harpe with at least four apical setae oriented distally, including one broadened seta (broadening only visible in CLSM image Suppl. material 3); harpe with one lateral seta close to apex, oriented distolaterally. Gonossiculus length $0.46 \times$ harpe length; gonossiculus J-shaped with knob-like apex, at least one digital tooth, tip oriented dorso-laterally. Aedeagus straight.

Female. Body length: 0.90 mm.

Colour (Fig. 6): Body light brown except metasoma and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 6): F8 length half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 6): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein distinctly oriented towards anterior wing margin. Two basal longitudinal carinae on syntergum.

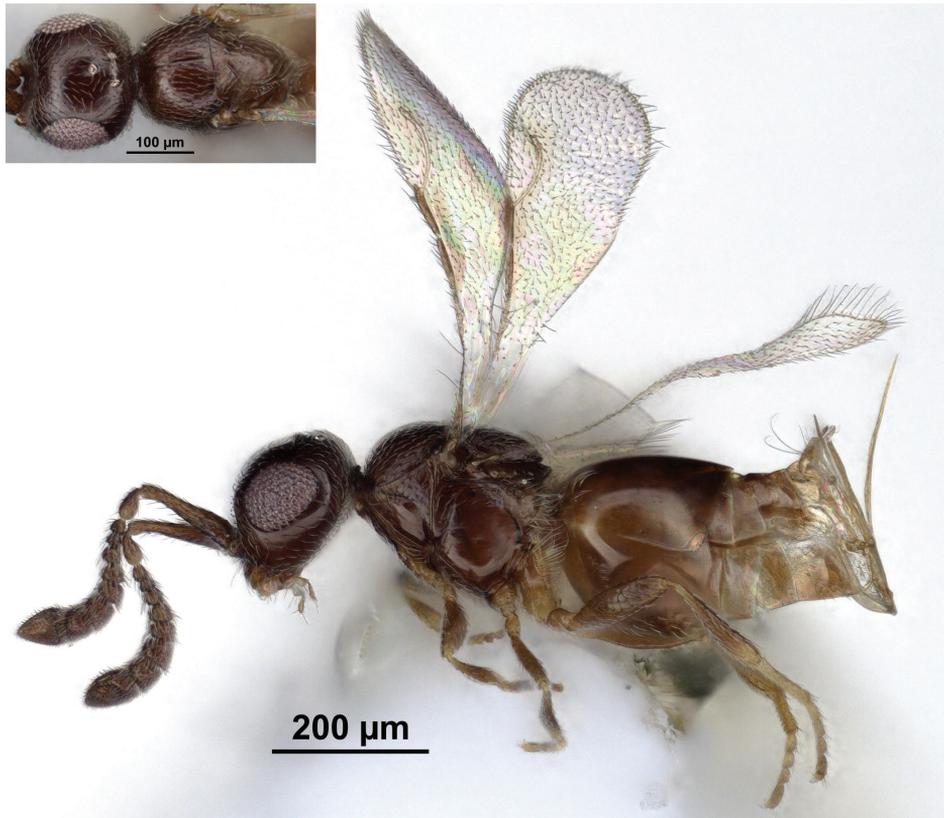


Figure 6. Female *Aphanogmus crispy* sp. nov. (paratype: ZFMK-HYM-00042484), head and mesosoma in dorsal view, habitus in lateral view.

COI barcode. Maximum intraspecific barcode distance: 3.3% (n = 15).

Minimum interspecific barcode distance: 10.5% (putative species consisting of NOCER-771 and NOCER-389).

Consensus sequence: 5'- AGCTGGACTTAGCCTGATCATCCGCTTAGAAC-
 TAAGGTCTCCCCCAATAATTTAATAAATAATGACCTAATCTACAATACT-
 GTAATTACTAACCATGCCTTTCTAATAATTTTTTTCCTAGTCATACCT-
 GTTATAATGGGGGGTTTCGGTAATTGACTAACCCCTGTAATAATTGGC-
 GCCCCTGACCTCTCCTTCCCCCGAATAAACAACATGAGATTGTGGT-
 TACTCCCCCCTCTCTTCTATACTTTAATAAGAATAACAACACTAACACTGG-
 AGTAGGAGCAGGATGAACCCTTTACCCCCCCTTAACCCTTGCCCCCTTC-
 CATGATGGAATATCAATAGATATAACAATTTTCTCTCTCCATATCGCTG-
 GCATCAGCTCAATTATAGGCTCAATTAATTTTCTAGTAACTATCATAAAAAT-
 AAGACCCTCCCCCAAGCACTAATCACCCCTCCCTTTATTTTGCTGATC-
 TATCATAATCACCTCCCTTCTTCTCCTCCTTTCCCTTACCTGTCTTAGCAG-
 GAGCTGTAACCATACTTCTGACTGACCGTAACATAAATACCTCTTTTTTC-
 GACCCCGAAGGGGGAGGAGACCCCTCCTCTACCAACACCTATTT -3'

Variation. The anteromedian projection of the metanoto-propodeo-metaplecto-mesopectal complex is more distinct in ZFMK-HYM-00042490 than in the holotype (ZFMK-HYM-00042477) and seemingly absent in 10022906, 10022913, and 10022925 (visible in μ CT image Suppl. material 4).

Biology. Unknown.

Distribution. Palaearctic: Czech Republic, Georgia, Germany, Norway, Sweden, and Switzerland.

Etymology. The species name is inspired by the shape of the harpe of the male genitalia with a distinct median ‘spine’. It was selected by acclamation from a short-list by fifth and sixth grade students of the Elisabeth-Selbert-Gesamtschule in Bonn, Germany. This was part of the school’s “Biodiversity Day”, aiming at increasing species knowledge and re-connecting kids to nature.

Remarks. *Aphanogmus crispy* can be distinguished from all other species of the *A. fumipennis* species group by the combination of the median spine of the harpe oriented distomedially and the distinct V-shaped mediodorsal notch of the harpe (Fig. 5D).

For further comparisons, see remarks under *A. tkheliharpus*.

***Aphanogmus digitangulus* Salden, Staverløkk, Mikó & Peters, sp. nov.**

<https://zoobank.org/9D260B82-FD02-40A1-98FF-08A1688ACF7C>

Figs 7, 8; Suppl. materials 5, 6

Material examined. Holotype: NORWAY • ♂; Trøndelag, Malvik: Buåsen; 63.3939°N, 10.6526°E; ca. 210 m a.s.l.; 5–27 Aug. 2019; A. Staverløkk leg.; Malaise trap; NINA; NOCER-081. **Paratypes:** NORWAY • 1 ♀; Telemark, Drangedal: Sannes gård; 59.0296°N, 9.2955°E; ca. 80 m a.s.l.; 23 Jun.–19 Jul. 2021; A. Staverløkk leg.; Malaise trap; NINA; NOCER-376 • 1 ♀; Aurskog-Høland, Mikkelsrud; 59.9754°N, 11.6683°E; ca. 300 m a.s.l.; 1 Aug.–12 Sep. 2022; A. Staverløkk leg.; Malaise trap; NINA; NOCER-809. GEORGIA • 1 ♂; Adjara, Kintrishi; 41.7372°N, 41.9792°E; ca. 400 m a.s.l.; 5–19 Oct. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042447 (without DNA barcode).

Other material examined. CZECH REPUBLIC • 1 ♂; South Moravia, Lednice, riparian forest; 9 Aug. 1991; L. Masner leg.; sweep net; UNHC; UNHC_1000014 (without DNA barcode). GERMANY • 1 ♂; Saxony, Bautzen, Driewitz; 51.3456°N, 14.4348°E; ca. 150 m a.s.l.; 30 Jul. 2013; L. Krogmann, T. Kothe leg.; sweep net; UNHC; 10022921 (without DNA barcode) • 1 ♂; Baden-Württemberg, Tübingen, Bebenhausen, Golder sbachtal; 48.5586°N, 9.0522°E; ca. 370 m a.s.l.; 22 Jun. 2012; L. Krogmann, T. Kothe, S. Kurz leg.; sweep net; UNHC; 10022929 (without DNA barcode). SWEDEN • 2 ♂♂; Stenbrohult, Djäkånabygds bokbacke, heath with old beeches; 1–18 Aug. 2003; UNHC; IM2146, IM2148 (without DNA barcodes) • 2 ♂♂; same collection data as for preceding; 1–15 Jul. 2003; UNHC; IM2155, IM2156 (without DNA barcodes) • 1 ♂; Vindelns kommun, Kulbäckslidens försökspark, dense mixed coniferous 20–25 yr old forest, Trap ID 60; 18 Aug.–1 Sep. 2003; UNHC; IM2151 (without DNA barcode).

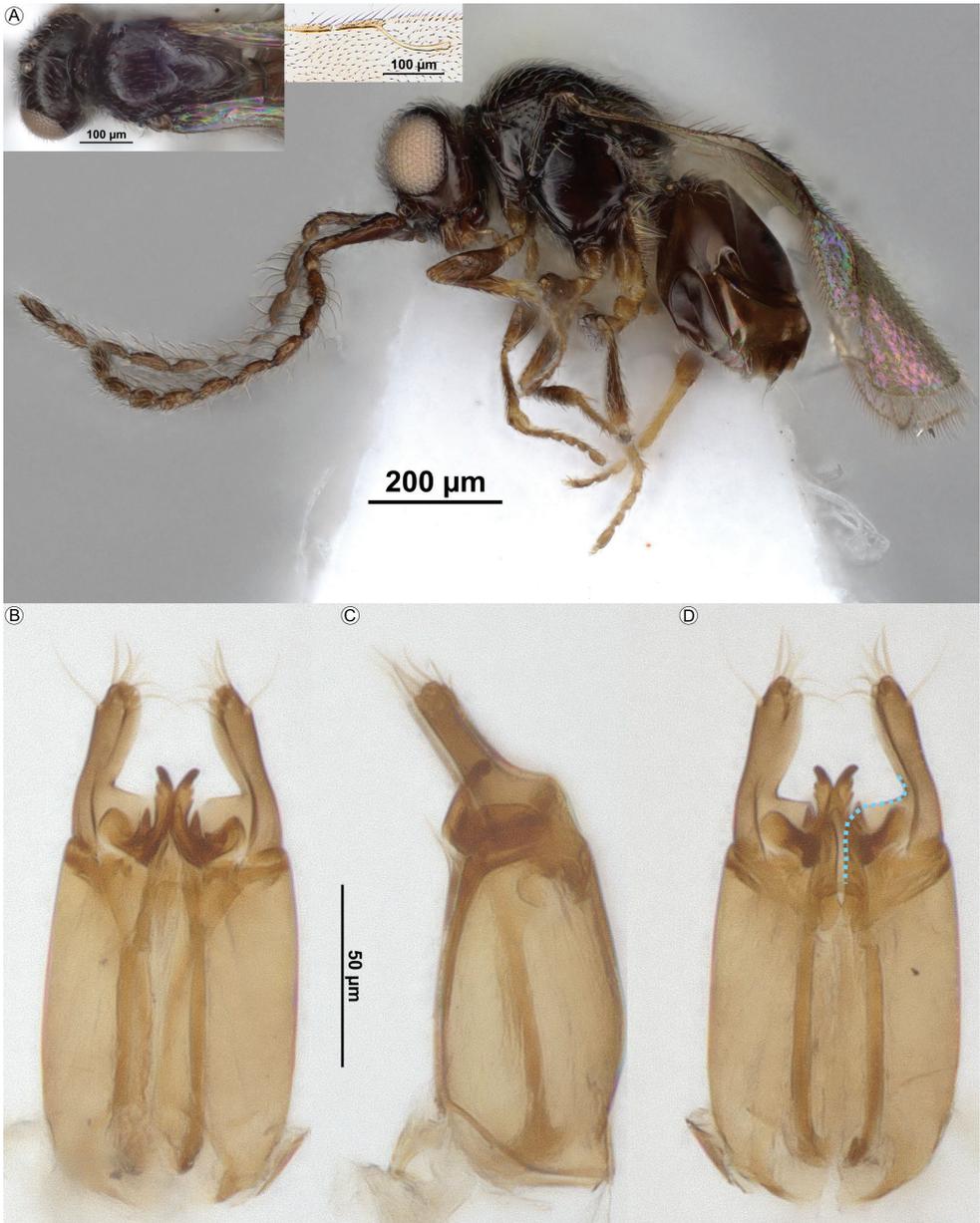


Figure 7. Male *Aphanogmus digitangulus* sp. nov. (paratype: ZFMK-HYM-00042447, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (holotype: NOCER-081), habitus in lateral view. **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with rectangular median extension.

Diagnostic description. Male. Body length: 0.80 mm.

Colour (Fig. 7A): Body brown. Antenna and legs slightly lighter and legs with lighter joints and tarsi.

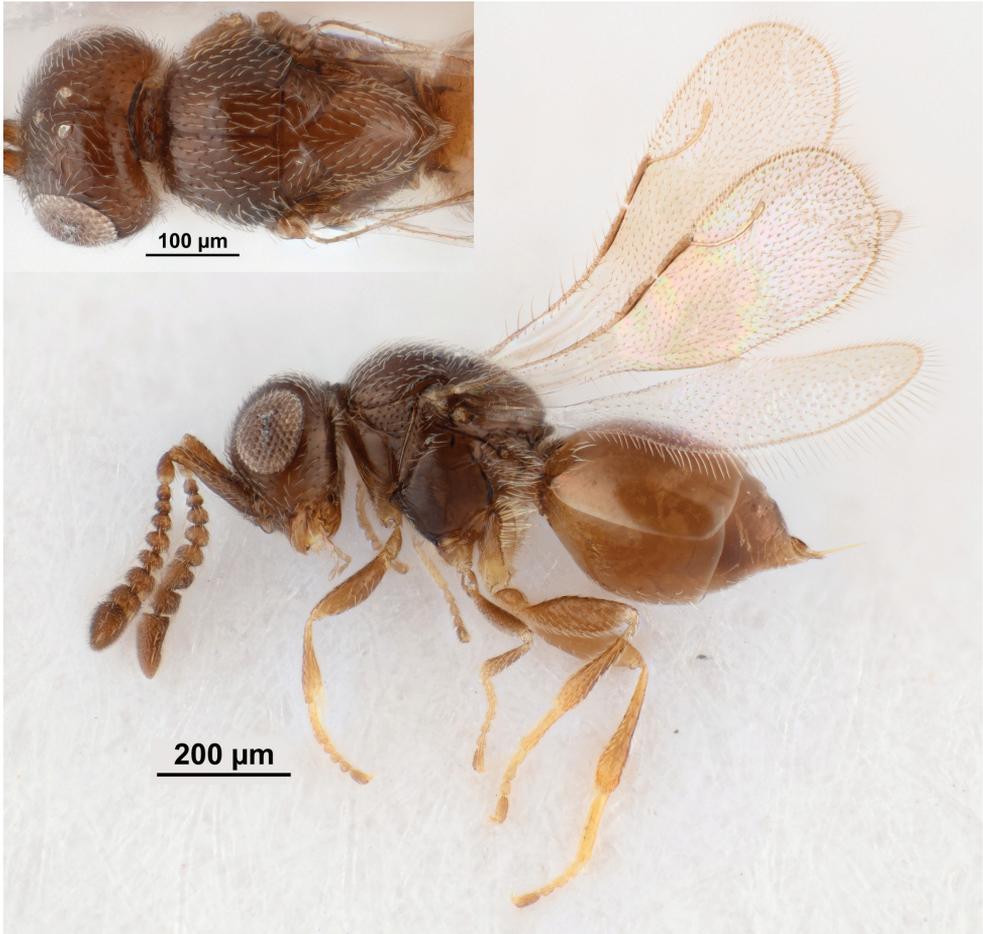


Figure 8. Female *Aphanogmus digitangulus* sp. nov. (paratype: NOCER-376), head and mesosoma in dorsal view, habitus in lateral view.

Antenna, head (Fig. 7A): F1 with sensillae arranged in three whorled rows, F1 length half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 7A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex short. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Four basal longitudinal carinae on syntergum.

Male genitalia (Fig. 7B–D): Gvc length one third of mesonotum length. Gvc width $0.69 \times$ gvc length; harpe/gvc index 0.46. Harpe finger-shaped, distoventrally oriented;

lateral margin of harpe slightly convex in basal third, concave in apical two-thirds, and slightly oriented distomedially; median margin of harpe slightly convex and slightly converging distomedially. Harpe without spines along median margin; harpe with rectangular median extension along basal third. Proximodorsal notch of harpe absent. Harpe width (above rectangular median extension) $0.13 \times$ gvc width, and $0.19 \times$ harpe length. Harpe with three median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least four apical setae oriented distoventrally; harpe with one distinct lateral seta close to apex, oriented distolaterally. Gonossiculus length $0.61 \times$ harpe length; gonossiculus J-shaped with at least two digital teeth and apically slightly serrated, tip oriented distodorsally and distolaterally. Aedeagus straight.

Female. Body length: 0.85 mm.

Colour (Fig. 8): Body light brown except metasoma and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 8): F8 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 8): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus indistinct. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Two basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 1.2% ($n = 3$). Minimum interspecific barcode distance: 14.9% (*A. ventricoharpus*).

Consensus sequence: 5'- AGCCGGATTAAGACTAATTATCCGCCTT-GAACTTAGATCCCCCCTAATACCATAATTAATAATGACCTAATCTA-CAACTCTGTAATCACAAACCATGCCTTCCTAATAATTTTTTTCCTAGT-TATACCTATTATACTAGGAGGATTCGGAAACTGATTAATCCCTAT-TATAATCGGGGCCCTGATTTAGCCTTCCCTCGTATAAATAATATA-AGACTATGATTACTCCCCCCTCTTTAACCCTCCTCCTAATA-AGAATAATAACCAACACAGGGGTGGGGGCAGGATGAACCCTT-TACCCCTTTAACTTTAATVCCCTTTTCATGACGGCATATCAATAGACT-TAACAATTTACTCTCTCCATATGTCAGGAGTTAGCTCAATTATAG-GCTCAATTAATTTTATAGTAACAACCTTATAAAATAAAACCCCTTCCCT-CAACTAATAATATCCCTCCCCCTATTTTGTGTTGATCAATCATAAT-TACCTCCCTCCTCCTTTTACTATCTCTCCCTGTACTAGCTGGTGCCG-TAACAATAATCCTTACCGACCGAAACTTAAATACTTCCTTTTTTCGATC-CAGAGGGGGGAGGGGACCCCTTACTTTACCAACATCTATTC -3'

Variation. The interaxillar sulcus is present in 10022921 and 10022929 (visible in μ CT image Suppl. material 6).

Biology. Unknown.

Distribution. Palaearctic: Czech Republic, Georgia, Germany, Norway, and Sweden.

Etymology. The species name is a composition of the Latin words ‘*digitus*’ and ‘*rectangulus*’, meaning ‘finger’ and ‘rectangular’, with reference to the male genitalia with a finger-shaped harpe and a rectangular median extension along the basal third of the harpe.

Remarks. *Aphanogmus digitangulus* is unique among all species of the *A. fumipennis* species group by its rectangular median extension along the basal third of the harpe, combined with the harpe lacking both spines and a proximodorsal notch (Fig. 7D).

For further comparisons, see remarks under *A. fumipennis*.

***Aphanogmus hafti* Salden, Mikó & Peters, sp. nov.**

<https://zoobank.org/47C44327-9B6D-4844-9F30-7311DC47206B>

Figs 9, 10; Suppl. materials 7, 8

Material examined. **Holotype:** GERMANY • ♂; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.16754°N, 8.7903°E; ca. 180 m a.s.l.; 2–16 Jul. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_T00805 (=SMNS_Hym_Cer_001108). **Paratypes:** GEORGIA • 1 ♀; Racha-Lechkhumi & Kvemo Svaneti, Doghurashi; 42.6782°N, 42.8101°E; ca. 1470 m a.s.l.; 17–24 May 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042444 • 1 ♀; same collection data as for preceding; 18–24 Aug. 2020; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042443 • 1 ♀; Racha-Lechkhumi & Kvemo Svaneti, Doghurashi; 42.6990°N, 42.8267°E; ca. 1800 m a.s.l.; 20–26 Jun. 2020; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042442 • 1 ♂; Adjara, Kintrishi; 41.7554°N, 42.1130°E; ca. 2280 m a.s.l.; 25 Aug.–8 Sep. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042441 (without DNA barcode).

Other material examined. GERMANY • 1 ♂; Baden-Württemberg, Esslingen, Oberboihingen, meadow orchard; 48.6506°N, 9.3689°E; ca. 310 m a.s.l.; 10–23 Jun. 2012; T. Kothe, G. Schweizer leg.; Malaise trap; UNHC; PSUC_FEM 10022947 (without DNA barcode) • 1 ♂; same collection data as for preceding; 12–26 Aug. 2012; T. Kothe, G. Schweizer leg.; Malaise trap; UNHC; PSUC_FEM 10022845 (without DNA barcode).

Diagnostic description. Male. Body length: 0.90 mm.

Colour (Fig. 9A): Body brown except metasoma and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 9A): F1 with sensillae arranged in three whorled rows, F1 length slightly shorter than half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 9A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex short. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent.

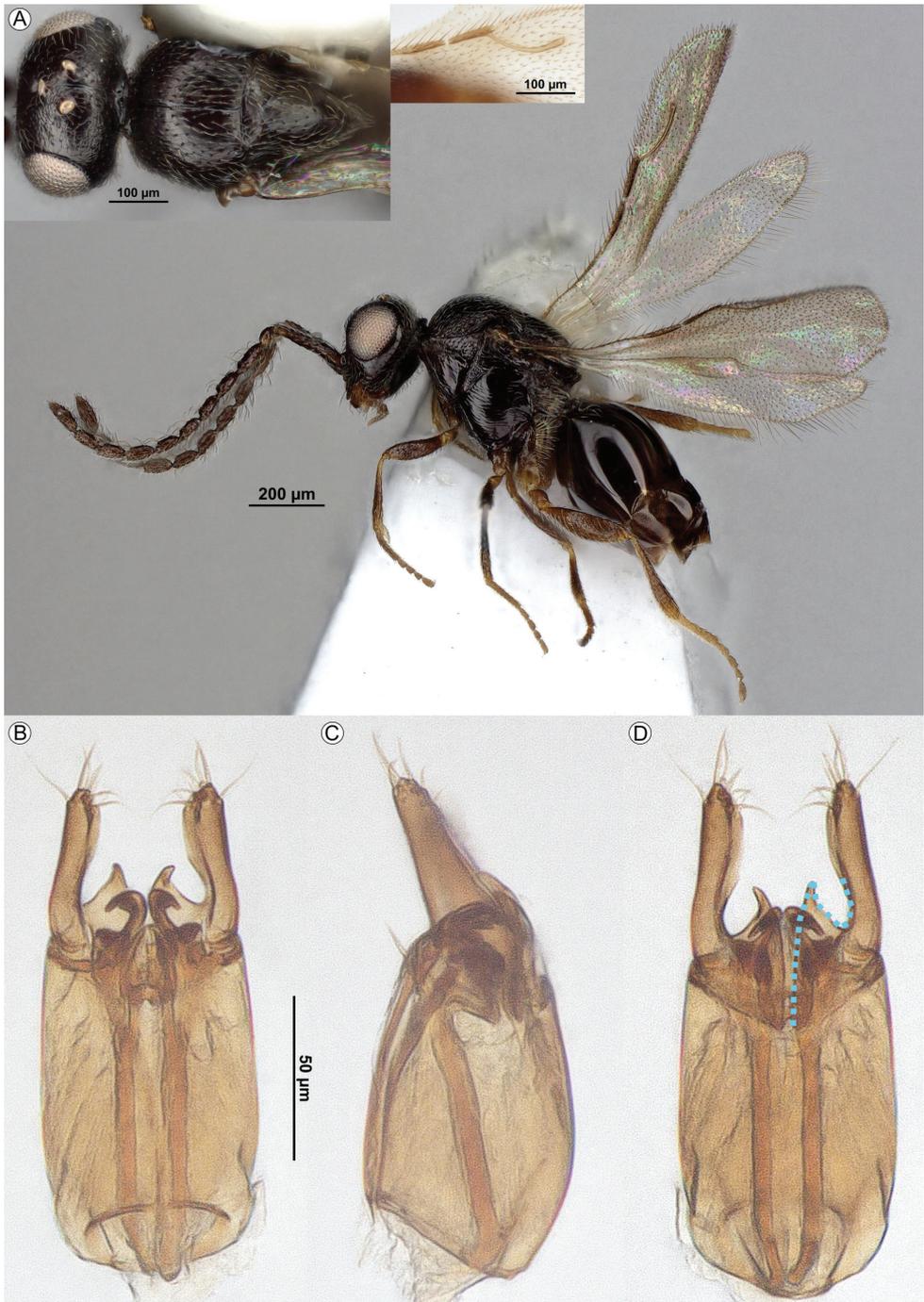


Figure 9. Male *Aphanogmus hafii* sp. nov. (paratype: ZFMK-HYM-00042441, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (holotype: SMNS_Hym_T00805, in glycerol), habitus in lateral view. **B–D.** Male genitalia (holotype: SMNS_Hym_T00805): **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine and proximodorsal notch of harpe.

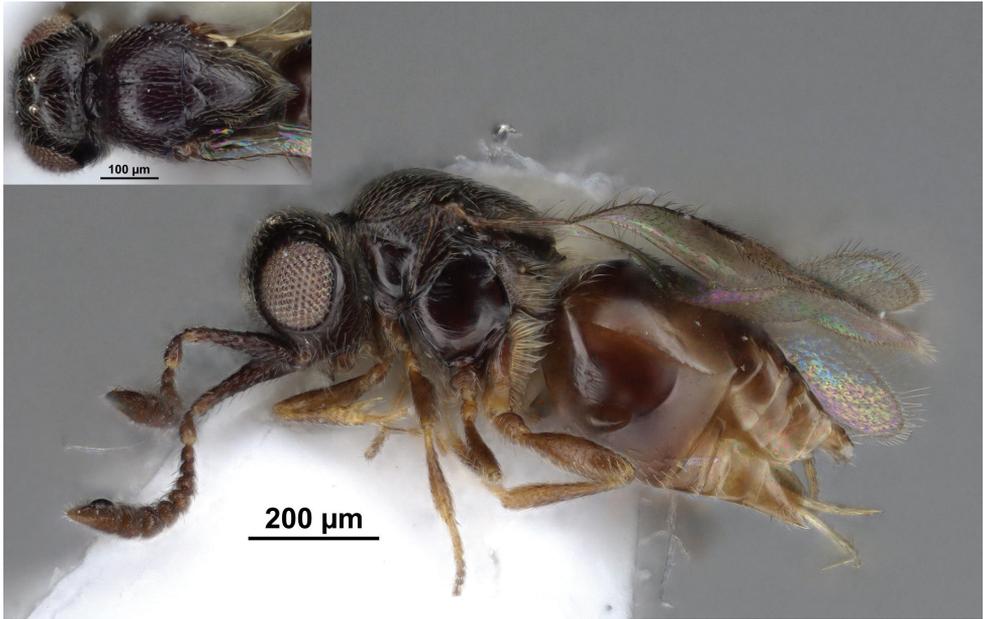


Figure 10. Female *Aphanogmus hafii* sp. nov. (paratype: ZFMK-HYM-00042444), head and mesosoma in dorsal view, habitus in lateral view.

Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Indistinct basal longitudinal carinae on syntergum.

Male genitalia (Fig. 9B–D): Gvc length one third of mesonotum length. Gvc width $0.70 \times$ gvc length; harpe/gvc index 0.48. Harpe finger-shaped, distoventrally oriented; lateral margin of harpe convex in basal half, straight in apical half, and oriented distally; median margin of harpe concave in basal quarter, convex in apical three-quarters, and slightly oriented distolaterally. Harpe with basomedian spine; tip of basomedian spine more distal than tip of gonossiculus and oriented distolaterally; harpe with slim median lamella-like extension along apical half. Proximodorsal notch of harpe U-shaped and $0.37 \times$ as long as harpe length. Harpe width (above basomedian spine) $0.19 \times$ gvc width, and $0.23 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least four apical setae oriented distally; harpe with one lateral seta close to apex, oriented distolaterally. Gonossiculus length $0.46 \times$ harpe length; gonossiculus C-shaped with at least two digital teeth, tips oriented dorsolaterally. Aedeagus indistinct.

Female. Body length: 1.00 mm.

Colour (Fig. 10): Body brown except legs lighter.

Antenna, head (Fig. 10): F8 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 10): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex distinct. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Four basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 2.9% (n = 4). Minimum interspecific barcode distance: 15.1% (*A. digitangulus*).

Consensus sequence: 5'- AGCTGGACTTAGCCTAATTATTCGCT-TAGAATTAAGATCCCCCCTAATAACATAATAACAATGACCTRATT-TACAACTCTGTAATCACCAATCATGCATTTTTAATAATTTTTTTCCTT-GTTATGCCAGTYATACTAGGGGGATTTGGAACTGACTAATCCCTAT-TATAATTGGTGCCCCAGATTTAGCTTTCCCTCGAATAACAATATA-AGTCTTTGACTACTCCCYCCCTCTTTAACCCCTCCTTCTCACAGAATA-ATAACCAATACCGGAGTCGGAGCAGGRTGAACCCTTTACCCCCCCT-TAACTCTAACCCCTTCCATGATGGAATATCAATAGACCTCACAAATT-TACTCCCTTCATATTGCAGGTCTTAGCTCAATTATAGGATCTAT-TAATTTTCATAGTAACAACCTACAAAATAAAAACCTTCCCCTCAATC-CATTCTATCCCTCCCCCTATTCTGTTGATCAATTATAATTACCTCCT-TACTCCTACTTCTATCCCTCCCCGTCTTAGCTGGAGCCATTACAATA-ATCCTCACTGACCGAAATTTAAATACTTCATTTTTTTGACCCAGA-AGGRGGGGGAGACCCCTTCTTTACCAACATTTATTC-3'

Variation. The colouration of the male specimen ZFMK-HYM-00042441 is dark brown and the specimen is equipped with four basal longitudinal carinae on the syntergum. F8 is as long as half of the scape length in ZFMK-HYM-00042442 and ZFMK-HYM-00042443. The interaxillar sulcus is present in PSUC_FEM 10022947 and PSUC_FEM 10022845 (visible in μ CT image Suppl. material 8).

Biology. Unknown.

Distribution. Palaearctic: Georgia and Germany.

Etymology. The species is named after the nature-enthusiastic documentary filmmaker Jan Haft. With his camera, he opens doors to countless hidden stories of nature.

Remarks. *Aphanogmus hafii* can be distinguished from all other species of the *A. fumipennis* species group by the distolaterally oriented basomedian spine of the harpe and the slim median lamella-like extension along the apical half of the harpe (Fig. 9D).

***Aphanogmus hamatogonus* Salden, Staverløkk, Mikó & Peters, sp. nov.**

<https://zoobank.org/C4B0006F-934F-4AB5-887E-480E68D0B7E6>

Figs 11, 12; Suppl. material 9

Material examined. *Holotype*: NORWAY • ♂; Trøndelag, Soknedal; 62.9786°N, 10.2206°E; ca. 210 m a.s.l.; 8 Jul.–11 Aug. 2020; A. Staverløkk leg.; Malaise trap; NINA; NOCER-09. *Paratypes*: NORWAY • 1 ♀; same data as for holotype; NINA;

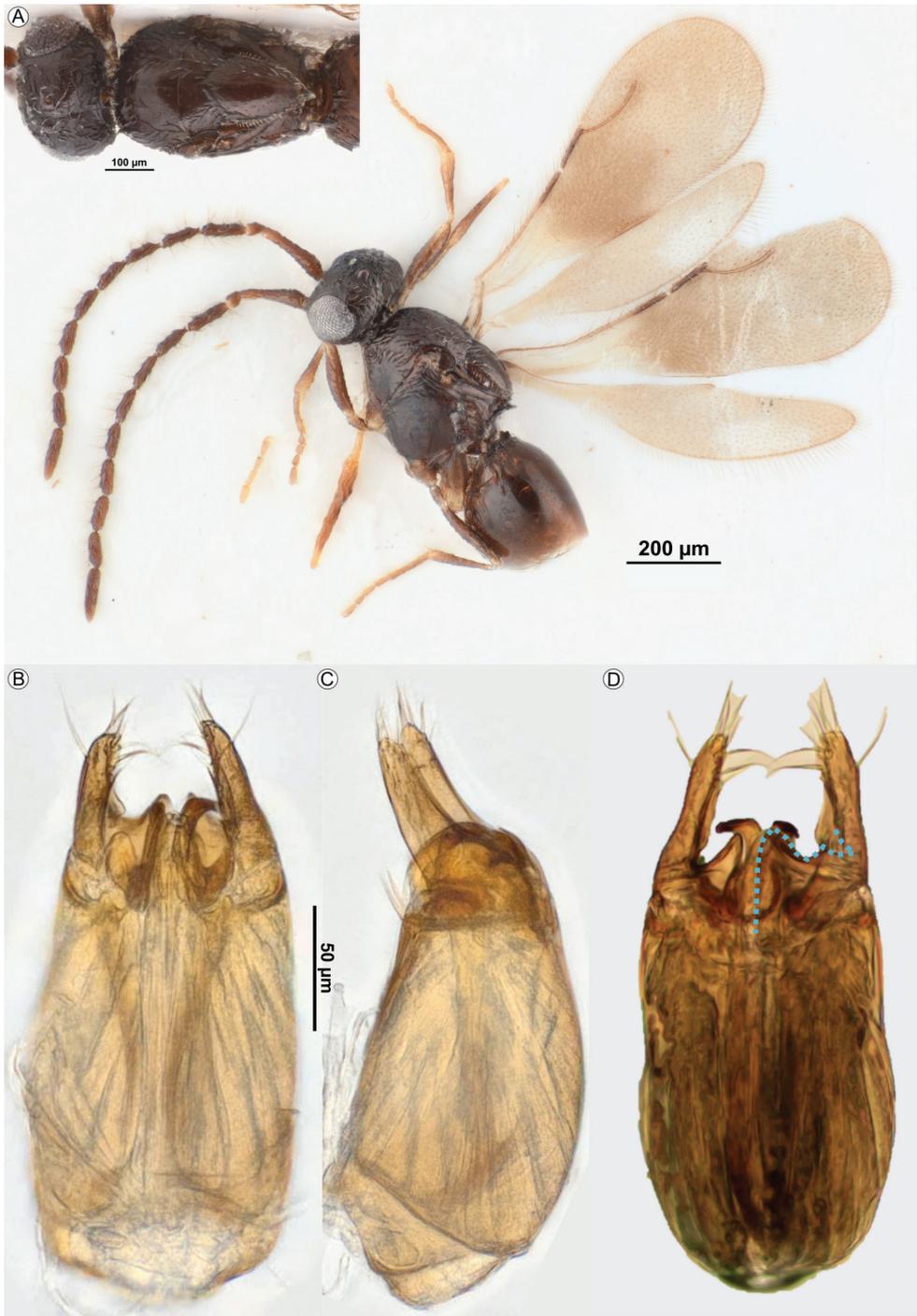


Figure 11. Male *Aphanogmus hamatogonus* sp. nov. (holotype: NOCER-09, unless noted otherwise). **A.** Head and mesosoma in dorsal view, habitus in lateral view. **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view (non-type: PSUC_FEM 10022812), blue dashed line with basomedian spine, small spine-like structure, and proximodorsal notch of harpe.

NOCER-550 • 1 ♀; Aurskog-Høland, Mikkelsrud; 59.9754°N, 11.6683°E; ca. 300 m a.s.l.; 9 May–13 Jun. 2022; A. Staverløkk leg.; Malaise trap; NINA; NOCER-852.

Other material examined. GERMANY • 1 ♂; North Rhine-Westphalia, Eifel National Park, Döppeskaul; 21 Sep.–5 Oct. 2009; J. Esser leg.; Malaise trap; UNHC; PSUC_FEM 10022941 (without DNA barcode) • 1 ♂; Saxony, Bautzen, Driewitz; 51.3456°N, 14.4348°E; ca. 150 m a.s.l.; 30 Jul. 2013; L. Krogmann, T. Kothe leg.; sweep net; UNHC; PSUC_FEM 10022914 (without DNA barcode) • 1 ♂; Baden-Württemberg, Lörrach, nature reserve Buchswald Grenzach; 47.5575°N, 7.6972°E; ca. 370 m a.s.l.; 6 Aug. 2013; T. Kothe, P. Bergmann leg.; sweep net; UNHC; PSUC_FEM 10022812 (without DNA barcode).

Diagnostic description. Male. *Body length*: 0.90 mm.

Colour (Fig. 11A): Body brown except legs and antenna lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 11A): F1 with sensillae arranged in at least four whorled rows, F1 longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 11A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus slightly visible. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. No basal longitudinal carinae on syntergum.

Male genitalia (Fig. 11B–D): Gvc length slightly less than half of mesonotum length. Gvc width $0.63 \times$ gvc length; harpe/gvc index 0.36. Harpe finger-shaped, distoventrally oriented; lateral margin of harpe slightly concave at mid-length and slightly oriented distomedially; median margin of harpe with small extension in basal quarter, straight in apical three-quarters, and slightly converging distomedially. Harpe with basomedian spine and small spine-like structure lateral to basomedian spine; tip of basomedian spine about as distal as tip of gonossiculus and oriented distally; tip of small spine-like structure more proximal than tip of gonossiculus, gradually narrowing towards apex, and oriented distally. Proximodorsal notch of harpe lateral to small spine-like structure, V-shaped, and $0.16 \times$ as long as harpe length. Width of harpe (above small median extension in basal quarter of harpe) $0.12 \times$ gvc width, and $0.17 \times$ harpe length. Harpe with three median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least four apical setae oriented distally; harpe with one lateral seta close to apex, oriented distolaterally. Gonossiculus length $0.52 \times$ harpe length; gonossiculus C-shaped with at least one digital hook-shaped tooth, tip oriented dorsally. Aedeagus straight.

Female. *Body length*: 0.90 mm.

Colour (Fig. 12): Body brown except metasoma, antenna and legs lighter. Legs with lighter joints and tarsi. Antenna with slightly darker F6–F8.



Figure 12. Female *Aphanogmus hamatogonus* sp. nov. (paratype: NOCER-852), head and mesosoma in dorsal view, habitus in lateral view.

Antenna, head (Fig. 12): F8 length half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 12): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Two basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 2.5% (n = 3). Minimum interspecific barcode distance: 15.1% (*A. digitangulus*).

Consensus sequence: 5'-GGCAGGCCTTAGCCTCATTATTCGTCTTGAATTAAGRTCCCCCCCCAATAACATAATAAATAACGATTTAATCTATAACTCTGTAATTACCAATCATGCCTTTTTAATAATTTTTTTCTGGTCATACCTAT-

TATATTGGGGGGCTTTGGAAATTGACTAATCCCCATTATAATTGGGGCTC-
CGGATCTAGCCTTCCCTCGAATAAATAATATGAGACTGTGAT-
TACTCCCCCCTCTTTAACCCCTCCTTCTAATAAGTATAATAACTAATACGGG-
TGTAGGAGCAGGTTGGACCCTTTACCCCCCTTTAACTTTAATACCCTTC-
CATGATGGAATATCAATAGACTTAACAGTTTATTCCTCCATATTGCAG-
GAATTAGCTCAATTATAGGCTCAATCAATTTTCATAGTTACCACTTATAAAAT-
AAAACCCTCCCCCAAATTTAACATCCCTCCCTCTATTTCTGTTGATCAAT-
TATAATTACTTCCCTTCTCCTCATCCTCTCCCTACCCGTCTTAGCCG-
GAGCTGTAACAATAATTCTCACCGATCGCAACTTAAATACTTCATTTTTT-
GATCCAGAAGGGGGGGGTGACCCCTACTCTATCAACATTTATTC -3'

Variation. Unknown.

Biology. Unknown.

Distribution. Palaearctic: Germany and Norway.

Etymology. The species name is a composition of the Latin word '*hamatus*', meaning 'hooked', and a short form of the anatomical term gonossiculus, with reference to the hook-shaped tooth of the gonossiculus of the male genitalia.

Remarks. *Aphanogmus hamatogonus* can be distinguished from all other species of the *A. fumipennis* species group by its small spine-like structure lateral to the baso-median spine of the harpe, in combination with a small median extension in the basal quarter of the harpe, and a hook-shaped tooth of the gonossiculus (Fig. 11D).

For further comparisons, see remarks under *A. fumipennis*.

Aphanogmus harpagodalis Salden, Mikó & Peters, sp. nov.

<https://zoobank.org/A02AEEB3-5567-42F8-BC3C-6F06F103E285>

Fig. 13; Suppl. material 10

Material examined. **Holotype:** GERMANY • ♂; Hesse, Werra-Meißner-Kreis, Großalm-erode, private garden, Siedlerweg, semi-abandoned garden with wet spot, ivy hedge and salix; 51.2591°N, 9.7871°E; ca 380 m a.s.l.; 12–20 Jul. 2022; J. Vogel leg.; Malaise trap; ZFMK; ZFMK-HYM-00042640 (without DNA barcode). **Paratypes:** GERMANY • 4 ♂♂; same data as for holotype; ZFMK; ZFMK-HYM-00042649, ZFMK-HYM-00042651, ZFMK-HYM-00042652, ZFMK-HYM-00042653 (without DNA barcodes) • 1 ♂; North Rhine-Westphalia, ZFMK garden; 50.7216°N, 7.1141°E; ca 60 m a.s.l.; 30 Aug. 2022; T. Salden leg.; sweep net; ZFMK; ZFMK-HYM-00042659 (without DNA barcode). SWEDEN • 1 ♂; Gotland, Eksta socken, Stora Karlsö; 57.2841°N, 17.9700°E; ca. 30 m a.s.l.; 15 Aug.–3 Sep. 2023; Hym inventory 2023 leg.; Malaise trap; NHRS; NHRS-HEVA000023404 (without DNA barcode).

Other material examined. GERMANY • 2 ♂♂; Baden-Württemberg, Esslingen, Oberboihingen, meadow orchard; 48.6506°N, 9.3689°E; ca. 310 m a.s.l.; 10–23 Jun. 2012; T. Kothe, G. Schweizer leg.; Malaise trap; UNHC; PSUC_FEM 10022950, PSUC_FEM 10022725 (without DNA barcodes).

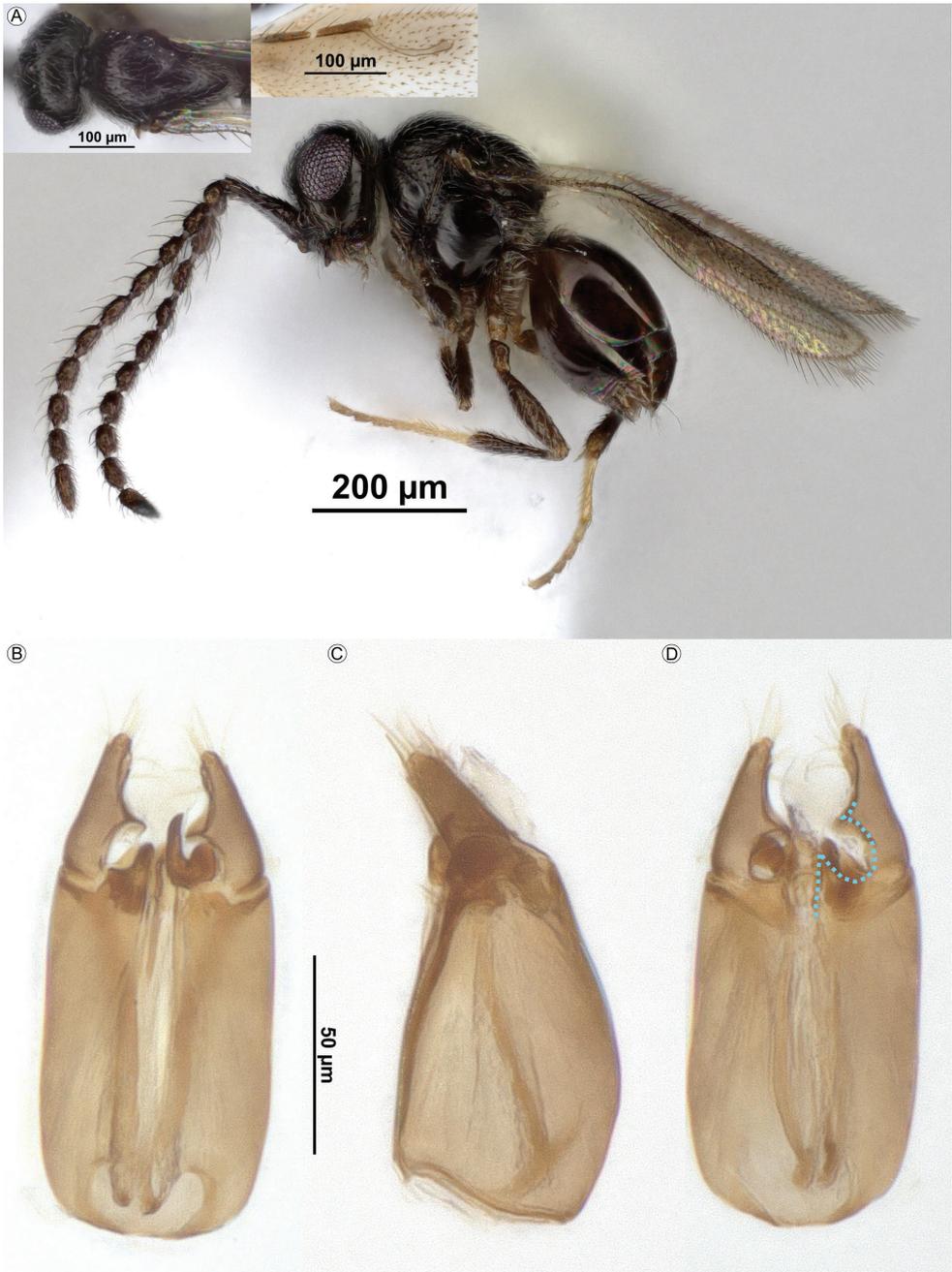


Figure 13. Male *Aphanogmus harpagodalis* sp. nov. (holotype: ZFMK-HYM-00042640, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (paratype: ZFMK-HYM-00042651, in glycerol), habitus in lateral view. **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine, proximodorsal notch of harpe, and median spine.

Diagnostic description. Male. *Body length*: 0.70 mm.

Colour (Fig. 13A): Body dark brown. Legs with lighter joints and tarsi.

Antenna, head (Fig. 13A): F1 with sensillae arranged in three whorled rows, F1 length slightly shorter than half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 13A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus present. Anteromedian projection of the meta-noto-propodeo-metapecto-mesopectal complex absent. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. No basal longitudinal carinae on syntergum.

Male genitalia (Fig. 13B–D): Gvc length one third of mesonotum length. Gvc width $0.62 \times$ gvc length; harpe/gvc index 0.37. Harpe finger-shaped, distoventrally oriented; lateral margin of harpe convex in basal third, straight in apical two-thirds, and oriented distomedially; median margin of harpe concave in basal half, concave in apical half, with median spine in-between, and slightly converging distomedially. Harpe with basomedian and median spine; tip of basomedian spine more proximal than tip of gonossiculus and oriented distally; median spine arising from mid-length of harpe and pagoda-shaped, gradually narrowing towards apex; tip of median spine more proximal than tip of gonossiculus and oriented medially. Proximodorsal notch of harpe U-shaped and $0.22 \times$ as long as harpe length. Harpe width (above median spine) $0.13 \times$ gvc width, and $0.20 \times$ harpe length. Harpe with three median setae oriented proximomedially and distomedially, extending to apical third; harpe with at least three apical setae oriented distally; harpe with one lateral seta close to apex, oriented distolaterally. Gonossiculus length $0.55 \times$ harpe length; gonossiculus J-shaped with at least one digital tooth, tip oriented distodorsally. Aedeagus straight.

Female. Unknown.

COI barcode. Unknown.

Variation. Unknown.

Biology. Unknown.

Distribution. Palaearctic: Germany.

Etymology. The species name is a composition of the anatomical term ‘harpe’ and the pagoda-shaped median spine of the harpe.

Remarks. *Aphanogmus harpagodalis* can be easily distinguished from all other species of the *A. fumipennis* species group by its two spines along the median margin of the harpe with the median spine being pagoda-shaped and oriented medially (Fig. 13D).

***Aphanogmus karlazani* Salden, Mikó & Peters, sp. nov.**

<https://zoobank.org/D89616DB-6EC7-4F03-9ECB-67D1B4F954C6>

Fig. 14; Suppl. material 11

Material examined. *Holotype*: GEORGIA • ♂; Kakheti, Vashlovani, near Alazani river; 41.1241°N, 46.6523°E; ca. 100 m a.s.l.; 21–28 Jun. 2021; G. Japoshvili leg.; Malaise trap; ECAUG; ZFMK-HYM-00042565 (without DNA barcode). ***Paratypes*:** GERMANY

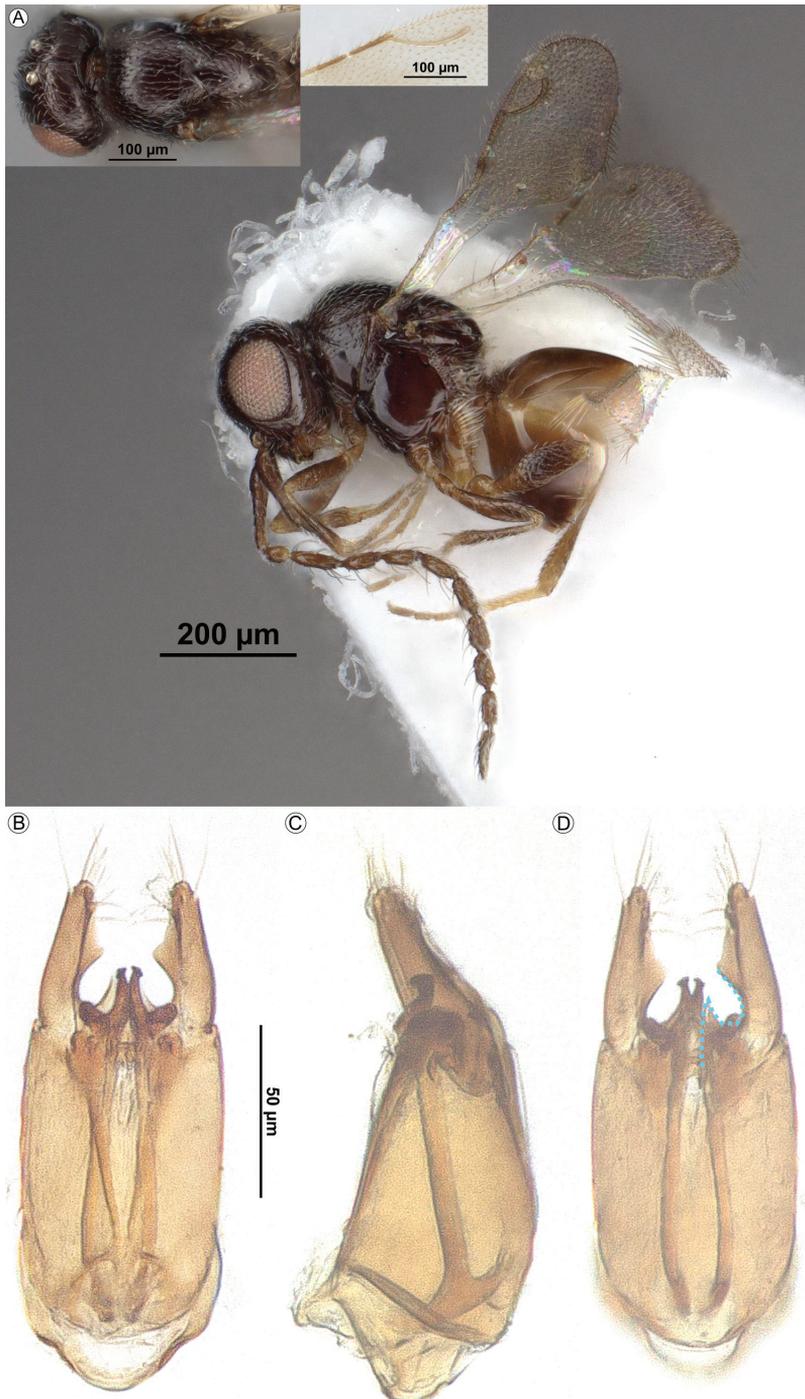


Figure 14. Male *Aphanogmus karlazani* sp. nov. (holotype: ZFMK-HYM-00042565). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (in glycerol), habitus in lateral view. **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine, proximodorsal notch of harpe, and triangular median lamella-like extension.

• 1 ♂; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.1675°N, 8.7903°E; ca. 180 m a.s.l.; 13–27 Aug. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001034.

Other material examined. HUNGARY • 2 ♂♂; Bács-Kiskun, Miklapusza; 1 Oct. 1997; É. Kovács leg.; yellow pan trap; UNHC; PSUCIM_3145, IM1079 (without DNA barcodes) • 2 ♂♂; Bács-Kiskun, Gara; 46.035°N, 19.020°E; ca. 90 m a.s.l.; 26–30 Jun. 2009; I. Mikó leg.; yellow pan trap; UNHC; UNHC_1000023, UNHC_1000024 (without DNA barcodes).

Diagnostic description. Male. *Body length*: 0.75 mm.

Colour (Fig. 14A): Body brown except metasoma and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 14A): F1 with sensillae arranged in three whorled rows, F1 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 14A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex virtually absent. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Four basal longitudinal carinae on syntergum.

Male genitalia (Fig. 14B–D): Gvc length one third of mesonotum length. Gvc width $0.69 \times$ gvc length; harpe/gvc index 0.47. Harpe finger-shaped, oriented distoventrally, and gradually narrowing towards apex; lateral margin of harpe slightly convex in basal half, straight in apical half, and oriented distomedially; median margin of harpe concave in basal half, slightly concave in apical half, with lamella-like extension in-between, and slightly diverging distolaterally. Harpe with basomedian spine; tip of basomedian spine slightly more proximal than tip of gonossiculus and oriented distally; harpe with distinct triangular median lamella-like extension at mid-length; tip of triangular median lamella-like extension pointed and oriented medially. Proximodorsal notch of harpe U-shaped and $0.36 \times$ as long as harpe length. Harpe width (above basomedian spine) $0.19 \times$ gvc width, and $0.26 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least four apical setae oriented distally, including one broadened seta (broadening only visible in CLSM image Suppl. material 11); harpe with one lateral seta close to apex, oriented distally. Gonossiculus length $0.48 \times$ harpe length; gonossiculus J-shaped with knob-like apex, with indistinct digital teeth, tip oriented distolaterally. Aedeagus straight.

Female. Unknown.

***COI* barcode.** Unknown.

Variation. Unknown.

Biology. Unknown.

Distribution. Palaearctic: Georgia, Germany, and Hungary.

Etymology. The species name is a composition of ‘Karlsruhe’ (Germany) and ‘Alazani River’ (Georgia), with reference to the localities of one paratype and the holotype.

Remarks. The male genitalia of *A. karlazani* have a distinct triangular median lamella-like extension at mid-length of the harpe (Fig. 14D), a character shared with *A. kintrishi* (Fig. 15D). However, in *A. karlazani*, the median margin of the triangular lamella-like extension is slightly concave in apical half (straight in *A. kintrishi*), the tip of the extension is pointed (rounded in *A. kintrishi*), and the median setae of the harpe are extending to the apical third in *A. karlazani* (restricted to the apical quarter in *A. kintrishi*). Additionally, the gonossiculus is differently shaped in both species (with indistinct digital teeth and a knob-like apex in *A. karlazani* (Fig. 14D) and at least three digital teeth without a knob-like apex in *A. kintrishi* (Fig. 15D)).

All six examined specimens can be unambiguously assigned to *A. karlazani* based on morphological characters, particularly the male genitalia. Only one DNA barcode (SMNS_Hym_Cer_001034) is available for *A. karlazani*. The molecularly closest specimen to SMNS_Hym_Cer_001034 is ZFMK-HYM-00042561 (with only 1% difference), which is a singleton with distinctly different male genitalia (Fig. 31B–D, an additional undescribed putative species). Integrating the data we have at hand, we decide to describe this species based on the distinct morphological characters shared by a series of six males from three countries, resulting in a clear morphological diagnosis, and acknowledge that molecular characterization of *A. karlazani* (and putative additional close species) needs additional specimens and sequence data. Consequently, given the still unclear molecular characterization of *A. karlazani*, we do not provide the DNA barcode as part of the description and do not highlight the single specimen/sequence as belonging to *A. karlazani* in Fig. 1.

***Aphanogmus kintrishi* Salden, Mikó & Peters, sp. nov.**

<https://zoobank.org/19113C9F-C2FD-4ECC-8FE9-EDBEEC46CD74>

Figs 15, 16; Suppl. material 12

Material examined. Holotype: GEORGIA • ♂; Adjara, Kintrishi; 41.7372°N, 41.9792°E; ca. 400 m a.s.l.; 27 Jul.–10 Aug. 2018; L. Mumladze leg.; Malaise trap; ZFMK; ZFMK-HYM-00042502. **Paratypes:** GEORGIA • 1 ♀; same data as for holotype; ECAUG; ZFMK-HYM-00042503 • 1 ♂; same data as for holotype; 13–27 Jul. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042505 • 1 ♂; same data as for holotype; 10–24 Aug. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042504 • 1 ♀, 1 ♂; same data as for holotype; 24 Aug.–7 Sep. 2018; L. Mumladze leg.; Malaise trap; ZFMK; ZFMK-HYM-00042506, ZFMK-HYM-00042509 • 1 ♂; same data as for holotype; 7–21 Sep. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042510 (without DNA barcode) • 1 ♀; same data as for holotype; 5–19 Oct. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042508.

Diagnostic description. Male. Body length: 0.85 mm.

Colour (Fig. 15A): Body brown except scape and legs yellowish.

Antenna, head (Fig. 15A): F1 with sensillae arranged in at least four whorled rows, F1 length longer than half of scape length. Preoccipital lunula absent. Preoccipital

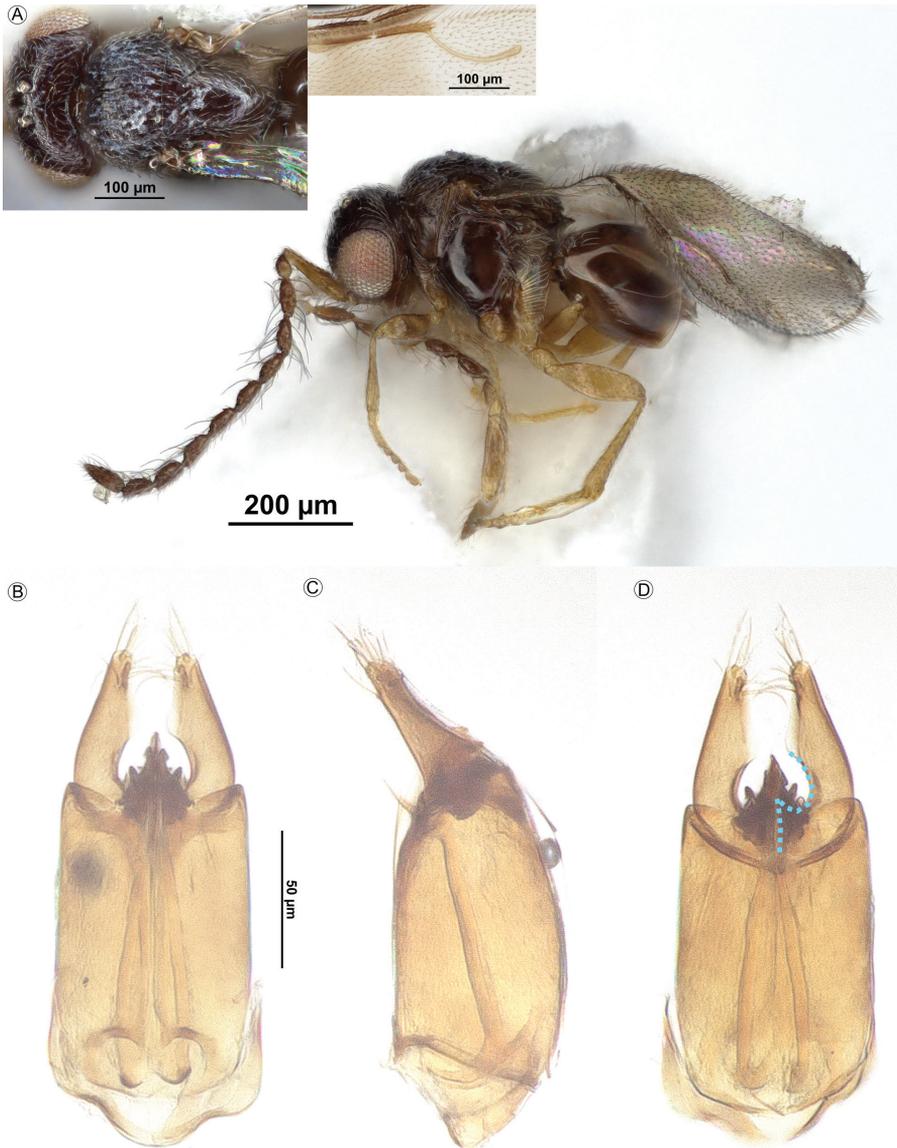


Figure 15. Male *Aphanogmus kintrishi* sp. nov. (paratype: ZFMK-HYM-00042505, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (holotype: ZFMK-HYM-00042502, in glycerol), habitus in lateral view. **B–D.** Male genitalia (holotype: ZFMK-HYM-00042502): **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine, proximodorsal notch of harpe, and triangular median lamella-like extension.

furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea present. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 15A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus present. Anteromedian projection of the

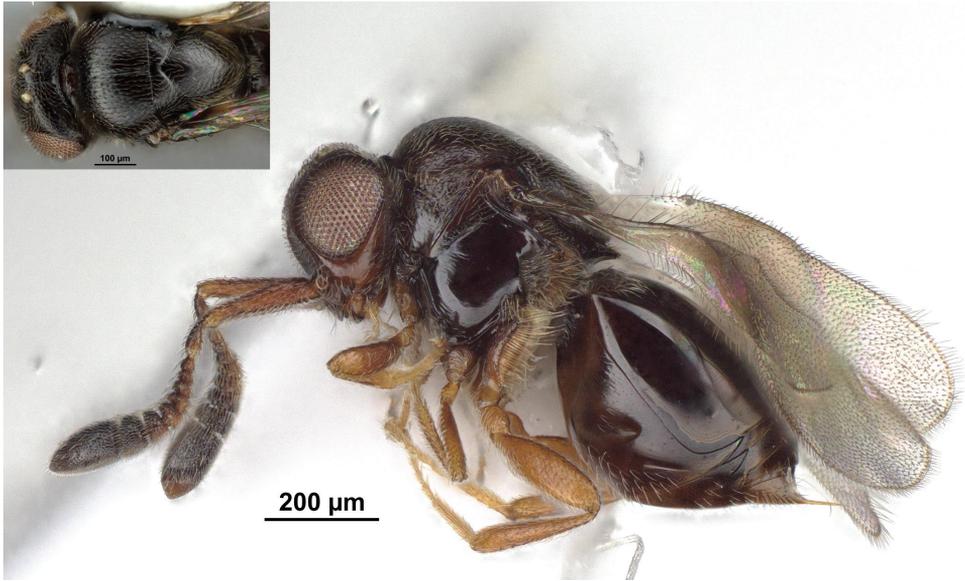


Figure 16. Female *Aphanogmus kintrishi* sp. nov. (paratype: ZFMK-HYM-00042506), head and mesosoma in dorsal view, habitus in lateral view.

metanoto-propodeo-metapecto-mesopectal complex straight and distinct. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent, with small setal patch at posterior margin of the mesometapleuron next to base of metacoxa. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Two basal longitudinal carinae on syntergum.

Male genitalia (Fig. 15B–D): Gvc length one third of mesonotum length. Gvc width $0.67 \times$ gvc length; harpe/gvc index 0.45. Harpe finger-shaped, oriented distoventrally, and gradually narrowing towards apex; lateral margin of harpe convex in basal third, straight in apical two-thirds, and oriented distomedially; median margin of harpe concave in basal half, straight in apical half, and oriented distally. Harpe with basomedian spine; tip of basomedian spine distinctly more proximal than tip of gonossiculus and oriented distally; harpe with distinct triangular median lamella-like extension at mid-length; tip of triangular median lamella-like extension rounded and oriented medially. Proximodorsal notch of harpe U-shaped and $0.30 \times$ as long as harpe length. Harpe width (above basomedian spine) $0.22 \times$ gvc width, and $0.29 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least five apical setae oriented distally, including one distinctly broadened seta with blunt end (visible only in CLSM image Suppl. material 12); harpe with one ventral seta, oriented distolaterally. Gonossiculus length $0.40 \times$ harpe length; gonossiculus J-shaped with three digital teeth, tips oriented dorsolaterally. Aedeagus straight.

Female. Body length: 1.00 mm.

Colour (Fig. 16): Body brown except scape and legs yellowish. F6–F8 darker than scape, pedicel, and F1–F5.

Antenna, head (Fig. 16): F8 length longer than half of scape length. Preoccipital lunula present. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea present. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 16): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight and distinct. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent, with small setal patch at posterior margin of the mesometapleuron next to base of metacoxa. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Five basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 0.0% (n = 7). Minimum interspecific barcode distance: 16.8% (*A. latiharpus*).

Consensus sequence: 5'-AGCCAGTTTAAAGAATCCTAGTTCGACTT-GAGCTAAGAAGACCCCCCAATAATATAATCAATAATGATCTAATTTA-CAATTCAATTATCACAGCCCATGCCTTTGTAATAAATTTTTTTTTAGT-CATACCCATCATACTGGGAGGATTTGGAACTGGCTCCTGCCCTAATA-ATTGGATCCCCGGATCTAGCCTTTCCCCGAATAAATAACATAAGATTTT-GACTCCTCCCTCCCTCCCTTACCCTACTAATCAATAGGATAATTATA-AACTCAGGGACTGGCGCTGGATGAACTCTTTACCCCCCCTCACCTC-CAATCTTCATCATTCCGGCATAGCAATAGATCTAACCATTTTCTCCCTA-CACGTAGCAGGAATTAGATCCATCATAGGCTCCATCAACTTCT-TAGTTACCCTATATAAAATAAAACCCCCCGCCTTCACCCCGGAAAT-CATGCCCTTTTCTGTTGATCAGTAGTAATCACCACCCTTCTACT-TATCCTATCTCTCCCGGTCTTAGCTGGAGCTATTACCATAATCTTAACA-GATCGCAACTTAAACACTTCCTTTTTTGACCCTAGTGGAGGTGGAGA-CCCATTCTTTACCAGCATCTTTTT -3'

Variation. Unknown.

Biology. Unknown.

Distribution. Palaearctic: Georgia.

Etymology. The species is named after the Kintrishi river and the Kintrishi National Park, where the type series were collected. The species epithet is treated as a noun in apposition.

Remarks. *Aphanogmus kintrishi* can be distinguished from all other species of the *A. fumipennis* species group by a striking and unique character, i.e. the presence of a small setal patch at the posterior margin of the mesometapleuron next to the base of the metacoxa, which is present in both males and females (Figs 15A, 16).

The male genitalia of *A. kintrishi* may be confused with those of the Afrotropical species *A. pilosicoxa* Salden & Peters, 2023, as both species exhibit a similar overall morphology, including comparable setal arrangements on the harpes, similar gonosculi, and a median extension on the harpe (Fig. 15D). However, closer examination reveals several diagnostic differences (Fig. 15D): A basomedian spine of the harpe is

present in *A. kintrishi* but absent in *A. pilosicoxa*, the harpe width to length ratio is higher in *A. kintrishi* (0.29) than in *A. pilosicoxa* (0.20), in *A. kintrishi* the harpes have a distinct triangular median lamella-like extension at mid-length, in *A. pilosicoxa* the harpes have a median extension at the base and a slim convex median lamella-like extension in the apical two-thirds.

In the molecular analyses, one female specimen from Norway (NOCER-435) is also included in this species, but only when using mPTP. It is delimited by the other two methods ASAP and objective clustering, its distance to the type series is 6.5%. Morphological examination of this singleton female does not allow reliable assessment. Integrating all data, this specimen is not considered as part of the species *A. kintrishi*.

For further morphological comparisons, see remarks under *A. karlazani*.

***Aphanogmus latiharpus* Salden & Peters, sp. nov.**

<https://zoobank.org/AB7B111E-050B-4736-8115-9249FBE7E8CF>

Figs 17, 18

Material examined. *Holotype*: GERMANY • ♂; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.16754°N, 8.7903°E; ca. 180 m a.s.l.; 2–16 Jul. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_T00806 (=SMNS_Hym_Cer_001136). *Paratypes*: GEORGIA • 1 ♀; Im-ereti, Mukhura; 42.3194°N, 43.0613°E; ca. 780 m a.s.l.; 13–20 Jun. 2020; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042492 • 1 ♀; Tbilisi, Agricultural University of Georgia; 41.8061°N, 44.7700°E; ca. 450 m a.s.l.; 21–28 Apr. 2022; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042494 • 1 ♂; Kakheti, Vashlovani, near Alazani river; 41.1241°N, 46.6523°E; ca. 100 m a.s.l.; 21–28 Jun. 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042491 (without DNA barcode). GERMANY • 1 ♀; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.16754°N, 8.7903°E; ca. 180 m a.s.l.; 9–23 Apr. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001613 • 1 ♀; same collection data as for preceding; 4–18 Jun. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001587 • 1 ♂; Baden-Württemberg, Tübingen, Hirschau, Oberes Tal, plot number 4244; 48.5050°N, 8.9935°E; ca. 370 m a.s.l.; 26 Sep.–9 Oct. 2014; T. Kothe, M. Engelhardt, D. Bartsch leg.; Malaise trap; SMNS; SMNS_Hym_Cer_000507. NORWAY • 1 ♀; Telemark, Drangedal: Sannes gård; 59.0296°N, 9.2955°E; ca. 80 m a.s.l.; 23 Jun.–19 Jul. 2021; A. Staverløkk leg.; Malaise trap; NINA; NOCER-371 • 4 ♀♀; same collection data as for preceding; 4 Aug.–22 Sep. 2021; A. Staverløkk leg.; Malaise trap; NINA; NOCER-295, NOCER-313, NOCER-335, NOCER-288. SWEDEN • 1 ♂; Gotland, Eksta socken, Stora Karlsö; 57.2846°N, 17.9718°E; ca. 30 m a.s.l.; 15 Aug. 2023; Hym inventory 2023 leg.; sweep net; NHRS; NHRS-HEVA000023408 (without DNA barcode) • 4 ♂♂; Gotland, Eksta socken, Stora Karlsö; 57.2848°N, 17.9701°E; ca. 30 m a.s.l.; 15 Aug.–3 Sep. 2023; Hym inventory 2023 leg.; Malaise trap; NHRS; NHRS-HE-

VA000023409, NHRS-HEVA000023410, NHRS-HEVA000023411, NHRS-HEVA000023412 (without DNA barcodes) • 1 ♂; Gotland, Eksta socken, Stora Karlsö; 57.2841°N, 17.9700°E; ca. 30 m a.s.l.; 15 Aug.–3 Sep. 2023; Hym inventory 2023 leg.; Malaise trap; NHRS; NHRS-HEVA000023413 (without DNA barcode).

Diagnostic description. Male. *Body length*: 0.60 mm.

Colour (Fig. 17A): Body light brown except antenna and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 17A): F1 with sensillae arranged in two whorled rows, F1 length half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 17A): Scutoscuteellar sulcus and transscutal articulation not adjacent, interaxillar sulcus present. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight and distinct. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein distinctly curved, tip of vein slightly oriented towards anterior wing margin. No basal longitudinal carinae on syntergum.

Male genitalia (Fig. 17B–D): Gvc length one third of mesonotum length. Gvc width $0.78 \times$ gvc length; harpe/gvc index 0.62. Harpe finger-shaped, occasionally with distinct diagonal striations along the basal two-thirds of the harpe, oriented from basolateral to apicomedial, harpe oriented distoventrally; lateral margin of harpe convex in basal two-thirds, straight in apical third, and oriented distomedially; median margin of harpe concave apically from basomedian spine, convex in apical third, and slightly diverging distolaterally. Harpe with distinctly sclerotized basomedian spine; tip of basomedian spine distinctly more proximal than tip of gonossiculus and oriented medially. Proximodorsal notch of harpe L-shaped. Harpe width (above basomedian spine) $0.23 \times$ gvc width, and $0.34 \times$ harpe length. Harpe with three median setae oriented proximomedially and distomedially, extending to apical third; harpe with at least four apical setae oriented distally; harpe with one ventral seta, oriented distolaterally. Gonossiculus length $0.64 \times$ harpe length; gonossiculus distinct, with at least two large digital teeth, tips oriented distodorsally and dorsolaterally. Aedeagus straight.

Female. *Body length*: 0.65 mm.

Colour (Fig. 18): Body brown except scape and legs lighter.

Antenna, head (Fig. 18): F8 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends at anterior ocellus. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 18): Scutoscuteellar sulcus and transscutal articulation not adjacent, interaxillar sulcus slightly visible. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight and distinct. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present.

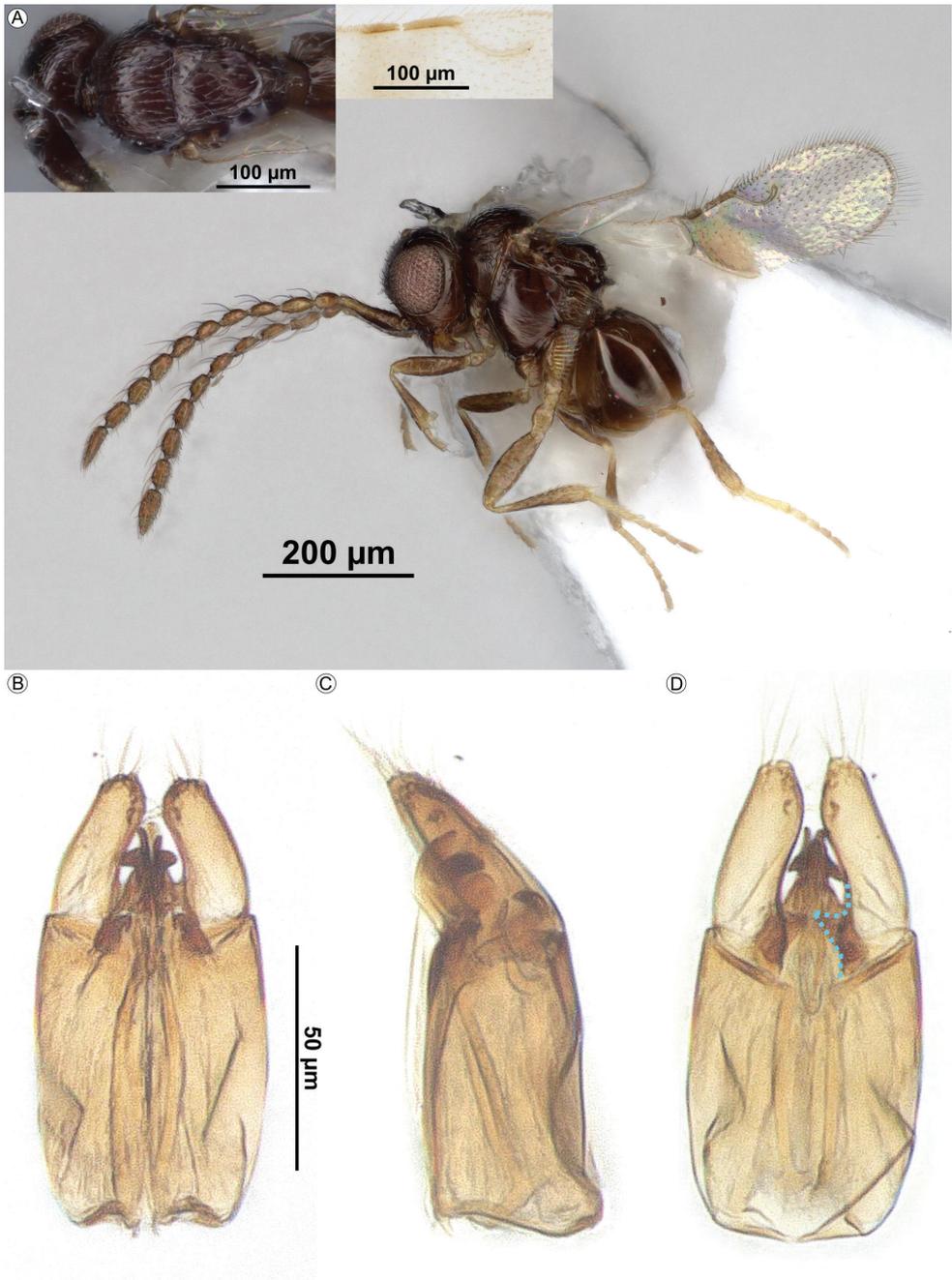


Figure 17. Male *Aphanogmus latiharpus* sp. nov. (paratype: NHRS-HEVA000023410, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (holotype: SMNS_Hym_T00806, in glycerol), habitus in lateral view. **B–D.** Male genitalia (holotype: SMNS_Hym_T00806): **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine and proximo-dorsal notch of harpe.

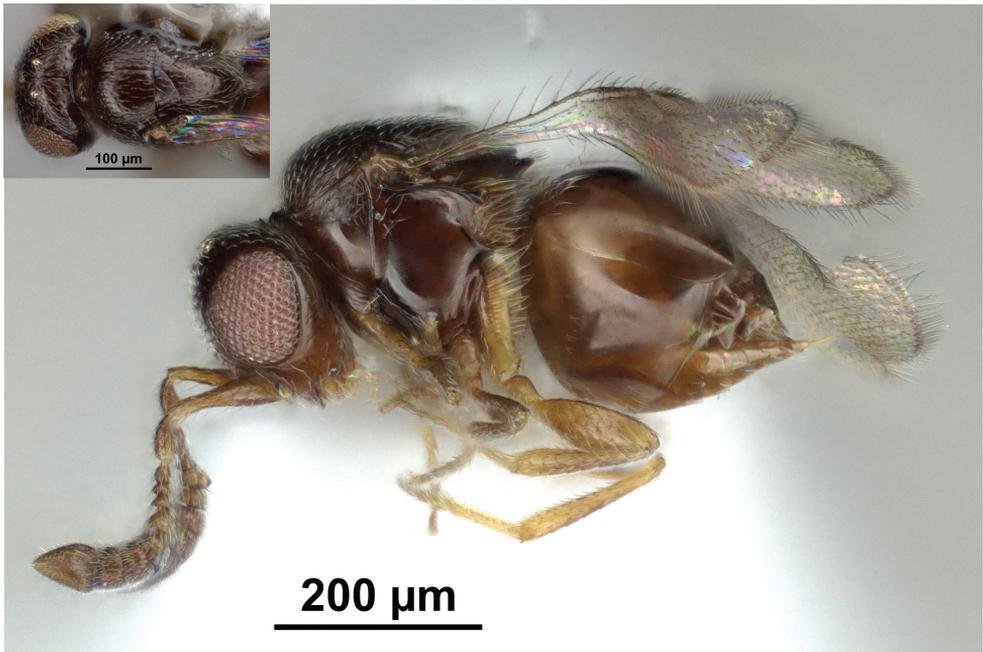


Figure 18. Female *Aphanogmus latiharpus* sp. nov. (paratype: ZFMK-HYM-00042492), head and mesosoma in dorsal view, habitus in lateral view.

Epicnemial pit absent. Stigmal vein distinctly curved, tip of vein slightly oriented towards anterior wing margin. Four basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 1.8% (n = 11). Minimum interspecific barcode distance: 16.8% (*A. kintrishi*).

Consensus sequence: 5'- AGCYAGTCTAAGACTCCTAATTTCGACTTGAATTAAGAAGACCCCCTAATAATCTAATTAATAATGACTTAATCTATAATTCAATTATCACTGCTCATGCTTTCGTAATAATTTTCTTTTTAGTATATACCCATTATACTGGGAGGATTTGGTAATTGGCTCCTCCCCCTAATGATTGGTTCCCCGATCTAGCCTTCCCTCGAATAAACAACATAAGATTCTGACTTTTACCCCCCTCCCTTACCTTACTAATCAATAGAATAATCACAACTCAGGAACGGGAGCAGGATGAACCCTTACCCTCCCCTTACATCCAACCTTAAACCATTCAGGAATAGCAATAGATCTAAC-TATTTTTTCCCTCCACATCGCAGGAATTAGATCAATTATAGGATCCATCAATTTTTTAGTTACTTTATACAAAATGAAACCCCTAGCCTTCACTCAAGAAATGATAACATTATTCTGTTGATCCGTTGTAATCACTAC-CATTCTTTTAATCCTATCCCTCCCCGTCCTAGCGGGGGCAATCACCATAATCTTAACAGATCGAACTTAAATACCTCCTTCTTTGACCCAAGAGGGGGGGGGGACCCCATTTTATATCAACATCTTTTT -3'

Variation. In ZFMK-HYM-00042491, the interaxillar sulcus is indistinct and three basal longitudinal carinae on the syntergum are present.

Biology. Unknown.

Distribution. Palaearctic: Georgia, Germany, Norway, and Sweden.

Etymology. The species name is a composition of the Latin word ‘*latus*’, which means ‘broad’, and the anatomical term ‘harpe’, with reference to the broad harpe.

Remarks. *Aphanogmus latiharpus* is a small-bodied species with only two whorled rows of sensillae on F1 of the male, and a distinctly curved stigmal vein on the fore wing (Fig. 17A). It can be distinguished from all other species of the *A. fumipennis* species group by characters of the male genitalia, i.e. the unique combination of broad, finger-shaped harpes (harpe width $0.34 \times$ harpe length), occasionally with distinct diagonal striations along the basal two-thirds of the harpe, oriented from proximolateral to distomedial, and a medially oriented basomedian spine of the harpe, accompanied by an L-shaped proximodorsal notch (Fig. 17D).

The imaged specimen NHRS-HEVA000023410 has a slightly deformed dorsal mesosoma.

***Aphanogmus tkheliharpus* Salden, Mikó & Peters, sp. nov.**

<https://zoobank.org/F449C353-BE50-4B01-88A3-C10EF02A6E43>

Figs 19, 20; Suppl. material 13

Material examined. **Holotype:** GEORGIA • ♂; Kakheti, Gombori; 41.8678°N, 45.2644°E; ca. 1490 m a.s.l.; 21–28 Jul. 2021; G. Japoshvili leg.; Malaise trap; ECAUG; ZFMK-HYM-00042459. **Paratypes:** GEORGIA • 1 ♀; same data as for holotype; ZFMK; ZFMK-HYM-00042460 • 1 ♀; Kakheti, Batsara Nature Reserve; 42.2222°N, 45.3029°E; ca. 800 m a.s.l.; 28 May 2022; T. Salden leg.; sweep net; ZFMK; ZFMK-HYM-00042465 • 3 ♀♀; Kakheti, Telavi; 41.9132°N, 45.4556°E; ca. 820 m a.s.l.; 29 May 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK; ZFMK-HYM-00042467, ZFMK-HYM-00042469, ZFMK-HYM-00042471 • 5 ♀♀; same collection data as for preceding; 30 May 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK; ZFMK-HYM-00042472, ZFMK-HYM-00042473, ZFMK-HYM-00042474, ZFMK-HYM-00042475, ZFMK-HYM-00042476.

Diagnostic description. Male. **Body length:** 0.70 mm.

Colour (Fig. 19A): Body light brown except metasoma and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 19A): F1 with sensillae arranged in three whorled rows, F1 length half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 19A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex distinctly short. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior margin of wing. No basal longitudinal carinae on syntergum.

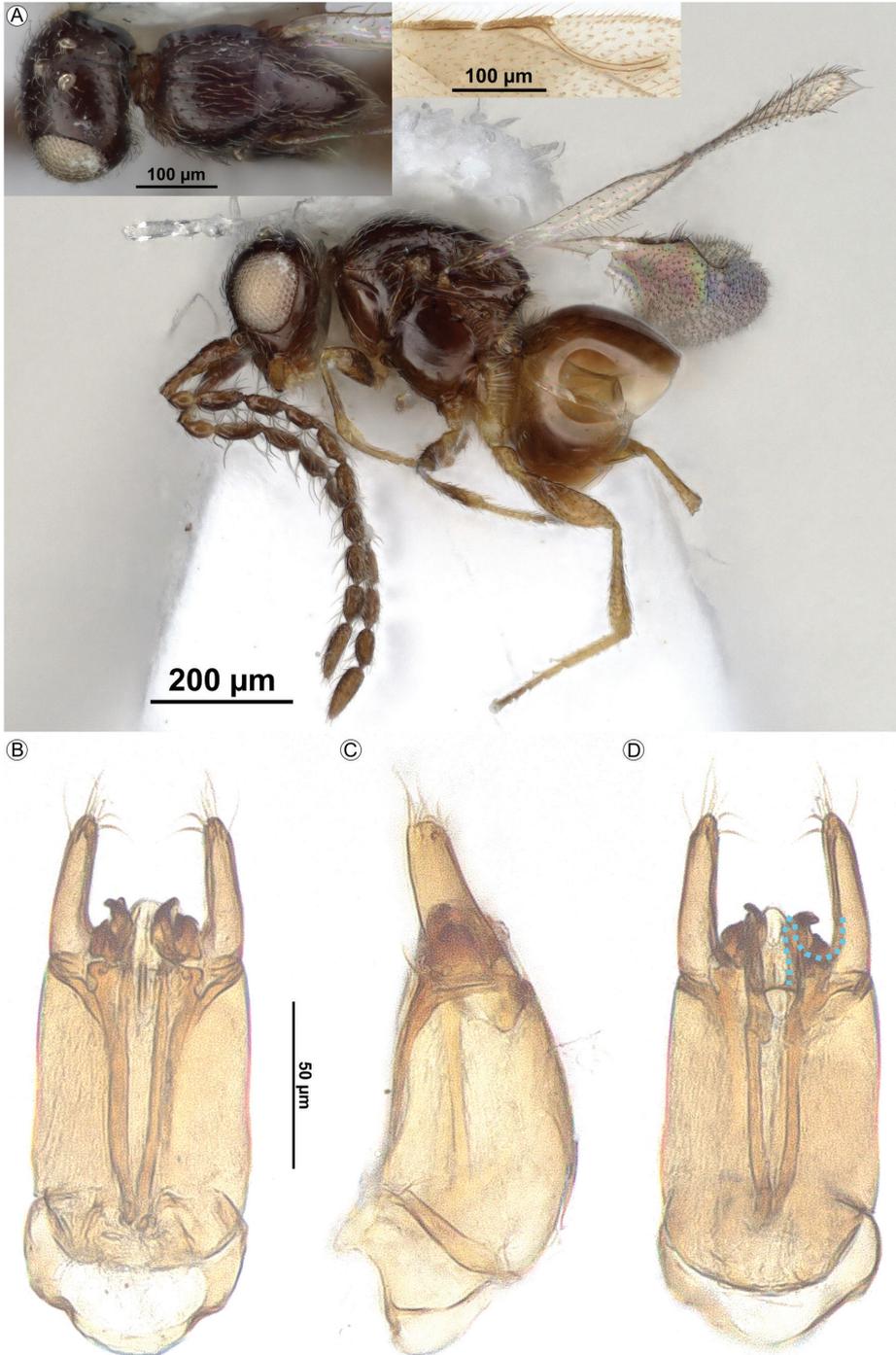


Figure 19. Male *Aphanogmus tkheliharpus* sp. nov. (holotype: ZFMK-HYM-00042459). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (in glycerol), habitus in lateral view. **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine and proximodorsal notch of harpe.

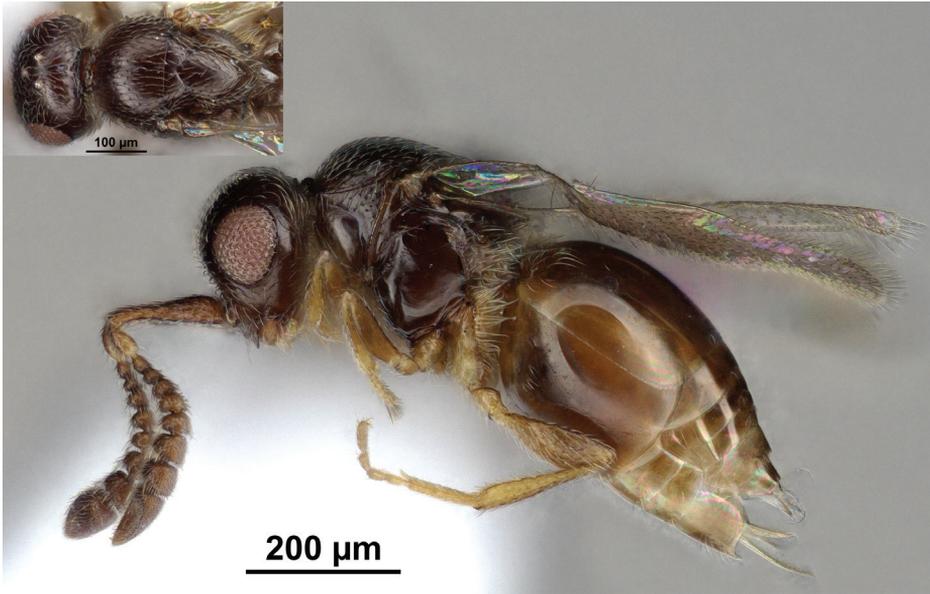


Figure 20. Female *Aphanogmus tkheliharpus* sp. nov. (paratype: ZFMK-HYM-00042469), head and mesosoma in dorsal view, habitus in lateral view.

Male genitalia (Fig. 19B–D): Gvc length slightly shorter than half of mesonotum length. Gvc width $0.72 \times$ gvc length; harpe/gvc index 0.51. Harpe finger-shaped, distoventrally oriented; lateral margin of harpe slightly convex in basal half, straight in apical half, and slightly oriented distomedially; median margin of harpe straight and oriented distally. Harpe with basomedian spine; tip of basomedian spine about as proximal as tip of gonossiculus and oriented distally. Proximodorsal notch of harpe U-shaped and $0.25 \times$ as long as harpe length. Harpe width (above basomedian spine) $0.15 \times$ gvc width, and $0.20 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least three apical setae oriented distally, including one broadened seta (broadening only visible in CLSM image Suppl. material 13); harpe with one lateral seta close to apex, oriented distally. Gonossiculus length $0.35 \times$ harpe length; gonossiculus C-shaped with at least one digital tooth, tip oriented dorsally. Aedeagus broadened and rounded.

Female. Body length: 0.70 mm.

Colour (Fig. 20): Body light brown except scape, pedicel, metasoma, and legs lighter.

Antenna, head (Fig. 20): F8 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 20): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-

mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Two basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 1.8% (n = 11). Minimum interspecific barcode distance: 13.7% (*A. zefranki*).

Consensus sequence: 5'- AGCAGGGCTAAGACTTATCATTCGTCCTT-
GAATTAAGATCCCCCCTAATAATAATAAATAATGACTTAATTTA-
CAACTCTGTAATTACCAATCACGCTTTCCTAATAATTTTTTTTTT-
TAGTTATACCCATTATACTGGGAGGTTTTTGAAATTGACT-
CATCCCTATTATGATTGGGGCCCCAGATTTAGCCTTCCCCC-
GAATAACAATATAAGATTATGATTCCTCCCCCCTTCTTTGACTCT-
GCTCCTCACAAGAATAAATACTAACACAGGCGTGGGGGCAGGGT-
GAACCCTCTACCCCCCCTGACTCTAATACCCTTTCACGATG-
GAATATCTATAGATCTAACAATCTACTCCCTTCACATCGCTGGAAT-
CAGTTCAATCATAGGTTCAATCAATTTTATAGTAACTTACAAAAT-
GAAGCCCTCCTCCCAAACCCTAGTCTCCCTGCCTCTATTCTGTTGATC-
TATTATAATCACCTCCCTTCTTCTTCTTCTTCCCTCCCCGTTTTAGCTG-
GAGCTGTAACAATAATCTTAACTGACCGAACTTAAATACTTCTTTTTTT-
GACCCAGAGGGGGGGGGGACCCCTACTTTACCAGCATTATTT -3'

Variation. Unknown.

Biology. Unknown.

Distribution. Palaearctic: Georgia.

Etymology. The species name is a composition of the Georgian word ‘თხელი’ (pronounced like ‘*tkheli*’, with a soft ‘t’ and the ‘kh’ like the ‘ch’ in German *Bach*, [x] after the International Phonetic Alphabet), which means ‘thin’, and the anatomical term ‘harpe’, with reference to the thin harpe.

Remarks. Superficially, *A. tkheliharpus* can be confused with *A. crispy*, as both species have comparatively thin harpes (Figs 5D, 19D). However, closer examination reveals diagnostic differences: the basomedian spine of the harpe is oriented distally in *A. tkheliharpus* (Fig. 19D) and the median spine is oriented distomedially in *A. crispy* (Fig. 5D). Additionally, the proximodorsal notch of the harpe is clearly U-shaped in *A. tkheliharpus* (Fig. 19D), in contrast to the V-shaped mediodorsal notch in *A. crispy* (Fig. 5D). Further distinguishing characters include the arrangement of the median setae of the harpe, which are restricted to the apical quarter in *A. tkheliharpus* and extending to the apical third in *A. crispy*. Moreover, the harpe has a uniform thin profile, while in *A. crispy* it is narrowed along the apical two-thirds.

***Aphanogmus trigoharpus* Salden, Mikó & Peters, sp. nov.**

<https://zoobank.org/F7543E6B-2F4D-46EB-9967-32312408FE1A>

Figs 21, 22; Suppl. material 14

Material examined. *Holotype*: GEORGIA • ♂; Adjara, Kintrishi; 41.7294°N, 42.0775°E; ca. 1020 m a.s.l.; 1–15 Jun. 2018; L. Mumladze leg.; Malaise trap; ZFMK;

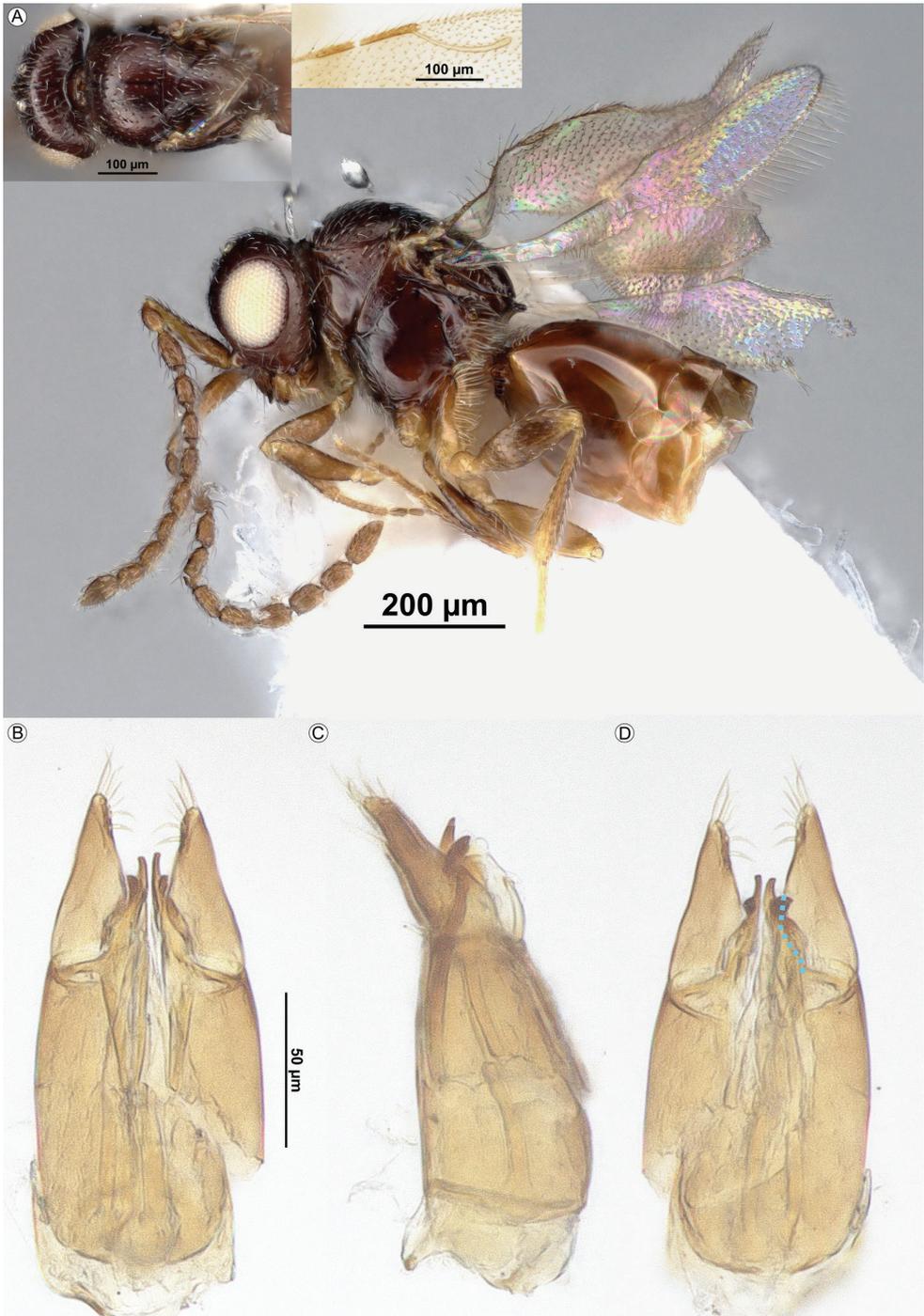


Figure 21. Male *Aphanogmus trigoharpus* sp. nov. (holotype: ZFMK-HYM-00042511). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (in glycerol), habitus in lateral view. **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with triangular median extension of harpe.

ZFMK-HYM-00042511. **Paratypes:** GEORGIA • 1 ♀; Adjara, Kintrishi; 41.7372°N, 41.9792°E; ca. 400 m a.s.l.; 13–27 Jul. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042514 • 1 ♀; same collection data as for preceding; 27 Jul.–10 Aug. 2018; L. Mumladze leg.; Malaise trap; ZFMK; ZFMK-HYM-00042516 • 1 ♀; same collection data as for preceding; 10–24 Aug. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042513 • 1 ♀; same collection data as for preceding; 7–21 Sep. 2018; L. Mumladze leg.; Malaise trap; ZFMK; ZFMK-HYM-00042517 • 1 ♀; same collection data as for preceding; 21 Sep.–5 Oct. 2018; L. Mumladze leg.; Malaise trap; ECAUG; ZFMK-HYM-00042518. GERMANY • 1 ♀; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.16754°N, 8.7903°E; ca. 180 m a.s.l.; 16–30 Jul. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_000918.

Diagnostic description. Male. Body length: 0.85 mm.

Colour (Fig. 21A): Body light brown except metasoma, antenna, and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 21A): F1 with sensillae arranged in three whorled rows, F1 length shorter than half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 21A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Median mesoscutal sulcus indicated. Anteromedian projection of the metanoto-propodeo-metaplecto-mesopectal complex straight and distinct, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metaplecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Four basal longitudinal carinae on syntergum.

Male genitalia (Fig. 21B–D): Gvc length one third of mesonotum length. Gvc width $0.63 \times$ gvc length; harpe/gvc index 0.52. Harpe triangular in apical two-thirds, distoventrally oriented, and gradually narrowing towards apex; lateral margin of harpe straight and oriented distomedially; median margin of harpe concave in basal third and straight in apical two-thirds, oriented distolaterally. Harpe without spines along median margin; harpe with distinct triangular median extension at mid-length; tip of distinct triangular median extension rounded and oriented medially. Proximodorsal notch of harpe absent. Harpe width (below distinct triangular median extension) $0.24 \times$ gvc width, and $0.33 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least six apical setae oriented distally, including one broadened seta (broadening visible only in CLSM image Suppl. material 14); harpe with one ventral seta, oriented distolaterally. Gonossiculus length $0.66 \times$ harpe length; gonossiculus with at least two digital teeth, tips oriented distodorsally. Aedeagus straight.

Female. Body length: 0.90 mm.

Colour (Fig. 22): Body brown except metasoma, scape, and legs yellowish.

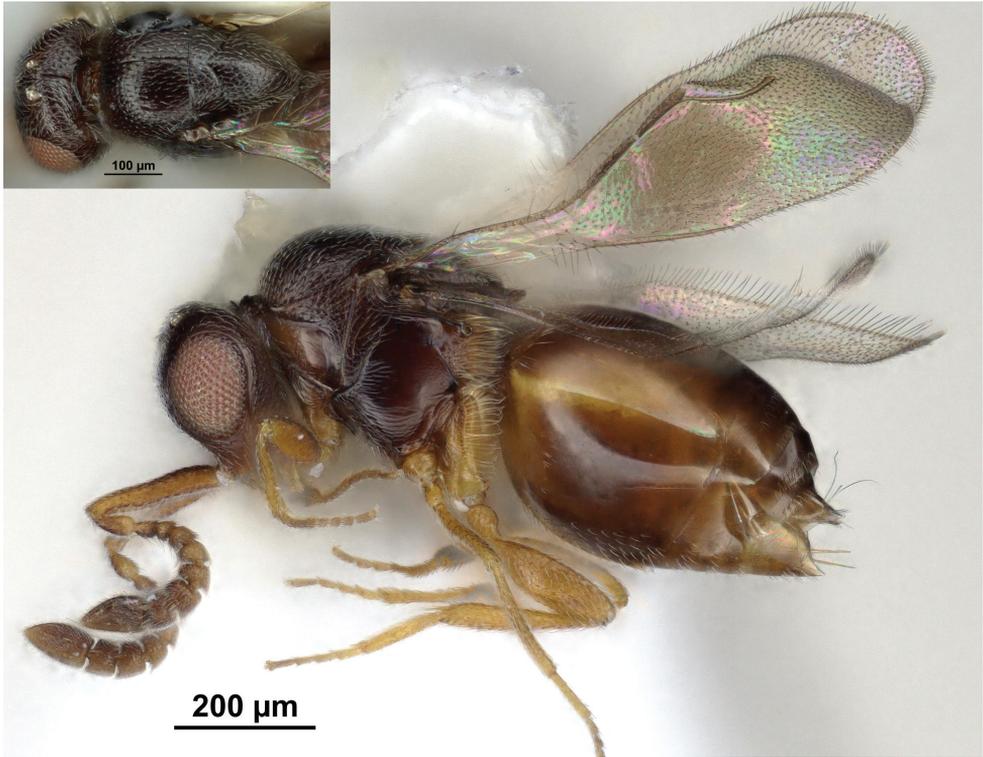


Figure 22. Female *Aphanogmus trigoharpus* sp. nov. (paratype: ZFMK-HYM-00042517), head and mesosoma in dorsal view, habitus in lateral view.

Antenna, head (Fig. 22): F8 length half of scape length. Preoccipital lunula present. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 22): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus present. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight and distinct, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Five basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 0.7% (n = 7). Minimum interspecific barcode distance: 8.1% (putative species consisting of ZFMK-HYM-00042521, ZFMK-HYM-00042522, ZFMK-HYM-00042519, ZFMK-HYM-00042520, NOCER-374, and NOCER-388).

Consensus sequence: 5'- TGCAAGTTTAAGCCTATTAATTTCGCCTAGAAT-TAAGTAGCCCCCCTAATAACCTAATTAACAATGATTTAATTTATA-ACTCTATATTACCGCCCATGCCTTTGTAATAATTTTCTTCCTTGT-

CATACCTATTATATTAGGAGGATTTGGCAACTGACTACTCCCCCTA-
ATAATTGGCTCCCCAGACTTAGCCTTCCCCCGAATAAATAATATAA-
GATTCTGATTACTCCCCCGCATTAATCCTTTTGATAAACAGAAT-
GATAATAAACTCTGGCACTGGAGCAGGATGAACCCTCTATCCCCCCT-
TACATCTAATCTCCATCACTCCGGCATCGCAATAGACTTAAC-
TATCTTTTCCCTTCATGTAGCAGGAATTAGCTCAATCATAGGGTCAAT-
TAATTTCCCTAGTCACCCTTTATAAAAATAAAACCCTTAAACTTCCAA-
CAAGAAATAATACCTCTATTTTGTTGATCCGTAGTAATCACAACAATCT-
TACTCATTCTCTCCCTCCCAGTTCTAGCAGGAGCTATCACTATGATTT-
TAACAGACCGAAATCTTAATACCTCCTTCTTCGACCCCAGAGGTGGAG-
GAGACCCTGTTTATACCAACACTTATTT -3'

Variation. Unknown.

Biology. Unknown.

Distribution. Palaearctic: Georgia, Germany, and Norway.

Etymology. The species name is a composition of the Greek word 'τρίγωνος' (trígōnos), which means 'triangular', and the anatomical term 'harpe', with reference to the triangular harpe.

Remarks. *Aphanogmus trigoharpus* is clearly differentiated from the other species of the *A. fumipennis* species group by a triangular harpe in the apical two-thirds, combined with the absence of spines and of a proximodorsal notch of the harpe (Fig. 21D).

In the molecular analyses, one female specimen from Georgia (ZFMK-HYM-00042523) is also included in this species, but only when using ASAP. It is delimited by the other two methods mPTP and objective clustering, its minimum distance to the type series is 5.3%. Morphological examination of this singleton female does not allow reliable assessment. Integrating all data, this specimen is not considered as part of the species *A. trigoharpus*.

***Aphanogmus vashlovani* Salden, Mikó & Peters, sp. nov.**

<https://zoobank.org/D3632C23-64CF-4006-AF5A-AC729ED8336A>

Figs 23, 24; Suppl. material 15

Material examined. Holotype: GEORGIA • ♂; Kakheti, Vashlovani, near Alazani river; 41.1241°N, 46.6523°E; ca. 100 m a.s.l.; 21–28 Jun. 2021; G. Japoshvili leg.; Malaise trap; ECAUG; ZFMK-HYM-00042529. **Paratype:** GEORGIA • 1 ♀; same data as for holotype; ZFMK; ZFMK-HYM-00042530.

Other material examined. GEORGIA • 1 ♀; Mtskheta-Mtianeti, Tbilisi National Park; 41.8797°N, 45.0216°E; ca 1280 m a.s.l.; 27 May 2022; T. Salden leg.; sweep net; ZFMK; ZFMK-HYM-00042534 • 1 ♀; Kakheti, Batsara Nature Reserve; 42.2229°N, 45.3029°E; ca 810 m a.s.l.; 28 May 2022; T. Salden, R.S. Peters leg.; Winkler leaf litter extraction; ZFMK; ZFMK-HYM-00042535 • 1 ♀; Kakheti, Batsara Nature Reserve; 42.2244°N, 45.3003°E; ca 820 m a.s.l.; 28 May 2022; T. Salden, R.S. Peters leg.; Winkler leaf litter extraction; ZFMK; ZFMK-HYM-00042536 • 2 ♀♀; Kakheti,

Telavi; 41.9134°N, 45.4588°E; ca. 820 m a.s.l.; 28 May 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK; ZFMK-HYM-00042537, ZFMK-HYM-00042538 • 1 ♀; same collection data as for preceding; 29 May 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK-HYM-00042533 • 21 ♀♀; Kakheti, Telavi; 41.9132°N, 45.4556°E; same collection data as for preceding; ZFMK; ZFMK-HYM-00042539, ZFMK-HYM-00042540, ZFMK-HYM-00042541, ZFMK-HYM-00042542, ZFMK-HYM-00042543, ZFMK-HYM-00042544, ZFMK-HYM-00042546, ZFMK-HYM-00042547, ZFMK-HYM-00042548, ZFMK-HYM-00042549, ZFMK-HYM-00042550, ZFMK-HYM-00042553, ZFMK-HYM-00042554, ZFMK-HYM-00042555, ZFMK-HYM-00042556, ZFMK-HYM-00042559, ZFMK-HYM-00042560, ZFMK-HYM-00042566, ZFMK-HYM-00042567, ZFMK-HYM-00042569, ZFMK-HYM-00042570 • 15 ♀♀; same collection data as for preceding; 30 May 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK; ZFMK-HYM-00042575, ZFMK-HYM-00042576, ZFMK-HYM-00042577, ZFMK-HYM-00042579, ZFMK-HYM-00042580, ZFMK-HYM-00042581, ZFMK-HYM-00042582, ZFMK-HYM-00042584, ZFMK-HYM-00042585, ZFMK-HYM-00042586, ZFMK-HYM-00042587, ZFMK-HYM-00042588, ZFMK-HYM-00042589, ZFMK-HYM-00042591, ZFMK-HYM-00042592 • 2 ♀♀; Kakheti, Lagodekhi National Park; 41.8091°N, 46.3224°E; ca. 500 m a.s.l.; 30 May 2022; T. Salden, R.S. Peters leg.; sweep net; ZFMK; ZFMK-HYM-00042572, ZFMK-HYM-00042574 • 2 ♀♀; Kakheti, Sighnaghi; 41.6233°N, 45.9184°E; ca. 770 m a.s.l.; 1 Jun. 2022; T. Salden, R.S. Peters leg.; yellow pan trap; ZFMK; ZFMK-HYM-00042593, ZFMK-HYM-00042594 • 1 ♀; Kakheti, Vashlovani, Takhistskali; 41.1254°N, 46.6496°E; ca. 110 m a.s.l.; 21–28 Jun. 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042595 • 1 ♀; Tbilisi, Agricultural University of Georgia; 41.8061°N, 44.7700°E; ca. 450 m a.s.l.; 21–28 Apr. 2022; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042573 • 1 ♀; Kakheti, Babaneuri; 42.0757°N, 45.3677°E; ca. 440 m a.s.l.; 30 Jun.–9 Jul. 2022; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042597 • 2 ♀♀; Racha-Lechkhumi & Kvemo Svaneti, Onchevi, Shola; 42.5585°N, 43.5193°E; ca. 1160 m a.s.l.; 20–27 May 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042527, ZFMK-HYM-0004252 • 1 ♀; Imereti, Mukhura; 42.3194°N, 43.0613°E; ca. 780 m a.s.l.; 20–27 Jun. 2020; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042526 • 1 ♂; Racha-Lechkhumi & Kvemo Svaneti, Tsageri, Doghurashi; 42.6698°N, 42.7854°E; ca. 1000 m a.s.l.; 18–24 Aug. 2020; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042525. GERMANY • 1 ♀; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.16754°N, 8.7903°E; ca. 180 m a.s.l.; 16–30 Jul. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_000961 • 1 ♂; same collection data as for preceding; 27 Aug.–10 Sep. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001188 • 1 ♀; same collection data as for preceding; 9–23 Apr. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001614 • 1 ♀; same collection data as for preceding; 4–18 Jun. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001228.

Other material examined. HUNGARY • 2 ♂♂; Veszprém, Nyirád; 2 Jun. 2010; E. Talamas leg.; sweep net; UNHC; PSUC_FEM 10035329, PSUC_FEM 10035310 (without DNA barcodes).

Diagnostic description. Male. *Body length*: 0.65 mm.

Colour (Fig. 23A): Body brown except metasoma, antenna, and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 23A): F1 with sensillae arranged in at least three whorled rows, F1 length half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 23A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein distinctly curved, tip of vein slightly oriented towards anterior wing margin. Three basal longitudinal carinae on syntergum.

Male genitalia (Fig. 23B–D): Gvc length one third of mesonotum length. Gvc width $0.66 \times$ gvc length; harpe/gvc index 0.60. Harpe finger-shaped, distoventrally oriented; lateral margin of harpe slightly convex in basal half, straight in apical half, and slightly oriented distomedially; median margin of harpe convex in basal third, slightly concave in apical two-thirds, and slightly converging distomedially. Harpe without spines along median margin. Proximodorsal notch of harpe absent. Harpe width (above convex median extension) $0.26 \times$ gvc width, and $0.26 \times$ harpe length. Harpe with four median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least five apical setae oriented distally, including one broadened seta (broadening only visible in CLSM image Suppl. material 15); harpe with one distinct ventral seta, oriented distolaterally. Gonossiculus length $0.38 \times$ harpe length; gonossiculus bulbous with at least two digital teeth, tips oriented dorsally. Aedeagus straight.

Female. *Body length*: 0.80 mm.

Colour (Fig. 24): Body brown except metasoma and legs lighter.

Antenna, head (Fig. 24): F8 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow present. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 24): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus present. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight and distinct, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein distinctly curved, tip of vein slightly oriented towards anterior wing margin. Three basal longitudinal carinae on syntergum.

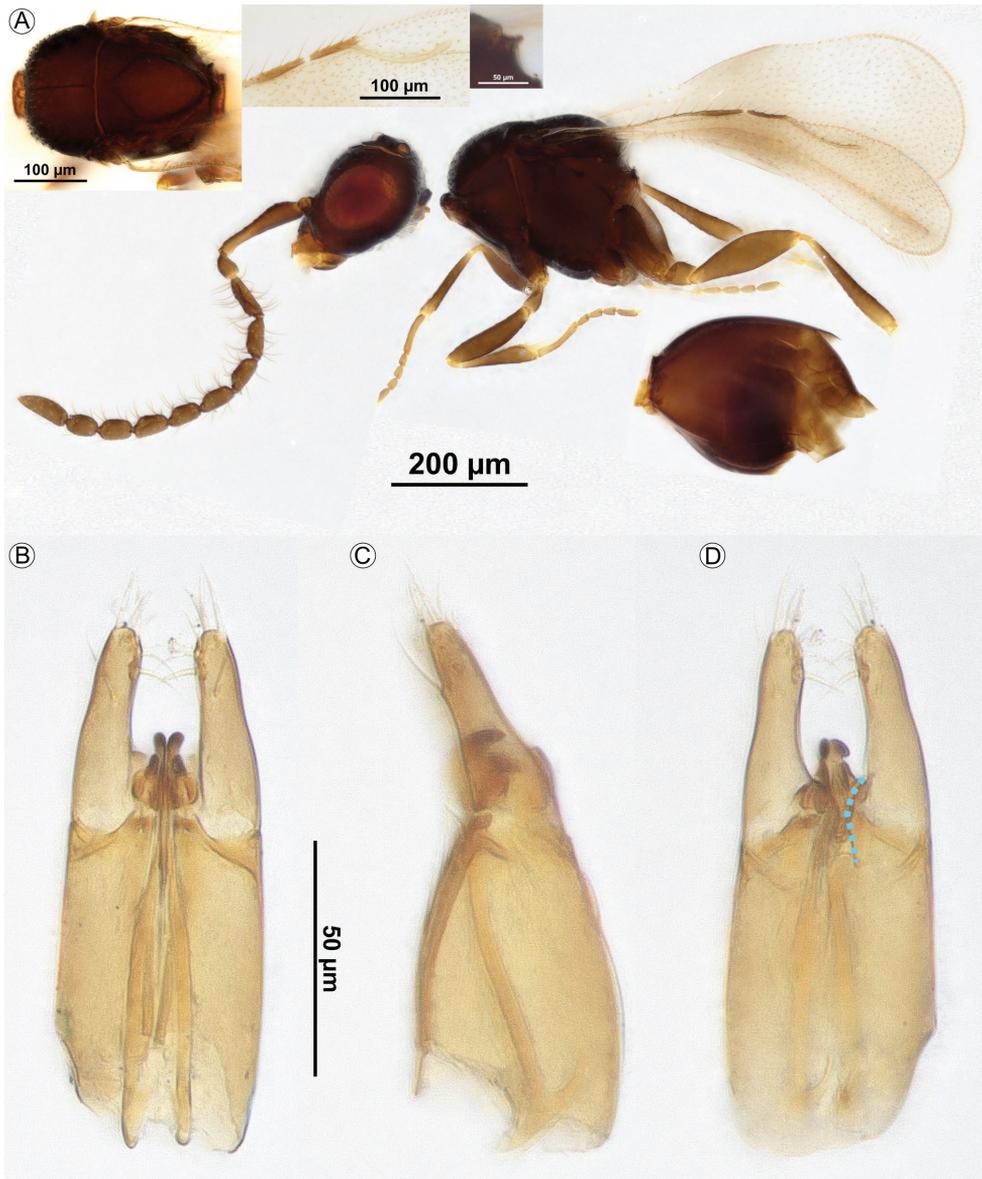


Figure 23. Male *Aphanogmus vashlovani* sp. nov. (holotype: ZFMK-HYM-00042529, in glycerol). **A.** Mesosoma in dorsal view, stigmal vein in lateral view, anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex in lateral view, habitus in lateral view. **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with convex median extension of harpe.

***COI* barcode.** Maximum intraspecific barcode distance: 5.1% (n = 59). Minimum interspecific barcode distance: 17.8% (putative species consisting of ZFMK-HYM-00042521, ZFMK-HYM-00042522, ZFMK-HYM-00042519, ZFMK-HYM-00042520, NOCER-374, and NOCER-388).

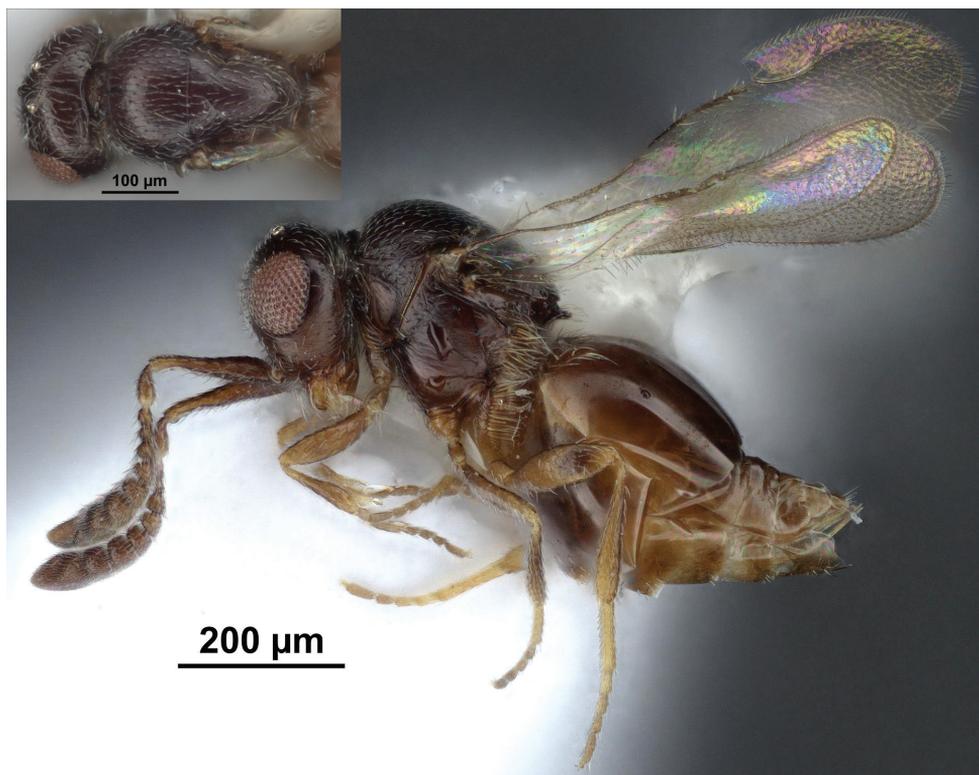


Figure 24. Female *Aphanogmus vashlovani* sp. nov. (paratype: ZFMK-HYM-00042530), head and mesosoma in dorsal view, habitus in lateral view.

Consensus sequence: 5'- AGCAAGTCTTAGATTATTAATCCGCCTT-GAGCTCAGAAGACCCCCCAATAACCTAATTAACAATGACTTAACCTATA-ACTCAATCATCACAGCCCACGCTTTTGTAATAATTTTCTTTCTTG-TAATACCCATCATACTGGGGGGGTTTGGAAATTGATTACTCCCCTA-ATAATTGGATCCCCCGACCTTGCATTCCCCCGGATAAATAATATAA-GATTCTGACTCCTCCCCCCTCCCTCACCTTCTAATAAATAGGATACT-CATAAACTCGGGAACCGGGGCAGGGTGGACCCTATACCCCCCT-GACATCCAATCTCCACCACGCTGGAATAGCCATAGATTTAA-CAATTTTCTCCCTTCACGTAGCTGGTATCAGTTCAATATAGGGTCAAT-CAACTTCCTGGTCACCCTATATAAAATAAAAACCAAGAAATTTAAATTAC-GAAATAATACCTCTTTTGTGTTGATCCGTAGCAGTTACTACTATCT-TACTAATTTTATCCCTCCCCGTCTAGCAGGTGCCATCACTATAATTT-TAACAGACC GAAATCTTAATACCTCCTTTTTCGATCCCGCCGGAGGAG-GAGACCCCGTATTATACCAGCACCTATTT -3'

Variation. Unknown.

Biology. Unknown.

Distribution. Palearctic: Georgia.

Etymology. The species is named after the Vashlovani National Park, where the type series were collected. The species epithet is treated as a noun in apposition.

Remarks. The convex median extension along the basal third of the harpe and the finger-shaped apical two-thirds of the harpe in *Aphanogmus vashlovani* (Fig. 23D) has some resemblance to the male genitalia of *A. fraterculus* Salden & Peters, 2023 from the Afrotropical *A. fumipennis* species group. However, the proportions and setal arrangement of the genitalia differ clearly between the two species.

The molecular species delimitation analyses result in different species clusters depending on the method applied. The mPTP analysis grouped 59 sequences into a single cluster, with an intraspecific barcode distance of 5.1%. The spID analysis split these 59 sequences into two clusters, one containing 51 sequences and the other eight sequences, with a barcode distance of 5.1% between the clusters. The ASAP analysis separated the same 59 sequences into four clusters: one cluster with two specimens, one cluster with 49 sequences, and two clusters with four sequences each. The two specimens ZFMK-HYM-00042529 (male), ZFMK-HYM-00042530 (female) are designated as holotype and paratype, because they consistently cluster together in all three delimitation methods and the male has well-diagnosable genitalia. The remaining 57 specimens are assigned to *A. vashlovani* but not designated as paratypes. Specifically, the cluster of 49 sequences found with ASAP has a maximum distance of 2.6% to the type series. Unfortunately, it includes only female specimens which are difficult to assess morphologically. The cluster of eight specimens found with spID includes a male ZFMK-HYM-00042525. Unfortunately, the dissected genitalia are slightly deformed. They at least closely resemble those of the holotype, and we assign this specimen to *A. vashlovani*, but we refrain from a taxonomic decision because of the deformation and do not designate the specimens as paratypes. Analyses of additional material will be necessary to further define the limits of *A. vashlovani* or to delimit additional species close to *A. vashlovani*.

***Aphanogmus ventricoharpus* Salden, Staverløkk, Mikó & Peters, sp. nov.**

<https://zoobank.org/8576A1B7-C470-42A2-AF2F-8AC6DFB4AF73>

Figs 25, 26; Suppl. materials 16, 17

Material examined. *Holotype:* NORWAY • ♂; Telemark, Drangedal: Sannes gård; 59.0296°N, 9.2955°E; ca. 80 m a.s.l.; 4 Aug.–22 Sep. 2021; A. Staverløkk leg.; Malaise trap; NINA; NOCER-291. *Paratypes:* NORWAY • 5 ♀♀; same data as for holotype; NINA; NOCER-333, NOCER-330, NOCER-331, NOCER-329, NOCER-328 • 1 ♀; same data as for holotype; 23 Jun.–19 Jul. 2021; A. Staverløkk leg.; Malaise trap; NINA; NOCER-392 • 1 ♂; same collection data as for preceding; NINA; NOCER-373 (without DNA barcode). GEORGIA • 1 ♀; Kakheti, Vashlovani; 41.1847°N, 46.5628°E; ca. 340 m a.s.l.; 20–28 Jun. 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042461 • 1 ♀; Racha-Lechkhumi & Kvemo Svaneti, Doghurashi; 42.6698°N, 42.7854°E; ca. 1000 m a.s.l.; 18–24 Aug. 2020;

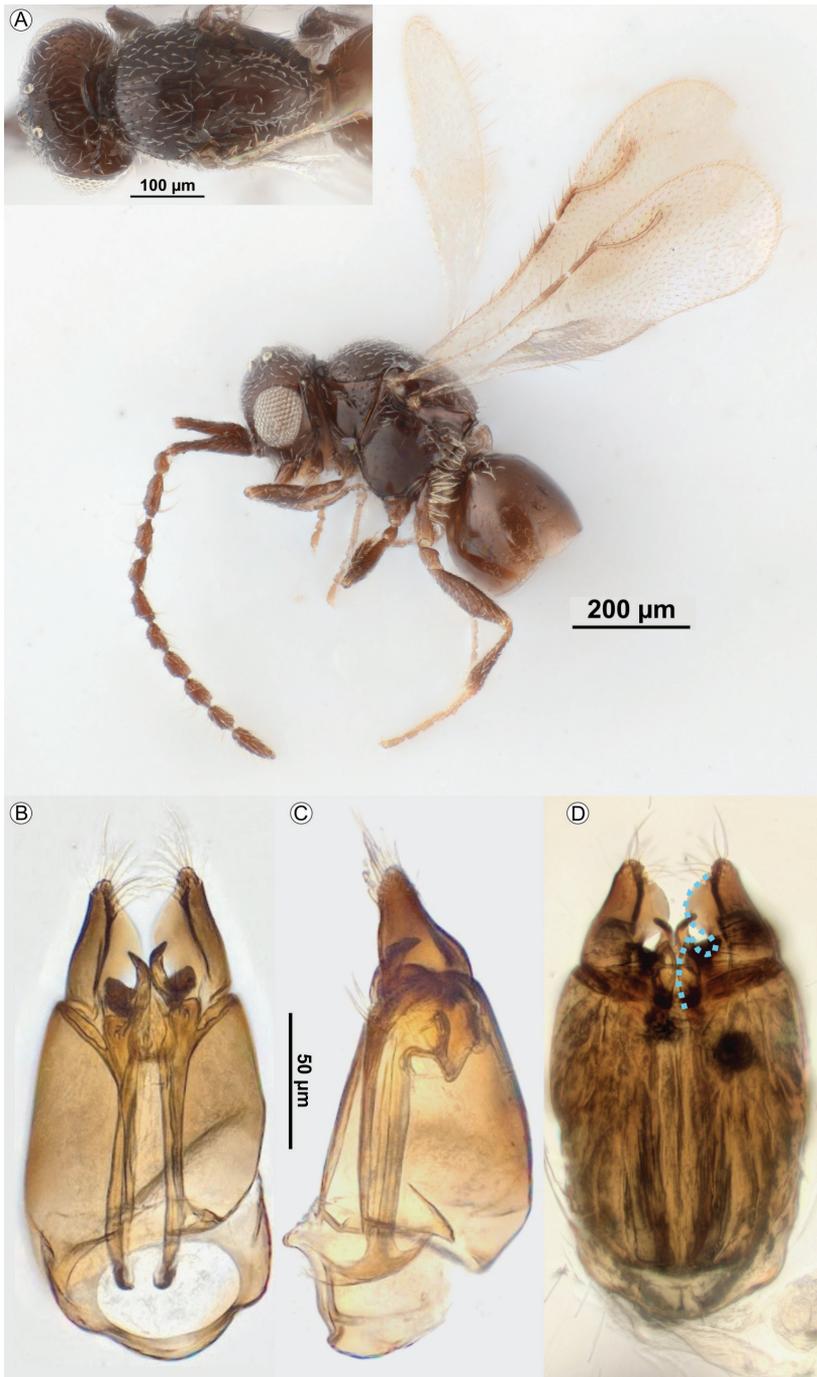


Figure 25. Male *Aphanogmus ventricoharpus* sp. nov. (holotype: NOCER-291, unless noted otherwise). **A.** Head and mesosoma in dorsal view, habitus in lateral view. **B–D.** Male genitalia (paratype: NOCER-373, unless noted otherwise): **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view (non-type: PSUC_FEM 10022748), blue dashed line with basomedian spine, proximodorsal notch of harpe, and convex and broad median lamella-like extension.

G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042463. GERMANY • 1 ♀; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.16754°N, 8.7903°E; ca. 180 m a.s.l.; 16–30 Jul. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_000905 • 1 ♀; same collection data as for preceding; 4–18 Jun. 2019; LUBW Insektenmonitoring leg.; Malaise trap; SMNS; SMNS_Hym_Cer_001240 • 1 ♂; Bavaria, Kronach, Küps; 50.21°N, 11.27°E; ca. 340 m a.s.l.; 04–10 Jul. 2022; NaPa Insektenmonitoring leg.; vane trap; ZFMK; ZFMK-HYM-00042670 (without DNA barcode) • 3 ♂♂; Saxony-Anhalt, Börde, Oschersleben; 52.00°N, 11.41°E; ca. 90 m a.s.l.; 18–24 Jul. 2022; NaPa Insektenmonitoring leg.; vane trap; ZFMK; ZFMK-HYM-00042671, ZFMK-HYM-00042672, ZFMK-HYM-00042674 (without DNA barcodes).

Other material examined. GERMANY • 1 ♂; Hesse, Hersfeld-Rotenburg, Rockensüß, doline; 51.0489°N, 9.8372°E; ca. 310 m a.s.l.; 16 Sep. –14 Nov. 2012; H.-J. Flügel leg.; Malaise trap; UNHC; PSUC_FEM 10022777 (without DNA barcode) • 1 ♂; Baden-Württemberg, Tübingen, Franz. Viertel, Aue Blaulach; 48.5089°N, 9.0786°E; ca. 340 m a.s.l.; 14 Jun. 2012; UNHC; PSUC_FEM 10022748. HUNGARY • 1 ♂; Bács-Kiskun, Miklapusztá; 1 Jul. 1997; É. Kovács leg.; yellow pan trap; UNHC; PSUC_FEM 10022764 (without DNA barcode) • 2 ♂♂; Bács-Kiskun, Gara; 46.035°N, 19.020°E; ca. 90 m a.s.l.; 26–30 Jun. 2009; I. Mikó leg.; yellow pan trap; UNHC; UNHC_1000079, UNHC_1000080 (without DNA barcodes).

Diagnostic description. Male. Body length: 0.70 mm.

Colour (Fig. 25A): Body brown. Legs with lighter joints and tarsi.

Antenna, head (Fig. 25A): F1 with sensillae arranged in four whorled rows, F1 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly before POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 25A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus slightly indicated. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex very short. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Two basal longitudinal carinae on syntergum.

Male genitalia (Fig. 25B–D): Gvc length slightly less than half of mesonotum length. Gvc width $0.95 \times$ gvc length; harpe/gvc index 0.49. Harpe bulbous, slightly distoventrally oriented, and gradually narrowing towards apex; lateral margin of harpe slightly convex in basal half, slightly concave in distal half, and oriented distally; median margin of harpe concave in basal third, strongly convex in apical two-thirds, and diverging distolaterally. Harpe with basomedian spine; tip of basomedian spine more proximal than tip of gonosticulus and oriented distally; harpe with distinctly convex and broad median lamella-like extension at mid-length. Proximodorsal notch of harpe U-shaped and $0.14 \times$ as long as harpe length. Harpe width (above basomedian spine) $0.29 \times$ gvc width, and $0.53 \times$ harpe length. Harpe with at least eight median setae oriented distomedially, extending to apical third; harpe with at least four apical setae

oriented distomedially; harpe with one lateral seta, oriented distolaterally. Gonossiculus length $0.53 \times$ harpe length; gonossiculus J-shaped with at least one digital tooth, tip oriented dorsolaterally. Aedeagus indistinct.

Female. Size: 0.65 mm.

Colour (Fig. 26): Body brown except metasoma lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 26): F8 length longer than half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends at anterior ocellus. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 26): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus slightly visible. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex straight, triangular in dorsal view. Dorsal region of anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex setose. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. Four basal longitudinal carinae on syntergum.

COI barcode. Maximum intraspecific barcode distance: 2.2% ($n = 11$). Minimum interspecific barcode distance: 11.8% (putative species consisting of SMNS_Hym_Cer_001242, SMNS_Hym_Cer_001698, and SMNS_Hym_Cer_001722).

Consensus sequence: 5'- AGCAGGATTAAGATTTATCATCCGTCTTGAATTAAGATCTCCCCCAACAACATAATAATAATGACCTAATTTATAATTCTGTTATCACCAATCATGCCTTCCTGATAATTTTTTTTTTAGTTATACCTATTATACTTGGAGGATTTGGAACTGACTTATCCCCCTTATAATTGGCTCCCCAGATTTAGCCTTCCCTCGAATAAATAACATAAGACTTTGACTCCTACCCCCCTCTTAAACCCTTCTCCTTATTAGAATAATAACCAATACAGGTGTGGGGGCAGGATGAACCCTTTATCCTCCCCTTACTTTTAGTCCCCTTTCATGATGGGATGTCAATAGATTTAACAATCTACTCTCTTCACATCGCAGGAATCAGTTCAATCATAGGTTCAATCAATTTTATAGTAACTACATACAAAATGAAACCCCCCTTCAAATATAATATATCCCTCCCTTTCTCTGTGATCAATATAAT-TACCTCCCTACTCCTTCTACTTTCTCTCCTGTTTTAGCTGGGGCTGTAACAATAATCCTAACAGACCGAACTTAAATACTTCTTTTTTTTGATC-CAGAAGGGGGGGAGACCCTCTCCTCTATCAACATTTATTC -3'

Variation. Unknown.

Biology. Unknown.

Distribution. Palaearctic: Georgia, Germany, Hungary, and Norway.

Etymology. The species name is a composition of the Latin word '*ventricosus*', which means 'bulging' and the anatomical term 'harpe', with reference to the convex median margin of the harpe.

Remarks. *Aphanogmus ventricoharpus* can be distinguished from all other species of the *A. fumipennis* species group by the conspicuous male genitalia, specifically by the distinctly convex and broad median lamella-like extension of the harpes, which are gradually narrowing towards the apex, giving the harpe a bulbous outline (Fig. 25D).



Figure 26. Female *Aphanogmus ventricoharpus* sp. nov. (paratype: ZFMK-HYM-00042461), head and mesosoma in dorsal view, habitus in lateral view.

Aphanogmus zefranki Salden, Mikó & Peters, sp. nov.

<https://zoobank.org/050B65AE-77E7-4BE4-8393-13B97D27A4C9>

Fig. 27; Suppl. material 18

Material examined. *Holotype*: GEORGIA • ♂; Kakheti, Vashlovani; 41.1570°N, 46.5601°E; ca. 290 m a.s.l.; 20–28 Jun. 2021; G. Japoshvili leg.; Malaise trap; ECAUG; ZFMK-HYM-00042448. *Paratypes*: GEORGIA • 2 ♂♂; same data as for holotype; ZFMK; ZFMK-HYM-00042450, ZFMK-HYM-00042453 • 2 ♂♂; Kakheti, Vashlovani, near Alazani river; 41.1241°N, 46.6523°E; ca. 100 m a.s.l.; 21–28 Jun. 2021; G. Japoshvili leg.; Malaise trap; ZFMK; ZFMK-HYM-00042454, ZFMK-HYM-00042455 • 1 ♂; same data as for holotype; ZFMK; ZFMK-HYM-00042457 (without DNA barcode).

Diagnostic description. Male. *Size*: 0.70 mm.

Colour (Fig. 27A): Body brown except metasoma, antenna and legs lighter. Legs with lighter joints and tarsi.

Antenna, head (Fig. 27A): F1 with sensillae arranged in three whorled rows, F1 length shorter than half of scape length. Preoccipital lunula absent. Preoccipital furrow slightly visible. Preoccipital furrow ends anteriorly at POL. Ocellar fovea margin absent. Anterior ocellar fovea slightly visible. Ocular impression and orbital carina absent.

Mesosoma, fore wing, metasoma (Fig. 27A): Scutoscutellar sulcus and transscutal articulation not adjacent, interaxillar sulcus absent. Anteromedian projection of the meta-

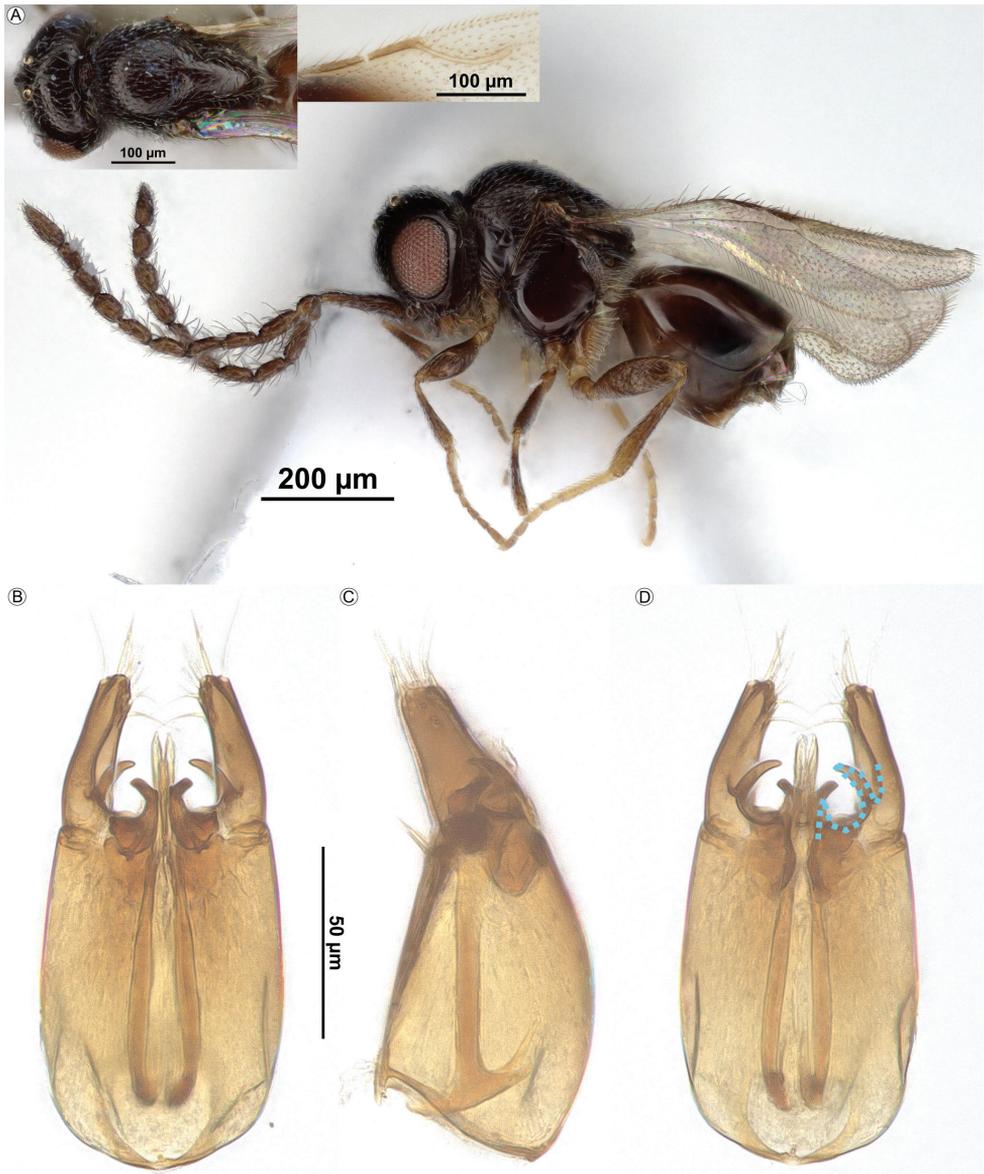


Figure 27. Male *Aphanogmus zefranki* sp. nov. (paratype: ZFMK-HYM-00042454, unless noted otherwise). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (holotype: ZFMK-HYM-00042448, in glycerol), habitus in lateral view. **B–D.** Male genitalia (holotype: ZFMK-HYM-00042448): **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine, proximodorsal notch of harpe, and median spine.

noto-propodeo-metapecto-mesopectal complex absent. Mesometapleural sulcus absent. Epicnemial carina present. Epicnemial pit absent. Stigmal vein curved, tip of vein slightly oriented towards anterior wing margin. No basal longitudinal carinae on syntergum.

Male genitalia (Fig. 27B–D): Gvc length one third of mesonotum length. Gvc width $0.76 \times$ gvc length; harpe/gvc index 0.47. Harpe finger-shaped, distoventrally oriented, and with straight apex in lateral view; lateral margin of harpe convex in basal half, straight in apical half, and oriented distomedially; median margin of harpe slightly concave and converging distomedially. Harpe with basomedian and median spine; tip of basomedian spine more proximal than tip of gonossiculus and oriented distally; median spine arising from basal third of harpe and $4 \times$ as long as wide and distinctly rounded; tip of median spine more distal than tip of gonossiculus and oriented medially. Proximodorsal notch of harpe U-shaped and $0.21 \times$ as long as harpe length. Harpe width (above median spine) $0.18 \times$ gvc width, and $0.28 \times$ harpe length. Harpe with five median setae oriented proximomedially and distomedially, restricted to apical quarter; harpe with at least three apical setae oriented distally, including one broadened seta (broadening only visible in CLSM image Suppl. material 18); harpe with one lateral seta close to apex, oriented distolaterally. Gonossiculus length $0.41 \times$ harpe length; gonossiculus C-shaped with at least one digital tooth, tip oriented dorso-laterally. Aedeagus straight.

Female. Unknown.

COI barcode. Maximum intraspecific barcode distance: 0.0% ($n = 5$). Minimum interspecific barcode distance: 12.1% (*A. ventricoharpus*).

Consensus sequence: 5'- AGCAGGATTAAGATTTATTATTTCGACTT-GAATTAAGATCCCCCCAAATAACCTAATAAACAATGATTTAATT-TATAACTCTGTAATTACTAATCATGCTTTCCTGATAATTTTTTTTT-TAGTTATACCCATTATACTTGGAGGATTTGGAAATTGACTA-ATCCCAATTATAATTGGATCACCAGATTTAGCCTTCCCTCGAATA-AATAATATAAGACTTTGATTACTTCCTCCTTCTTTGACTCTTCTCCT-TAGAAGAATAATAACTAATACAGGTGTAGGAGCAGGATGAACCCTT-TACCCTCCTCTAACTTTAGTACCCTTTCATGATGGTATATCAATAG-ATCTAACAATTTATTCTCTTCATATCGCAGGAATCAGTTCTATTATAG-GTTCAATTAATTTTATAGTAACAACCTTACAAAATAAAACCCTCCTTC-CAAAATCTAATTTCCCTCCCCTTATTCTGTTGATCAATTATAAT-TACATCCCTTCTTTTACTTTTATCCCTTCTGTTTTAGCGGGAGCTG-TAACAATAATTCTAACAGACCGAACTTAAATACTTCTTTTTTCGACCCG-GAAGGAGGGGGAGACCCCTTACTCTACCAACACCTATTT -3'

Variation. The anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex is present and short in ZFMK-HYM-00042454.

Biology. Unknown.

Distribution. Palaearctic: Georgia.

Etymology. The species is named after Hosea Jan Frank, better known as Ze Frank, a popular YouTube creator. He presents „True Facts“ about biodiversity and Morgan Freeman in an artistic, humorous, and scientific manner.

Remarks. *Aphanogmus zefranki* can be easily distinguished from all other species of the *A. fumipennis* species group by its distinct median spine of the harpe which is $4 \times$ as long as wide, distinctly rounded, and medially oriented (Fig. 27D).

Comments on undescribed putative species of the *A. fumipennis* species group

In addition to the newly described species above, we identified several additional specimens of the *A. fumipennis* species group that represent at least nine undescribed putative species, adding up to a minimum of 23 species on this species group in the Western Palaearctic. These putative species are well delimited by molecular sequence data analyses, but could not be diagnosed and then formally described based on morphology, because most are currently represented only by female specimens, which usually lack morphological characters with diagnostic value (Figs 28, 29). We also found single male specimens that exhibit a clearly distinct genitalia morphology and putatively belong to two different species but for which no molecular data are available (Fig. 30) or, in one case, molecular species delimitation was ambiguous (see remarks in *A. karlazani*) (Fig. 31). In such cases, we refrained from describing new species. Collection and integrative analysis of additional material will allow delimitation and description of these putative species and of potentially even more species in this species group.

Aphanogmus fumipennis Thomson, 1858

Aphanogmus fumipennis: Trietsch et al. 2019: 11–14.

Aphanogmus fumipennis: Salden and Peters 2023: 342, 343.²

Remarks. Originally described from a male and a female specimen (Thomson 1858). Male and female specimens assigned to each other by morphology. More than 100 years after the original description of *A. fumipennis*, Dessart (1963b) examined Thomson's type specimens and designated a female lectotype, which was until then designated as a syntype. The lectotype is slide mounted and identified as NHRS-HEVA000008194 (Dessart prep. nr. 6212/124), deposited in the collection of the NHRS (Fig. 32). In addition to the lectotype designation of *A. fumipennis*, Dessart (1963b, p. 403, 415) designated Thomson's original male *A. fumipennis* syntype as the new allotype of *A. fasciipennis*.

Unfortunately, the female lectotype lacks distinct morphological characters with clear diagnostic value that would allow reliable delimitation from other species in the *A. fumipennis* species group, or enable the assignment of other specimens to *A. fumipennis* as the nominal species. This limitation might be overcome in the future through molecular analysis of the lectotype. We refrained from an attempt because of the age, small size and delicateness of the lectotype specimen and the lab protocols not yet set up for these cases. Morphology of the Waterston's evaporatorium (WE) might also allow assigning females and males to each other (see Ulmer et al. 2021), but dissection of the WE results in (partial) damage of the (type) specimens and the species diagnostic value of the character is not fully explored and established, in contrast to the male genitalia. Ergo, we also refrained from an attempt to dissect the *A. fumipennis* type (as well as our holo- or paratypes or the types of synonyms, see below).

² see Johnson and Musetti 2004: 15–17.

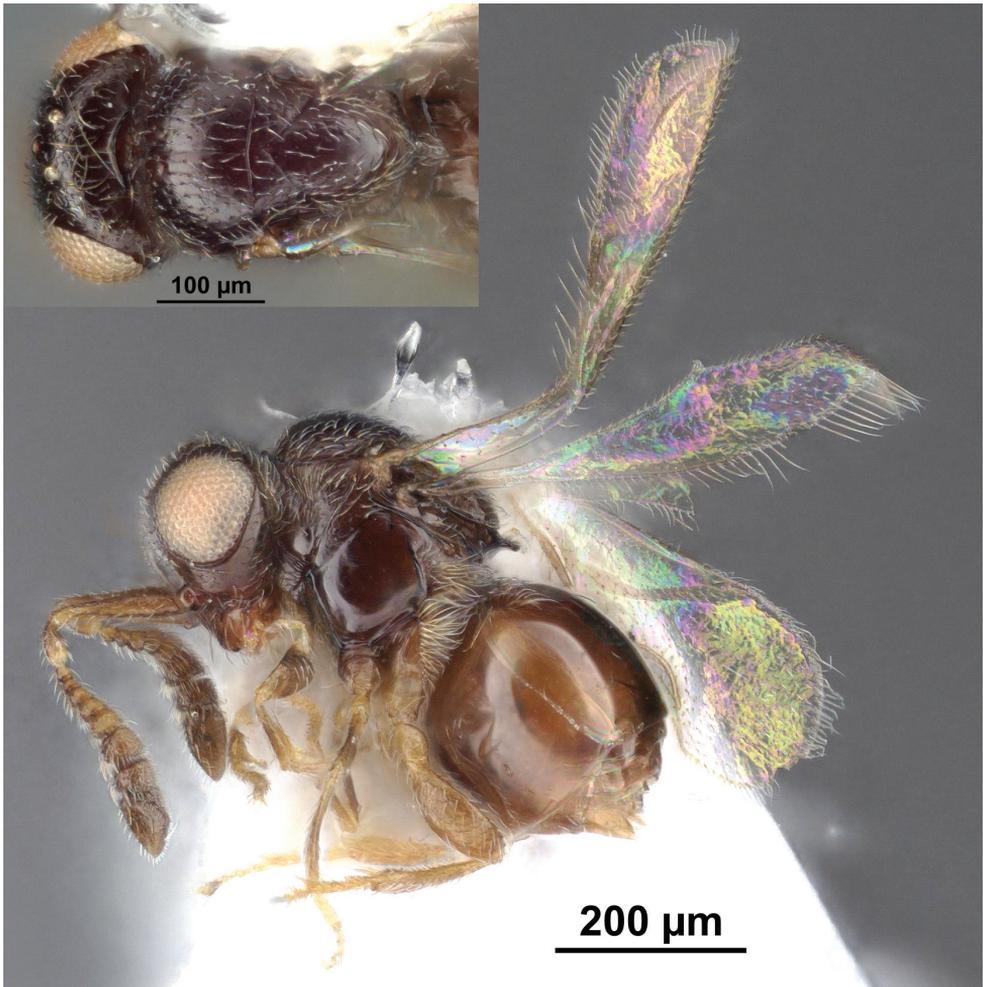


Figure 28. Female *Aphanogmus* sp. (ZFMK-HYM-00042496), head and mesosoma in dorsal view, habitus in lateral view. Representative specimen of a putative new species delimited by *COI* barcode analyses but not formally described due to insufficient morphological diagnostic characters.

Dessart (1963b) described a male allotype from Belgium (Dessart prep. no. 6302/151), whose genitalia he dissected and illustrated (p. 394, figs 12, 13). Unfortunately, we were unable to locate the specimen or the dissected genitalia in the RBINS, RMCA, or NHRS collections (Gerard Y., Hanot S., Vårdal H., pers. comm.). It is questionable whether the designated allotype from Belgium is even conspecific with the lectotype from Sweden, given our results that there are multiple morphologically similar species of the *A. fumipennis* species group distributed across Europe.

The illustration of the genitalia of the male allotype by Dessart is not sufficient to clarify the identity of *A. fumipennis*, in comparison with the newly described species. The illustrated genitalia of the *A. fumipennis* allotype show superficial resemblance to those of *A. digitangulus* sp. nov. and *A. hamatogonus* sp. nov. in terms of the large and distinct gonossiculus and the thin finger-shaped harpes. However, the distinct



Figure 29. Female *Aphanogmus* sp. (ZFMK-HYM-00042524), head and mesosoma in dorsal view, habitus in lateral view. Representative specimen of a putative new species delimited by *COI* barcode analyses but not formally described due to insufficient morphological diagnostic characters.

rectangular median extension in *A. digitangulus* is not present in Dessart's drawing of *A. fumipennis*. The gonossiculus of *A. hamatogonus* lacks the several distinct digital teeth that are clearly visible in the illustration of *A. fumipennis*. In addition, the illustration of *A. fumipennis* does not show any basomedian spine or small spine-like structure, as found in *A. hamatogonus*.

The complementary characters we use in the descriptions of females do not allow inferences on the status of the lectotype female. In summary, as long as the male allotype, particularly the associated genitalia, remains untraceable and a thorough diagnostic assessment of the female lectotype is not possible, we consider *A. fumipennis* a species inquirenda.

All geographic records of *A. fumipennis* published after Dessart (1963b), e.g., from Finland (Hellén 1966), Czech Republic (Zeman and Vaněk 2001), Germany (Dessart 2001), Britain and Ireland (Broad and Livermore 2014), Romania (Teodorescu 2020), have to be treated with caution, as they may belong to the *A. fumipennis* species group but cannot be reliably assigned to species level.

All synonymized species of *A. fumipennis* are considered to belong to the *A. fumipennis* species group, as Dessart was aware of the conspicuous diagnostic posterior mesosomal comb and synonymized (or confirmed synonymization) all of them (see below). A further taxonomic assessment of the synonymized species of *A. fumipennis* is currently not feasible, as they are known only from single female specimens and lack

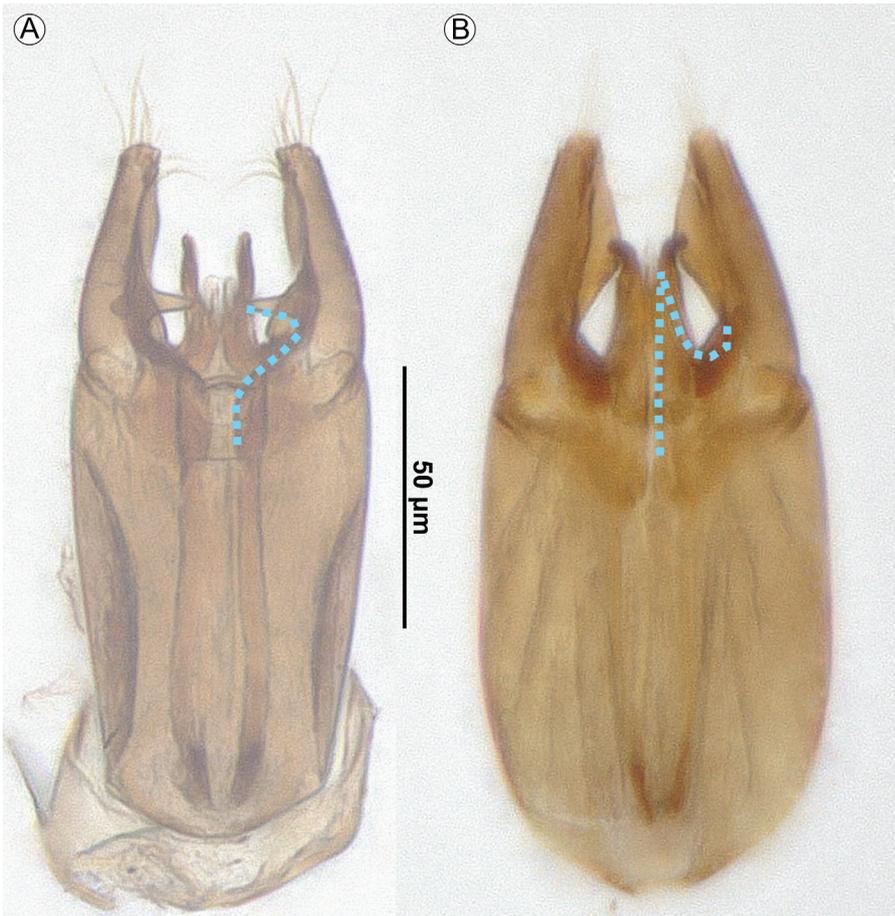


Figure 30. Male genitalia of *Aphanogmus* spp. in dorsal view. **A.** ZFMK-HYM-00042531; **B.** NHRS-HEVA000025258. Male genitalia of two specimens representing two putative new species recognized based on distinctive morphology but not formally described because only single male specimens without associated *COI* barcodes were available.

corresponding males with genitalia (exception *A. laevis*, see below). For now, we consider the synonymized species as species inquirendae.

The following synonyms are listed for *A. fumipennis*:

Aphanogmus hyalinipennis Thomson, 1858: described from a single female specimen from Sweden, near Lund and deposited at NHRS (NHRS-HEVA000008193, prép. n° 6212/122) (Fig. 33). The species was synonymized by Dessart (1963b).

Aphanogmus laevis Förster, 1861: described from a single male specimen from Switzerland and deposited at NHMW (NHMW-HYM#0030402). The species was synonymized by Szelényi (1940). After the examination of the type specimen, we can confirm that it belongs to the *A. fumipennis* species group by the presence of the posterior mesosomal comb and the posterodistal spine at the metacoxa (Fig. 34).

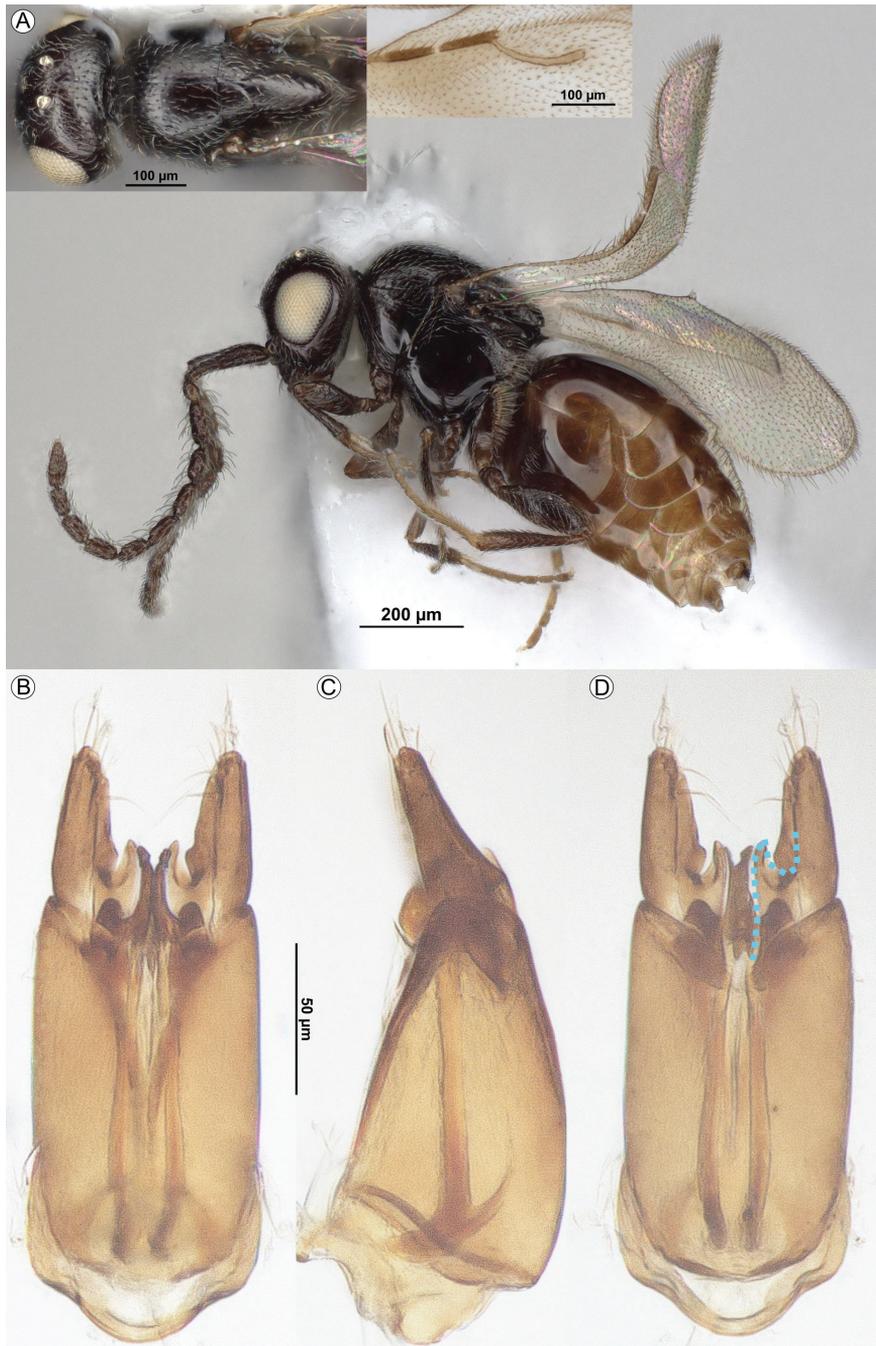


Figure 31. Male *Aphanogmus* sp. (ZFMK-HYM-00042561). **A.** Head and mesosoma in dorsal view, stigmal vein in lateral view (in glycerol), and habitus in lateral view; **B–D.** Male genitalia: **B.** Ventral view; **C.** Lateral view; **D.** Dorsal view, blue dashed line with basomedian spine and proximodorsal notch of harpe. Representative specimen of a putative new species with distinctive male genitalia morphology but not formally described because *COI* barcode analyses yielded ambiguous results.

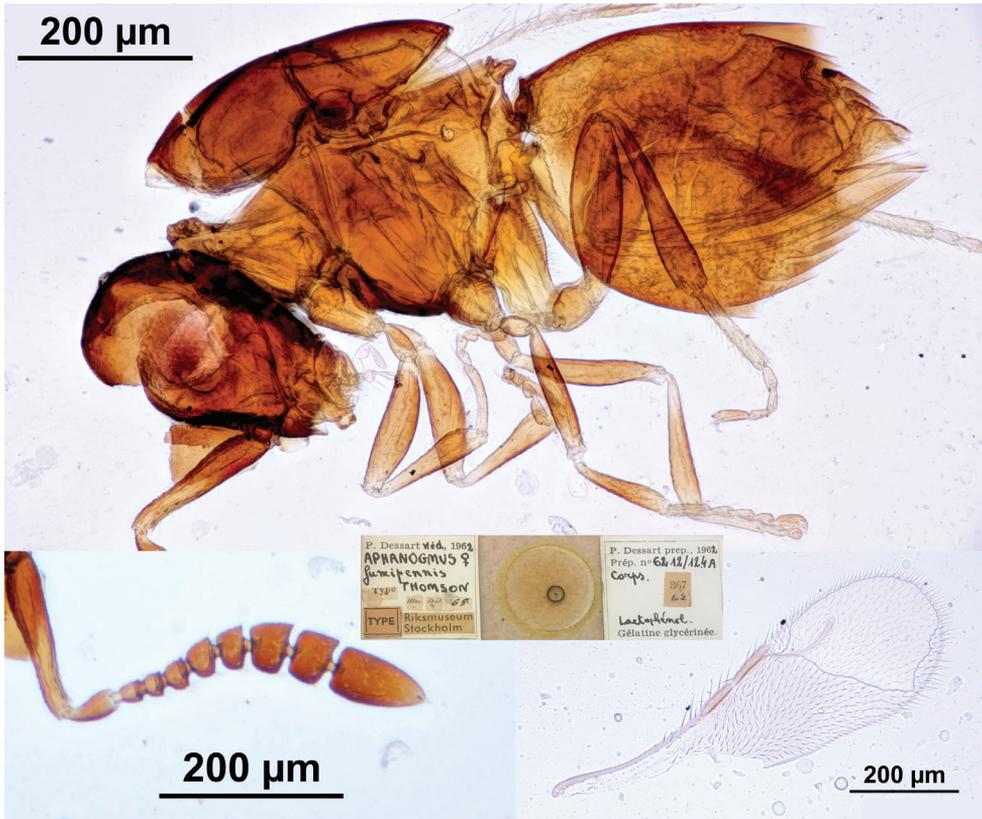


Figure 32. Female *Aphanogmus fumipennis* Thomson, 1858 (lectotype: NHRS-HEVA000008194, prép. n° 6212/124), habitus in lateral view, left antenna in lateral view, right fore wing in lateral view, and slide prép. n° 6212/124A.

However, we refrained from dissecting the male genitalia. The delicate procedure is likely to damage the genitalia and rather lose information than gain information. We follow decisions similar to Trietsch et al. 2020 (e.g., *Conostigmus californicus* (Ashmead, 1893)) and Salden and Peters 2023 (e.g., *Cyoceraphron fuscopleuralis* Dessart, 1978), and consider *A. laevis* as a species inquirenda.

Aphanogmus grenadensis Ashmead, 1896: described from two female specimens from Grenada (Neotropics) and deposited at NHMUK and USNM. The species was synonymized by Dessart (1975a, 1981).

Aphanogmus formicarius Kieffer, 1905: described from a single female specimen from Slovenia “Draufeld” and deposited in the MAAS. The species was synonymized by Dessart (1975a).

Aphanogmus clavatus Kieffer, 1907: described from a single female specimen from Italy and originally deposited in the MCSN. Dessart (1975a) synonymized the species and reported the type to be missing in the MCSN. Hellén (1966) added records of male and female specimens from Finland. Due to the lack of sufficient diagnostic characters, these species identifications are highly dubious.

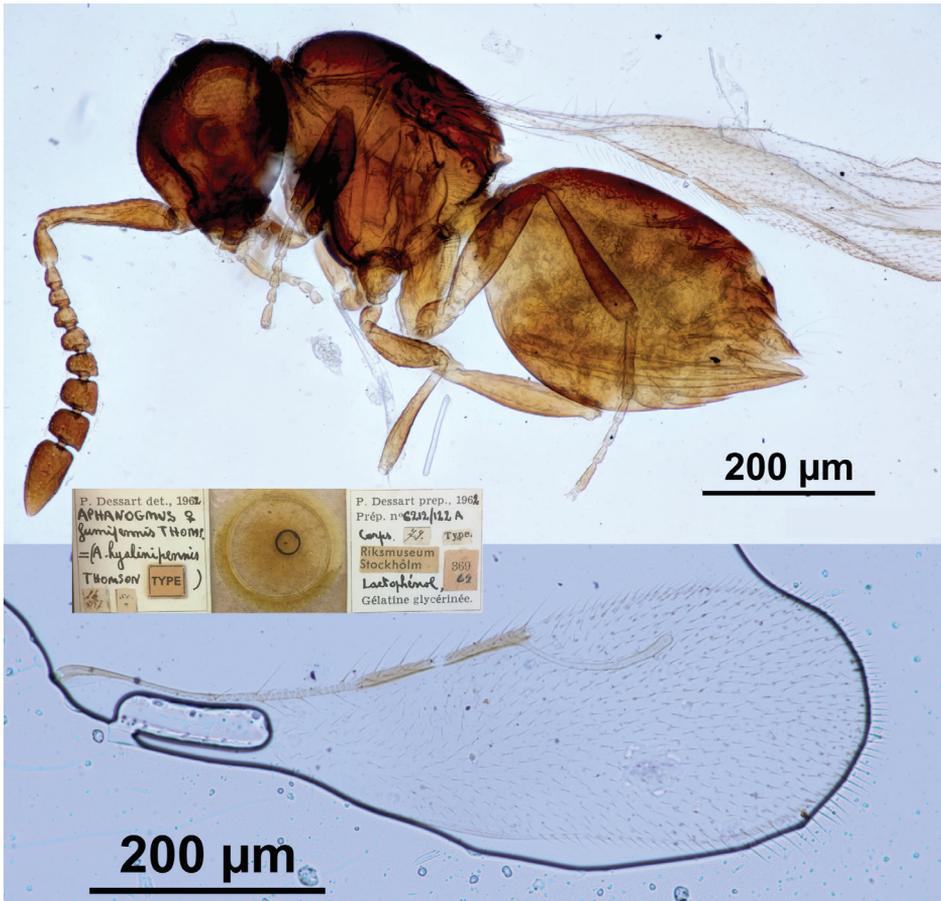


Figure 33. Female *Aphanogmus hyalinipennis* Thomson, 1858 (NHRS-HEVA000008193, prép. n° 6212/122, synonym of *A. fumipennis* Thomson, 1858), habitus in lateral view, right fore wing in lateral view, and slide prep. n° 6212/122A.

Ceraphron armatus Kieffer, 1907: described from a single female specimen from Scotland and deposited in the NHMUK. The species was synonymized by Dessart (1975a).

Ceraphron formicarium Kieffer, 1907: described from a single female specimen from England and deposited in the NHMUK. The species was synonymized by Dessart (1975a).

Ceraphron frenalís Kieffer, 1907: described from a single female specimen from Italy and deposited in the MCSN. The species was synonymized by Szélnyi, in Russo (1938) and synonymization was confirmed by Dessart (1965).

Ceraphron oriphilus Kieffer, 1913: described from a single female specimen from Kenya (Afrotropics) and deposited in the MNHN (Trietsch et al. 2019). The species was synonymized by Dessart (1966).

Ceraphron fuliginosi Box, 1921: described from a single female specimen from England and deposited in the NHMUK. The species was synonymized by Dessart (1975a).



Figure 34. Male *Aphanogmus laevis* Förster, 1861 (NHMW-HYM#0030402, synonym of *A. fumipennis* Thomson, 1858), mesosoma in dorsal view, stigmal vein in lateral view, habitus in lateral view, and label data.

Calliceras fasciata Fouts, 1924: described from two female specimens from the USA (Nearctic) and deposited in the LACM and USNM. The species was synonymized by Dessart (1981).

Calliceras boreale Whittaker, 1930: described from two female specimens from Canada (Nearctic) and deposited in the NHMUK. The species was synonymized by Dessart (1975a).

Allomicrops bemisiae Ghesquière, 1935: described from a single female specimen from the Democratic Republic of the Congo (Afrotropics) and deposited in the RMCA. The species was synonymized by Dessart (1963a). The species is listed as parasitoid or hyperparasitoid of *Bemisia tabaci* (Gennadius, 1889) (Hemiptera: Aleyrodidae) (Ghesquière 1935).

Biology. For a detailed list of recorded biological data associated with the name *A. fumipennis* (including synonyms/species inquirendae) see suppl. material 1 in Moser et al. (2024).

Key to males of the *Aphanogmus fumipennis* species group from the Western Palearctic

- 1 Male genitalia without spine on harpe (see blue dashed line Figs 7D, 21D, 23D)..... 2
- Male genitalia with spine on harpe (see blue dashed line e.g., Figs 4D, 9D, 27D)..... 4

- 2(1) Male genitalia with apical half of harpe finger-shaped (Figs 7B, D, 23B, D) ...3
 – Male genitalia with apical half of harpe triangular (Fig. 21B, D).....
 *A. trigoharpus* sp. nov.
- 3(2) Harpe with rectangular median extension along basal third; harpe slimmer,
 i.e., harpe width of narrowest finger-shaped part 0.30 × harpe width of widest
 medially extended part (Fig. 7D) *A. digitangulus* sp. nov.
 – Harpe with convex median extension along basal third; harpe wider, i.e.,
 harpe width of narrowest finger-shaped part 0.53 × harpe width of widest
 medially extended part (Fig. 23D) *A. vashlovani* sp. nov.
- 4(1) Harpe with basomedian and median spine or with basomedian spine and
 small spine-like structure (Figs 4D, 11D, 13D, 27D) 5
 – Harpe with only one spine (basomedian or median) (e.g., Figs 5D, 9D,
 15D)..... 8
- 5(4) Median spine of harpe equally wide along its length (Figs 4D, 27D) 6
 – Median spine or small spine-like structure of harpe gradually narrowing (Figs
 11D, 13D) 7
- 6(5) Median spine of harpe arising from mid-length of harpe and 2 × as long as
 wide (Fig. 4D) *A. bispinatus* sp. nov.
 – Median spine of harpe arising from basal third of harpe and 4 × as long as
 wide (Fig. 27D) *A. zefranki* sp. nov.
- 7(5) Median spine of harpe arising from mid-length of harpe, tip of median spine
 oriented medially (Fig. 13D)..... *A. harpagodalis* sp. nov.
 – Small spine-like structure arising laterally from basomedian spine, tip of small
 spine-like structure oriented distally (Fig. 11D) *A. hamatogonus* sp. nov.
- 8(4) Proximodorsal notch of harpe L- or U-shaped (visible in dorsal view, see blue
 dashed line e.g., Figs 15D, 17D, 19D)..... 9
 – Proximodorsal notch of harpe absent, mediodorsal notch of harpe V-shaped
 (visible in dorsal view, see blue dashed line Fig. 5D) *A. crispy* sp. nov.
- 9(8) Median margin of harpe not straight apically from proximodorsal notch of
 harpe (e.g., Figs 15D, 25D) 10
 – Median margin of harpe straight apically from proximodorsal notch of harpe
 (Fig. 19D)..... *A. tkbeliharpus* sp. nov.
- 10(9) Median margin of harpe with distinct triangular or convex lamella-like exten-
 sion (Figs 14B, D, 15B, D, 25B, D) 11
 – Median margin of harpe without or with only slim lamella-like extension
 (Figs 9B, D, 17B, D) 13
- 11(10) Median margin of harpe with distinct triangular lamella-like extension
 (Figs 14B, D, 15B, D) 12
 – Median margin of harpe with distinct convex lamella-like extension (Fig. 25B,
 D)..... *A. ventricoharpus* sp. nov.
- 12(11) Median setae of harpe restricted to apical quarter; median margin of harpe
 straight in apical half (Fig. 15B, D)..... *A. kintrishi* sp. nov.
 – Median setae of harpe extending to apical third; median margin of harpe
 slightly concave in apical half (Fig. 14B, D)..... *A. karlazani* sp. nov.

- 13(10) Proximodorsal notch of harpe U-shaped and apex of basomedian spine oriented distolaterally, median margin of harpe with slim lamella-like extension (Fig. 9D)..... *A. hafti* sp. nov.
- Proximodorsal notch of harpe L-shaped and apex of basomedian spine oriented medially, median margin of harpe without median extension (Fig. 17D) .
..... *A. latiharpus* sp. nov.

Discussion

Our integrative taxonomic analyses show that the herein defined *Aphanogmus fumipennis* species group represents at least 23 genetically and morphologically distinguishable species in the Western Palaearctic. Genetic and/or morphological data were sufficient to delimit and describe 14 species of the *A. fumipennis* species group new to science. These results cast significant doubts on the previous taxonomic identity of *A. fumipennis* Thomson, 1858 as a cosmopolitan species with conspicuous intraspecific morphological variation and a broad range of hosts.

The results follow Dessart (1963a) who already observed morphological variation in *A. fumipennis* and interpreted them as strong intraspecific variability but the integrative approach with molecular data analyses, and a detailed comparison of male genitalia morphology, strongly suggest that these variations already reflected interspecific differences. Consequently, we must assume that some synonyms of *A. fumipennis* may in fact represent distinct species within the *A. fumipennis* species group, in particular, with regard to *A. fumipennis* specimens recorded from localities around the world, e.g., from Canada, Congo, Grenada, Kenya, Peru, and the USA (California, Maryland) (Dessart 1963a, 1966, 1975a, 1981). This is also supported by further studies on the newly defined *A. fumipennis* species group, with focus on the eastern Nearctic region and South Korea (Mikó et al. unpublished data).

The recently described species *Aphanogmus fraterculus*, *A. pilosicoxa*, and *A. simbai* (Salden and Peters 2023) from Kenya are also members of the expanded and refined *A. fumipennis* species group, sharing the easily recognizable diagnostic posterior mesosomal comb.

The mesosomal comb harbours an area between the setal rows that is smooth and concave, somewhat reminiscent of the corbicula (pollen basket) of honey bees. It is certainly not used for pollen collection but we can only speculate on its function. It resembles the densely arranged setae present on the metacoxa and on the posterolateral surface of the metanoto-propodeo-mesopecto-metapectal complex in some *Ceraphron* species in the subgenus *Larsoceraphron* and in other unidentified *Ceraphron* species (Ghafouri Moghaddam et al. 2025). In these cases, solidification of a yellow secretion in dying specimens has been observed in the setae along both the metacoxal and the posterolateral surface of the metanoto-propodeo-mesopecto-metapectal complex, suggesting a possible link to a secretory gland (Salden unpublished data). However, in *Ceraphron*, the observed pilose body region lacks the smooth, concave area flanked by two distinct rows of setae present in the *A. fumipennis* species group. The function of the posterior mesosomal comb remains unknown and requires further study.

The host records attributed to *A. fumipennis* span several insect orders (Ghesquière 1935; Dessart and Bournier 1971; Dessart 1975b). Dessart (1963a, 1975a) suggested that the main hosts of *A. fumipennis* are likely coccid-feeding larvae of Cecidomyiidae (Diptera) and all other host records should be interpreted with caution as they might represent rare events or misidentifications. However, there is well-documented parasitoidism by *A. fumipennis* of *Thrips tabaci* Lindemann, 1889 (Thysanoptera: Thripidae) (Dessart and Bournier 1971). The biology of the newly discovered species within the *A. fumipennis* species group remains unknown. Future studies on their biology could further corroborate species limits and contribute to a more complete picture of diversification and distribution within *Aphanogmus* as well as of the species' roles in the ecosystems.

The workflows and technologies required for processing larger samples within an integrative taxonomic framework have been continuously improved in recent years, becoming more efficient and cost-effective (Hartop et al. 2022, 2024; Meier et al. 2025; Amorim et al. 2025). In particular, the dark taxa must be included (Hausmann et al. 2020; Srivathsan et al. 2023). Only then can we obtain a more realistic picture of the known unknown biodiversity “at our doorstep”. Recently, Moser et al. (2025) showed that even in a comparatively well-studied country such as Germany, Ceraphronoidea are one of the taxa in which the number of recorded species (38, including *Conostigmus franzinii* Trietsch & Mikó, 2020) and the number of species yet to be expected (322–493) strikingly differ. Moser et al. (2025) did not perform species-level treatments, but our results are in line with their general inferences. Our study provides the first description of more than a single Palaearctic *Aphanogmus* species in 66 years, since Parr (1960). It increases the number of Ceraphronidae species listed for Germany from 12 (including the nominal species *A. fumipennis* Thomson, 1858 with uncertain identity) to 22. Furthermore, it increases the number of *Aphanogmus* species known from Georgia from a single species to a total of 12, thereby raising the number of Ceraphronoidea species recorded for Georgia from three to 14. This represents a starting point for studying the Ceraphronoidea and other parasitoid wasp groups in Georgia and the Caucasus region, one of the global biodiversity hotspots harbouring a wealth of yet undiscovered endemic and potentially threatened species (Japoshvili and Ljubomirov 2021; Riedel et al. 2023; Rduch et al. 2024; Salden et al. 2024).

This study underscores the utility of integrative taxonomy in biodiversity discovery of dark taxa like Ceraphronidae as a prerequisite to all downstream research and application, including clarifying host ranges, unravelling the evolutionary history of the taxon, and using a more precise understanding of local and global biodiversity in conservation measures. In a world with an accelerating extinction rate, this is more important than ever.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the BMBF for funding the project Caucasus Barcode of Life (CaBOL – <https://ggbc.eu/>), grant number 01DK20014A, which financially supported the field work and for funding the German Barcode of Life III: Dark Taxa Project (FKZ 16LI1901C), which financially supported the molecular work performed at SMNS. We are grateful to all collectors of specimens and all people who helped sorting material. Samples from the insect monitoring BW were provided by the Landesanstalt für Umwelt Baden-Württemberg (LUBW, State Institute for Environment Baden-Württemberg). Furthermore, we would like to thank DBU Naturerbe GmbH (Osnabrück), the Nature Conservation Center of the District of Coesfeld, the Lower Nature Conservation Authorities of the Districts of Recklinghausen and Coesfeld, the Federal Forestry Service Rhein-Weser, and the Münster District Government for the good cooperation and for granting the necessary permits. We would like to thank the NaPa (Nature-Positive Agriculture) project, managed by Dr. Tamara Hartke and Vera Prenzel, as well as the collaborating farmers for granting access to their property and who kindly provided specimens and the student helpers who assisted in pre-sorting samples. We also thank Anja Bodenheim for the sequencing of the Georgian specimens. For processing the data into the GBOL and BOLD databases, we are indebted to Jana Thormann and Björn Rulik. The processing of Norwegian specimens for BOLD was supported by Prof. Torbjørn Ekrem (NorBOL/NTNU Museum) and Dr. Frode Ødegaard (Hymenoptera Collection at NTNU Museum). The project on Ceraphronoidea in Norway (9-20, NOCER) was financially supported by the Norwegian Taxonomy Initiative (Norwegian Biodiversity Centre). We thank all curators and assistants for the loan of type specimens and for their assistance in clarifying the availability and location of material. In particular, we are grateful to Hege Vårdal, Julia Stigenberg, and Mattias Forshage (NHRS); Dominique Zimmermann, Tamara Spasojevic, and Manuela Vizek (NHMW); Camille Locatelli, Tim Laebens, Yvonnick Gerard, and Wouter Dekoninck (RBINS); and Stéphane Hanot (RMCA). Special thanks go to Juliane Vehof for introducing us to the Keyence imaging system. We thank Tomáš Faragó for tomographic reconstruction and Angelica Cecilia and Marcus Zuber for the assistance at the beamline. We acknowledge the KIT Light Source for provision of instruments at their beamlines and we would like to thank the Institute for Beam Physics and Technology (IBPT) for the operation of the storage ring, the Karlsruhe Research Accelerator (KARA). We thank the reviewers Mostafa Ghafouri Moghaddam and Jonah Ulmer and the editor Tamara Spasojevic for their thoughtful and constructive feedback, which significantly improved this manuscript. We are grateful to the International Society of Hymenopterists for their support. Finally, we would like to thank all ceraphronids for being out there.

References

- Alekseev VN (1995) Superfam. Ceraphronoidea. In: Lehr PA (Ed.). Key to the Insects of the Russian Far East. Neuropteroidea, Mecoptera, Hymenoptera. Vol. IV, pt 2. Dal'nauka, Vladivostok: 24–37. [In Russian].

- Amorim DS, Oliveira SS, Balbi MIPA, Ang Y, Torres A, Yeo D, Srivathsan A, Meier R (2025) An integrative taxonomic treatment of the Mycetophilidae (Diptera: Bibionomorpha) from Singapore reveals 115 new species on 730 km² [Preprint]. bioRxiv. <https://doi.org/10.1101/2023.09.02.555672>
- Armstrong AL, Sones JE, Lohrmann V, Hebert PDN, Janzen DH, Hallwachs W, Blaschke JD (2024) Six in one: cryptic species and a new host record for *Olixon* Cameron (Rhopalosomatidae, Hymenoptera) revealed by DNA barcoding. *Journal of Hymenoptera Research* 97: 363–378. <https://doi.org/10.3897/jhr.97.116726>
- Ashmead WH (1893) A monograph of the North American Proctotrypidae. *Bulletin of the United States National Museum* 45: 1–472. <https://doi.org/10.5479/si.03629236.45.1>
- Ashmead WH (1904) Descriptions of Two New Hymenoptera from Japan – I. *Journal of the New York Entomological Society* 12: 65–84. https://digitalcommons.usu.edu/bee_lab_an/90/
- Astrin J, Stüben P (2008) Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorhynchinae (Coleoptera: Curculionidae). *Invertebrate Systematics* 22(5). <https://doi.org/10.1071/is07057>
- Box LA (1921) New species of myrmecophilous Hymenoptera-Proctotrypoidea. *Entomologist's Record and Journal of Variation* 33 (1): 15–17.
- Broad G, Livermore L (2014) Checklist of British and Irish Hymenoptera - Ceraphronoidea. *Biodiversity Data Journal* 2: e1167. <https://doi.org/10.3897/BDJ.2.e1167>
- Buffington ML, Polaszek A (2009) Recent occurrence of *Aphanogmus dictynna* (Waterston) (Hymenoptera: Ceraphronidae) in Kenya an important hyperparasitoid of the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae). *Zootaxa* 2214: 62–68. <https://doi.org/10.11646/zootaxa.2214.1.4>
- Buhl PN, O'Conner JP, Ashe P (2010) A new reared species of *Aphanogmus* (Hymenoptera, Ceraphronidae) from Ireland. *Entomologist's Monthly Magazine* 146: 53–55.
- Cecilia A, Rack A, Douissard P-A, Martin T, dos Santos Rolo T, Vagoič P, Hamann E, van de Kamp T, Riedel A, Fiederle M, Baumbach T (2011) LPE grown LSO:Tb scintillator films for high-resolution X-ray imaging applications at synchrotron light sources. *Nuclear Instruments and Methods in Physics Research Section A: Accelerators, Spectrometers, Detectors and Associated Equipment* 648: 321–323. <https://doi.org/10.1016/j.nima.2010.10.150>
- Debnath R, Rajmohana K, Sushama V, Dinesh KP (2025) DNA metabarcoding of spider egg sacs uncovers novel insights into host parasitoid complexes and trophic networks. *Scientific Reports* 15: 13608. <https://doi.org/10.1038/s41598-025-97799-2>
- Dessart P (1963a) Contribution à l'étude des Hyménoptères Proctotrupeoidea. (III). Révision du genre *Allomicrops* Kieffer, 1914, et description de *Ceraphron masneri* sp. nov. (Ceraphronidae). *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* 99: 513–539.
- Dessart P (1963b) Contribution à l'étude des Hyménoptères Proctotrupeoidea (II). Révision des *Aphanogmus* décrits par C. G. Thomson. *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* 99: 387–416.
- Dessart P (1965) Contribution à l'étude des Hyménoptères Proctotrupeoidea. (VI). Les Ceraphroninae et quelques Megaspilinae (Ceraphronidae) du Musée Civique d'Histoire Naturelle de Gênes. *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* 101: 105–192.

- Dessart P (1966) Contribution à l'étude des hyménoptères Proctotrupeoidea. (XI). revision des Ceraphronidae d'Afrique orientale décrits par l'Abbe Jaen-Jacques kieffer. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 42: 1–30.
- Dessart P (1975a) Matériel typique des microhyménoptera myrmécophiles de la Collection Wasmann déposé au Muséum Wasmannianum à Maastricht (Pays-Bas). Publicaties van Het Natuurhistorisch Genootschap in Limburg 24: 1–94.
- Dessart P (1975b) A propos du genre *Neoceraphron* Ashmead, 1893 (Hy., Ceraphronoidea, Ceraphronidae). Bulletin et Annales de la Société Royale Belge d'Entomologie 111: 163–177.
- Dessart P (1979) Suppression et demembrement du genre *Neoceraphron* Ashmead, 1893 (Hymenoptera Ceraphronoidea Ceraphronidae). Bulletin et Annales de la Société royale belge d'Entomologie 115: 161–168.
- Dessart P (1981) Notule hyménoptérologique no. 8. Bulletin et Annales de la Société Royale Belge d'Entomologie 117: 12–15.
- Dessart P (1994) Hyménoptera Ceraphronoidea nouveaux ou peu connus. New or unusual Hymenoptera Ceraphronoidea. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Entomologie. 64: 49–103.
- Dessart P (2001) Ceraphronoidea. In: Dathe H, Taeger A, Blank S (Eds) Verzeichnis der Hautflügler Deutschlands (Entomofauna Germanica 4). 7. Entomologische Nachrichten und Berichte, Dresden, 178 pp.
- Dessart P, Alekseev VN (1982) Deux especes nouvelles de Ceraphronidae de la region de l'amour (Hym. Ceraphronoidea). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 54: 1–4.
- Dessart P, Bournier A (1971) *Thrips tabaci* Lindman (Thysanoptera), hôte inattendu d'*Aphanogmus fumipennis* (Thomson) (Hym. Ceraphronidae). Bulletin et Annales de la Société royale entomologique de Belgique 107: 116–118.
- Dos Santos Rolo T, Ershov A, van de Kamp T, Baumbach T (2014) In vivo X-ray cine-tomography for tracking morphological dynamics. Proceedings of the National Academy of Sciences of the United States of America 111: 3921–3926. <https://doi.org/10.1073/pnas.1308650111>
- Douissard P-A, Cecilia A, Rochet X, Chapel X, Martin T, van de Kamp T, Helfen L, Baumbach T, Luquot L, Xiao X, Meinhardt J, Rack A (2012) A versatile indirect detector design for hard X-ray microimaging. Journal of Instrumentation 7: P09016. <https://doi.org/10.1088/1748-0221/7/09/P09016>
- Edgar RC (2004) MUSCLE: A multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics 5(1): 113. <https://doi.org/10.1186/1471-2105-5-113>
- Ernst A, Miko I, Deans A (2013) Morphology and function of the ovipositor mechanism in Ceraphronoidea (Hymenoptera, Apocrita). Journal of Hymenoptera Research 33: 25–61. <https://doi.org/10.3897/jhr.33.5204>
- Evans GA, Dessart P, Glenn H (2005) Two new species of *Aphanogmus* (Hymenoptera: Ceraphronidae) of economic importance reared from *Cybocephalus nipponicus* (Coleoptera: Cybocephalidae). Zootaxa 1018: 47–54. <https://doi.org/10.11646/zootaxa.1018.1.3>
- Faragó T, Gasilov S, Emslie I, Zuber M, Helfen L, Vogelgesang M, Baumbach T (2022) Tofu: a fast, versatile and user-friendly image processing toolkit for computed tomography. Journal of Synchrotron Radiation 29: 916–927. <https://doi.org/10.1107/S160057752200282X>

- Fergusson NDM (1980) A revision of the British species of *Dendrocerus* Ratzeburg (Hymenoptera: Ceraphronoidea) with a review of their biology as aphid hyperparasites. Bulletin of the British Museum (Natural History) Entomology 41: 255–314. <https://doi.org/10.5962/bhl.part.28549>
- Ghafouri Moghaddam M, Salden T, Heidari Latibari M, Butcher BA (2025) Review of the subgenus *Larsoceraphron* Dessart, 1981 of the genus *Ceraphron* Jurine, 1807 (Hymenoptera, Ceraphronidae) with the description of a new species from Thailand. Journal of Hymenoptera Research 98: 579–602. <https://doi.org/10.3897/jhr.98.151607>
- Ghesquière J (1935) Un Calliceratide (Hym. Poct.) nouveau du Congo belge. Bulletin de la Société Royale de Botanique de Belgique. 65: 59–61.
- Hartop E, Srivathsan A, Ronquist F, Meier R (2022) Towards Large-Scale Integrative Taxonomy (LIT): Resolving the Data Conundrum for Dark Taxa. Systematic Biology 71: 1404–1422. <https://doi.org/10.1093/sysbio/syac033>
- Hartop E, Lee L, Srivathsan A, Jones M, Peña-Aguilera P, Ovaskainen O, Roslin T, Meier R (2024) Resolving biology's dark matter: species richness, spatiotemporal distribution, and community composition of a dark taxon. BMC Biology 22: 215. <https://doi.org/10.1186/s12915-024-02010-z>
- Hausmann A, Krogmann L, Peters RS, Rduch V, Schmidt S (2020) GBOL III: DARK TAXA. iBOL Barcode Bulletin 10(1). <https://doi.org/10.21083/ibol.v10i1.6242>
- Haviland MD (1920) Memoirs: On the Bionomics and Development of *Lygocerus testaceimanus*, Kieffer, and *Lygocerus cameroni*, Kieffer (Proctotrypoidea-Ceraphronidae), parasites of *Aphidius* (Braconidae). Quarterly Journal of Microscopical Science 2: 101–127. <https://doi.org/10.1242/jcs.s2-65.257.101>
- Hellén W (1966) Fauna Fennica 20. Die Ceraphroniden Finnlands (Hymenoptera: Proctotrupoidea). Societas pro Fauna et Flora Fennica, Helsinki.
- Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. Molecular Biology and Evolution 35(2): 518–522. <https://doi.org/10.1093/molbev/msx281>
- Japoshvili G (2022) New data on some microhymenopteran families from Lagodekhi Protected Area, with new records for Georgia (Sakartvelo) and the Caucasus. Caucasia 1: 7–11. <https://doi.org/10.3897/caucasia.1.e81647>
- Japoshvili G, Ljubomirov T (2021) Wasps of the families Ampulicidae, Bembicidae, Bethyloidea, Chrysididae, Crabronidae, Evanidae, Gasteruptidae, Heloridae, Pemphredonidae, Pompilidae, Psenidae, Sphecidae and Vespidae (Hymenoptera) of Lagodekhi protected areas, from Georgia (Sakartvelo). Annals of Agrarian Science 19: 269–287.
- Johnson NF, Musetti L (2004) Catalog of systematic literature of the Superfamily Ceraphronoidea (Hymenoptera). Contributions of the American Entomological Institute 33: 1–149. <https://api.semanticscholar.org/CorpusID:92285669>
- Kapli P, Lutteropp S, Zhang J, Kobert K, Pavlidis P, Stamatakis A, Flouri T (2017) Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. Valencia A (Ed.). Bioinformatics 33 (11): 1630–1638. <https://doi.org/10.1093/bioinformatics/btx025>
- Kieffer JJ (1907) Proctotrypidæ (suite). Species des Hyménoptères d'Europe et d'Algérie 10: 145–288. <https://zenodo.org/records/24300>

- Kieffer JJ (1914) Serphidae (=Proctotrupidae) et Calliceratidae (=Ceraphronidae). Das Tierreich 42: 1–254. <https://doi.org/10.5962/bhl.title.1219>
- Larsson A (2014) AliView: a fast and lightweight alignment viewer and editor for large data sets. Bioinformatics 30(22): 3276–3278. <https://doi.org/10.1093/bioinformatics/btu531>
- Luhman JC, Holzenthal RW, Kjaerandsen JK (1999) New host record of a ceraphronid (Hymenoptera) in Trichoptera pupae. Journal of Hymenoptera Research 8(1): 126. <https://doi.org/10.5281/zenodo.16095912>
- Matsuo K, Ganaha-Kikumura T, Ohno S, Yukawa J (2016) Description of a new species of *Aphanogmus* Thomson (Hymenoptera, Ceraphronidae) that parasitizes acarivorous gall midges of *Feltiella* (Diptera, Cecidomyiidae) in Japan. ZooKeys 596: 77–85. <https://doi.org/10.3897/zookeys.596.8472>
- Meier R, Shiyang K, Vaidya G, Ng PKL (2006) DNA barcoding and taxonomy in Diptera: A tale of high intraspecific variability and low identification success. Systematic Biology 55(5): 715–728. <https://doi.org/10.1080/10635150600969864>
- Meier R, Srivathsan A, Oliveira SS, Balbi MIPA, Ang Y, Yeo D, Kjærandsen J, Amorim DS (2025) “Dark taxonomy”: A new protocol for overcoming the taxonomic impediments for dark taxa and broadening the taxon base for biodiversity assessment. Cladistics 41: 223–238. <https://doi.org/10.1111/cla.12609>
- Mikó I, Deans AR (2009) *Masner*, a new genus of Ceraphronidae (Hymenoptera, Ceraphronoidea) described using controlled vocabularies. ZooKeys 20: 127–153. <https://doi.org/10.3897/zookeys.20.119>
- Mikó I, Masner L, Johannes E, Yoder MJ, Deans AR (2013) Male terminalia of Ceraphronoidea: morphological diversity in an otherwise monotonous taxon. Insect Systematics & Evolution 44: 261–347. <https://doi.org/10.1163/1876312X-04402002>
- Mikó I, Trietsch C, Van De Kamp T, Masner L, Ulmer JM, Yoder MJ, Zuber M, Sandall EL, Baumbach T, Deans AR (2018) Revision of *Trassedia* (Hymenoptera: Ceraphronidae), an evolutionary relict with an unusual distribution. Insect Systematics and Diversity 2(6): 4. <https://doi.org/10.1093/isd/ixy015>
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Von Haeseler A, Lanfear R (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37(5): 1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- Mollaei M, Sadeghi-Namaghi H, Lotfalizadeh H, Minab F (2025) *Aphanogmus feltiellophagus* sp. nov. (Hymenoptera: Ceraphronidae), a parasitoid of the acarivorous gall midge, *Feltiella acarisuga* Vallot (Diptera: Cecidomyiidae) in Iran. Journal of Insect Biodiversity and Systematics 11 (3): 693–702. <https://doi.org/10.61186/jibs.11.3.693>
- Moser M, Ulmer J, Van de Kamp T, Vasilița C, Renninger M, Mikó I, Krogmann L (2023) Surprising morphological diversity in ceraphronid wasps revealed by a distinctive new species of *Aphanogmus* (Hymenoptera: Ceraphronoidea). European Journal of Taxonomy 864: 146–166. <https://doi.org/10.5852/ejt.2023.864.2095>
- Moser M, Salden T, Mikó I, Krogmann L (2024) Synthesis of the host associations of Ceraphronoidea (Hymenoptera): a key to illuminating a dark taxon. Insect Systematics and Diversity 8(6): 6. <https://doi.org/10.1093/isd/ixae039>

- Moser M, Vasilița C, Haas-Renninger M, Pirvu E, Haas M, Krogmann L (2025) German Barcode of Life reveals unexpected diversity of Ceraphronoidea (Hymenoptera). *Biodiversity Data Journal* 13: e159561. <https://doi.org/10.3897/BDJ.13.e159561>
- Müller B, Thormann J, Von Der Mark L, Astrin J, Rulik B (2024) Supplemental lab-protocol for barcoding primers: dEURYT-BRBM2, LCO1490-JJ, LCO1490-JJ2 & LCO1490-JJ3 v1. <https://doi.org/10.17504/protocols.io.6qpvr96kbvbk/v1>
- Parr MJ (1960) Three new species of *Aphanogmus* (Hymenoptera: Ceraphronidae) from Britain, with a re-description of *A. fumipennis* Thoms., 1858, a species new to Britain. *Transactions of the Society for British Entomology* 14: 115–130.
- Puillandre N, Brouillet S, Achaz G (2021) ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources* 21 (2): 609–620. <https://doi.org/10.1111/1755-0998.13281>
- Rambaut A (2018) FigTree. <https://github.com/rambaut/figtree/releases/tag/v1.4.4>
- Ranjith AP, Ayiswarya SV, Niveditha B, Priyadarsanan DR (2023) A new species of *Aphanogmus* Thomson (Hymenoptera: Ceraphronidae) parasitising predatory cecidomyiids in mite-induced galls of *Pongamia pinnata* in India. *Journal of Natural History* 57: 1963–1971. <https://doi.org/10.1080/00222933.2023.2279237>
- Ratnasingham S, Hebert PDN (2007) Barcoding BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes* 7(3): 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Rduch V, Dey L-S, Ghazaryan A, Husemann M, Iankoshvili G, Krammer H-J, Lambrecht M, Marabuto E, Mengual X, Müller B, Peters RS, Rulik B, Salden T, Silva-Brandão KL, Espeland M, Thormann J, Töpfer T, Weiss C, Żyła D, Hein N (2024) Exkursion in den Kaukasus: Der CaBOL BioBlitz 2022 in Armenien und Georgien. *Koenigiana* 18: 21–40.
- Riedel M, Penigot W, Schwarz M, Diller E, Johansson N, Japoshvili G (2023) Darwin wasps (Hymenoptera, Ichneumonidae) of the Kintrishi National Park, Sakartvelo (Georgia), with descriptions of six new species. *Linzer Biologische Beiträge* 55: 61–153. <https://doi.org/10.35011/lbb.55.1-05>
- Russo G (1938) Contributo alla conoscenza dei Coleotteri Scolitidi. Fleotribo: *Phloeotribus scarabaeoides* (Bern.) Fauv. Parte seconda. Biografia, simbionti, danni e lotta. *Laboratorio di Entomologia Agraria di Portici, Bollettino* 2: 1–420.
- Salden T, Peters RS (2023) Afrotropical Ceraphronoidea (Insecta: Hymenoptera) put back on the map with the description of 88 new species. *European Journal of Taxonomy* 884: 1–386. <https://doi.org/10.5852/ejt.2023.884.2181>
- Salden T, Müller B, Japoshvili G, Hein N, Ugrelidze A, Peters RS (2024) First records of the Hymenoptera superfamilies and families Mymarommatoidea: Mymarommatidae and Stephanoidea: Stephanidae in Georgia. *Caucasiana* 3: 145–150. <https://doi.org/10.3897/caucasiana.3.e124925>
- Sheikh SI, Ward AKG, Zhang YM, Davis CK, Zhang L, Egan SP, Forbes AA (2022) *Ormyrus labotus* (Hymenoptera: Ormyridae): Another generalist that should not be a generalist is not a generalist. *Insect Systematics and Diversity* 6: 8. <https://doi.org/10.1093/isd/ixac001>
- Srivathsan A, Ang Y, Heraty JM, Hwang WS, Jusoh WFA, Kutty SN, Puniamoorthy J, Yeo D, Roslin T, Meier R (2023) Convergence of dominance and neglect in flying insect diversity. *Nature Ecology and Evolution* 7: 1012–1021. <https://doi.org/10.1038/s41559-023-02066-0>

- Sternberg N, Bodenheim A, Oriowo TO, Podsiadlowski L, Stange M (2025) Human impacts on the distribution and genetic diversity of Eurasian minnows (*Phoxinus*: Leuciscidae) in the Rhenish Massif. *Knowledge and Management of Aquatic Ecosystems* 426: 20. <https://doi.org/10.1051/kmae/2025015>
- Szelényi G (1940) Die paläarktische Arten der Gattung *Aphanogmus* Thoms. (Hym. Proct.). *Annales Historico-Naturales Musei Nationalis Hungarici* 33: 122–136. <http://publication.nhmus.hu/Annales/cikkreszletes.php?idhoz=529>
- Teodorescu I (2020) Ceraphronidae and Megaspilidae (Hymenoptera: Ceraphronoidea)—The current state of knowledge in Romania. *Romanian Journal of Biology-Zoology* 65: 35–54. https://www.ibiol.ro/zoology/RJB-Z-65/RJBZ_65_art-3.html
- Thomson CG (1858) Sveriges Proctotruper. Tredje Gruppen Ceraphronini. Öfversigt af Kongl. Vetenskapsakademiens förhandlingar 15: 287–305.
- Trietsch C, Mikó I, Deans AR (2019) A photographic catalog of Ceraphronoidea types at the Muséum national d'Histoire naturelle, Paris (MNHN), with comments on unpublished notes from Paul Dessart. *European Journal of Taxonomy* 502: 1–60. <https://doi.org/10.5852/ejt.2019.502>
- Trietsch C, Mikó I, Ezray B, Deans AR (2020) A Taxonomic Revision of Nearctic *Conostigmus* (Hymenoptera: Ceraphronoidea: Megaspilidae). *Zootaxa* 4792(1): 1–155. <https://doi.org/10.11646/zootaxa.4792.1.1>
- Ulmer JM, Mikó I, Deans AR, Krogmann L (2021) The Waterston's evaporatorium of Ceraphronidae (Ceraphronoidea, Hymenoptera): A morphological barcode to a cryptic taxon. *Journal of Hymenoptera Research* 85: 29–56. <https://doi.org/10.3897/jhr.85.67165>
- Vasilița C, Moser M, Krogmann L (2022) Mission possible: an optimised protocol for the unbarcodable Ceraphronoidea (Hymenoptera). *Biodiversity Data Journal* 10: e84860. <https://doi.org/10.3897/bdj.10.e84860>
- Vasilița C, Feng V, Hansen AK, Hartop E, Srivathsan A, Struijk R, Meier R (2024) Express barcoding with NextGenPCR and MinION for species-level sorting of ecological samples. *Molecular Ecology Resources* 24: e13922. <https://doi.org/10.1111/1755-0998.13922>
- Vogelgesang M, Farago T, Morgeneyer TF, Helfen L, dos Santos Rolo T, Myagotin A, Baumbach T (2016) Real-time image-content-based beamline control for smart 4D X-ray imaging. *Journal of Synchrotron Radiation* 23: 1254–1263. <https://doi.org/10.1107/S1600577516010195>
- Ward AKG, Sheikh SI, Forbes AA (2020) Diversity, host ranges, and potential drivers of speciation among the Inquiline enemies of oak gall wasps (Hymenoptera: Cynipidae). *Insect Systematics and Diversity* 4: 3. <https://doi.org/10.1093/isd/ixaa017>
- Yoder MJ, Mikó I, Seltmann KC, Bertone MA, Deans AR (2010) A gross anatomy ontology for Hymenoptera. *PLoS ONE* 5(12): e15991. <https://doi.org/10.1371/journal.pone.0015991>
- Youssef RM, Kaf NHA, Abboud R, Al Tawaha ARM (2022) New record of *Aphanogmus clavicornis* Thomson (Hymenoptera: Ceraphronidae) as a larval parasitoid of tomato leaf miner *Tuta absoluta* (Meyrick) in Syria. *International Journal of Biology Sciences* 4: 181–185. <https://doi.org/10.33545/26649926.2022.v4.i2c.120>
- Zeman V, Vaněk J (2001) Hymenoptera (Braconidae, Aphidiidae, Ichneumonidae, Diapriidae, Scelionidae, Pltygasteridae, Ceraphronidae, Megaspilidae, Dryinidae, Mutillidae, Pemphredonidae) in pitfall traps in montane and sub-alpine zone in Giant Mts. *Východočeský sborník přírodovědný, Práce a studie* 9: 129–133.

Supplementary material 1

Full list of examined material

Authors: Tobias Salden, István Mikó, Arnstein Staverløkk, Marina Moser, Cristina Vasilița, Thomas van de Kamp, Jonathan Vogel, Lars Podsiadlowski, Nils Hein, George Japoshvili, Ralph S. Peters

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl1>

Supplementary material 2

Digital reconstruction of male *Aphanogmus bispinatus* sp. nov. (non-type: PSUC_FEM 10022848) based on synchrotron micro-CT

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Habitus in lateral view; **B.** Mesosoma in lateral view; **C.** Mesosoma in dorsal view; **D.** Head in frontal view; **E.** Head from posterior view; **F.** Mesosoma from posterior view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl2>

Supplementary material 3

CLSM micrographs of male genitalia of *Aphanogmus crispy* sp. nov. (non-type: 10022906)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl3>

Supplementary material 4

Digital reconstruction of male *Aphanogmus crispy* sp. nov. (non-type: 10022906) based on synchrotron micro-CT

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Habitus in lateral view; **B.** Mesosoma in lateral view; **C.** Mesosoma in dorsal view; **D.** Head in frontal view; **E.** Head from posterior view; **F.** Mesosoma from posterior view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl4>

Supplementary material 5

CLSM micrographs of male genitalia of *Aphanogmus digitangulus* sp. nov. (non-type: 10022929)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Lateral view; **C.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl5>

Supplementary material 6

Digital reconstruction of male *Aphanogmus digitangulus* sp. nov. (non-type: 10022921) based on synchrotron micro-CT

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Habitus in lateral view; **B.** Mesosoma in lateral view; **C.** Mesosoma in dorsal view; **D.** Head in frontal view; **E.** Head from posterior view; **F.** Mesosoma from posterior view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl6>

Supplementary material 7

CLSM micrographs of male genitalia of *Aphanogmus hafti* sp. nov. (non-type: PSUC_FEM 10022845)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventrolateral view; **B.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl7>

Supplementary material 8

Digital reconstruction of male *Aphanogmus hafti* sp. nov. (non-type: PSUC_FEM 10022845) based on synchrotron micro-CT

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Habitus in lateral view; **B.** Mesosoma in lateral view; **C.** Mesosoma in dorsal view; **D.** Head in frontal view; **E.** Head from posterior view; **F.** Mesosoma from posterior view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl8>

Supplementary material 9

Digital reconstruction of male *Aphanogmus hamatogonus* sp. nov. (non-type: PSUC_FEM 10022812) based on synchrotron micro-CT

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Habitus in lateral view; **B.** Mesosoma in lateral view; **C.** Mesosoma in dorsal view; **D.** Head in frontal view; **E.** Head from posterior view; **F.** Mesosoma from posterior view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl9>

Supplementary material 10

Digital reconstruction of male *Aphanogmus harpagodalis* sp. nov. (non-type: PSUC_FEM 10022950) based on synchrotron micro-CT

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Habitus in lateral view; **B.** Mesosoma in lateral view; **C.** Mesosoma in dorsal view; **D.** Head in frontal view; **E.** Head from posterior view; **F.** Mesosoma from posterior view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl10>

Supplementary material 11

CLSM micrograph of male genitalia of *Aphanogmus karlazani* sp. nov. (holotype: ZFMK-HYM-00042565) in ventral view

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl11>

Supplementary material 12

CLSM micrographs of male genitalia of *Aphanogmus kintrishi* sp. nov. (holotype: ZFMK-HYM-00042502)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl12>

Supplementary material I3

CLSM micrographs of male genitalia of *Aphanogmus tkbeliharpus* sp. nov. (holotype: ZFMK-HYM-00042459)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl13>

Supplementary material I4

CLSM micrographs of male genitalia of *Aphanogmus trigoharpus* sp. nov. (holotype: ZFMK-HYM-00042511)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl14>

Supplementary material 15

CLSM micrographs of male genitalia of *Aphanogmus vashlovani* sp. nov. (holo-type: ZFMK-HYM-00042529)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl15>

Supplementary material 16

CLSM micrographs of male genitalia of *Aphanogmus ventricoharpus* sp. nov. (non-type: PSUC_FEM 10022777)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Lateral view; **C.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl16>

Supplementary material 17

Digital reconstruction of male *Aphanogmus ventricoharpus* sp. nov. (non-type: PSUC_FEM 10022748) based on synchrotron micro-CT

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Habitus in lateral view; **B.** Mesosoma in lateral view; **C.** Mesosoma in dorsal view; **D.** Head in frontal view; **E.** Head from posterior view; **F.** Mesosoma from posterior view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl17>

Supplementary material 18

CLSM micrographs of male genitalia of *Aphanogmus zefranki* sp. nov. (holotype: ZFMK-HYM-00042448)

Authors: Tobias Salden, István Mikó, Thomas van de Kamp

Data type: tiff

Explanation note: **A.** Ventral view; **B.** Dorsal view.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.99.178410.suppl18>