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Surprising morphological diversity in ceraphronid wasps revealed by a distinctive new species of *Aphanogmus* (Hymenoptera: Ceraphronoidea)

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Abstract. Within the well-studied Palearctic entomofauna, it is often assumed that the discovery of new species is limited to resolving cryptic species complexes within dark taxa. Herein, we describe a highly distinctive species of *Aphanogmus* Thomson, 1858 (Hymenoptera: Ceraphronidae) from Germany and provide a COI barcoding sequence for the new species. We present a 3D reconstruction of the holotype based on micro-CT to serve as a cybertype. The females of *Aphanogmus kretschmanni* Moser sp. nov. are diagnosed by two rows of prominent spines on the ventral edge of the 7th metasomal sternite, a character set that has not previously been found in Hymenoptera. We analyse the functional morphology of the ovipositor mechanism and discuss hypotheses regarding the functional implications of the unique

modification of the 7th metasomal sternite. Possible host associations are reviewed and the taxonomic placement of the new species is discussed.

Keywords. Dark taxa, functional morphology, DNA barcoding, micro-CT scanning, insect decline.

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Introduction

The German entomofauna is generally considered relatively well-studied, especially within nature conservation areas (Dathe *et al.* 2001; Klausnitzer 2005; Gottschalk 2019). Despite this fact, there are still estimated to be thousands of species on which no basic taxonomic, biological and biogeographical information or taxonomic expertise is available. Being vastly understudied and taxonomically inaccessible, dark taxa such as many Diptera and parasitoid Hymenoptera, have categorically been neglected in biodiversity research and conservation efforts (Shaw & Hochberg 2001; IUCN 2021). In times of severe decline of insect biomass (Hallmann *et al.* 2017), it is of paramount importance to research dark taxa more closely in order to establish effective conservation strategies that will preserve biodiversity and consequently also the morphological diversity of these groups. With the recent advent of integrative taxonomy, classical morphological methods have progressively been complemented by digital 3D imaging and molecular (i.e., genetic and karyological), ecological, physiological, biogeographical, biochemical, and behavioural data (Gokhman 2018). Integrative taxonomy "aims to delimit the units of life's diversity from multiple and complementary perspectives" (Dayrat 2005) and therefore holds the potential to make taxa that are notoriously difficult to handle taxonomically accessible to science.

The introduction of DNA barcoding added a new component to taxonomy that potentially allows for robust and time-efficient species delimitation (Hebert *et al.* 2003). However, in recent years the growing output of DNA barcoding has led to a significant increase in the number of published Barcode Index Numbers (BINs) with no species names or taxonomic information attached (Page 2016). These dark taxa lack formal species names either because they cannot be identified on a species level or because they have remained entirely undescribed as of yet (Page 2016). DNA barcoding has proven particularly useful for species delimitation in cryptic species complexes with two or more distinct species whose external morphology is indistinguishable. Consequently, DNA barcoding has the potential to contribute to providing more realistic estimates on the true species diversity within a given geographic region (e.g., Hebert *et al.* 2004, 2016; Geiger *et al.* 2016).

Despite being semantically similar, 'dark taxa' and 'cryptic species' constitute two different concepts. 'Dark taxa' are a taxonomic phenomenon in which taxa cannot be identified to any known species either due to a lack of means for identification or because they are not formally described. This phenomenon can manifest itself through biological hurdles, such as a resistance to DNA barcoding, or unconventional morphological characters being necessary for identification; as well as historically, with literature being scarce and disjointed making entry into research on the group steep. This is in contrast to 'cryptic species', which is a biological concept. It is defined as morphologically indistinguishable taxa that are or have been classified as a single species (Bickford *et al.* 2007). Unresolved cryptic species complexes can aggravate the study of dark taxa. However, it is a common misconception that the challenge of dark taxa taxonomy lies solely in unravelling the multitude of cryptic species complexes found within these taxa. Whilst dark taxa are usually vastly understudied, cryptic species are found in all major biogeographical regions and taxonomic groups and have received considerable attention (Pfenninger & Schwenk 2007).

Herein, we provide an example of a dark taxon that is not cryptic at all and use an integrative taxonomic approach to describe it as a distinctive new species of Ceraphronidae Haliday, 1833.

Ceraphronidae is a relatively small, yet widespread family of parasitoid and hyperparasitoid wasps that is superficially monotonous (Mikó *et al.* 2013) and contains approximately 110 Palearctic species in six genera (Johnson & Musetti 2004). Yet, only ten species are included in the most recent German checklist (Dessart 2001) and one additional species was recently described from Lower Saxony (Ulmer *et al.* 2018). These numbers along with a lack of solid ecological information on the majority of described species attest to the need for basic research on this superfamily of parasitoid wasps.

The new species belongs to the genus *Aphanogmus* Thomson, 1858 and was sampled with Malaise traps as part of ongoing biodiversity monitoring projects in Baden-Wuerttemberg in south-western Germany. Females of this species are characterised by two prominent rows of spines along the 7th metasomal sternite, a feature that has not been observed in any other Hymenoptera before. A detailed morphological description is provided along with sequence data of the COI barcode. We also present a 3D cybertype based on synchrotron micro-CT data and discuss the functional implications of the diagnostic spines on the metasomal sternite with regard to ovipositor mechanics.

Material and methods

Species description and terminology

The holotype is deposited in the entomological collection of the State Museum of Natural History Stuttgart (SMNS). The morphological terminology in this study used mainly for the description in natural language as well as the machine-readable description in Supp. file 1 follows that of the Hymenoptera anatomy ontology (Yoder *et al.* 2010) and Mikó & Deans (2009) with some additional terms on ovipositor morphology from Ernst *et al.* (2013) and the Waterston's evaporatorium from Ulmer *et al.* (2021).

Imaging

Observations and descriptions were compiled using a Leica M205C stereo microscope with a 7.8 to 160x magnification. For habitus (Figs 1, 2B, D) and wing interference pattern (WIP) imaging (Fig. 2A), an MZ 16 APO Leica R microscope with an attached DXM 1200 Leica R camera was used with subsequent stacking of images in Helicon focus ver. 7.6.1 (Helicon Soft Ltd, Kharkov, Ukraine). Stacking followed the pyramid approach (method C) with a smoothing parameter setting of 4 to reduce image artefacts. Recording of WIP followed the protocol of Shevtsova *et al.* (2011) with wings taken from specimens in 99.6% pure ethanol. The wings were air-dried on the slide and photographed after white-balancing against a white background with the same exposure time and saturation to ensure comparability. Detailed images were taken with a Keyence VHX 5000 digital microscope. The same system was used for measuring key characters of 27 specimens to account for size variation. Image stacking artefacts were removed, contrast and tonality were adjusted and figures were assembled in Adobe Photoshop Elements 2020 (Adobe Systems Software Ireland Ltd, Dublin, Ireland).

CLSM imaging

Dissected specimens were placed in a drop of anhydrous glycerol between two #1.5 coverslips prior to imaging with a Nikon A1R-HD Confocal Laser Scanning Microscope (CLSM) at the Instrumentation Center of the University of New Hampshire. Two excitation wavelengths were used in the analysis (487 and 560 nm), and two emission ranges (500–540 and 570–645 nm). Volume rendered images were created with FIJI (Schindelin *et al.* 2012; Image/Stack/Zproject) using green and red lookup tables to match coloration with their respective fluorescence spectra (green for 500–540 and red for 570–645 nm).

Synchrotron X-ray microtomography

Synchrotron micro-CT was performed at the imaging cluster of the KIT light source at Karlsruhe Institute of Technology (KIT), Germany. We used a parallel polychromatic X-ray beam produced by a 1.5 T bending magnet that was spectrally filtered by 0.5 mm aluminium. A fast indirect detector system consisting of a 12 µm LSO:Tb scintillator (Cecilia *et al.* 2011) was employed along with a diffraction-limited optical microscope (Optique Peter) coupled with a 12 bit pco.dimax high speed camera with 2016 × 2016 pixels. Scans were done by taking 3000 projections at 70 fps and an optical magnification of 10x , resulting in an effective pixel size of 1.22 µm. Tomographic reconstruction was performed by the UFO framework (Vogelgesang *et al.* 2012). The tomographic volume was converted to 8 bit and cropped to the region of interest. In Amira 6.5 (Thermo Fisher Scientific, Waltham, MA, USA) all sclerites were pre-segmented in the software's segmentation editor. The labels served as input for automatic segmentation, which was performed using the online platform Biomedisa (biomedisa.org) (Lösel *et al.* 2020). Segmentation results were again imported into Amira 6.5 and minor errors were corrected. The final labels of all sclerites were converted into polygon meshes, exported as OBJ files and reassembled and smoothed in CINEMA 4D R20 (Fig. 3).

Exact measurements in Supp. file 2 are based on the 3D model of the holotype and were taken in Amira 6.5 with the 3D length measurement option from the toolbar. The length and width of antennal segments are given as the arithmetic mean of the individual measurements of each segment of the left and right antenna.

For DNA barcoding, the protocol developed by Vasilița *et al.* (2022) was used. All sequences are deposited at Barcode of Life Data (BOLD) Systems (Ratnasingham & Hebert 2007) (DOI: https://doi.org/10.5883/DS-CERAPKR), as well as in GenBank, the individual IDs for which are given in the type material section in the results.

Abbreviations

1vf = first valvifer
1vv = first valvulae
ang = anterior angle of the first valvifer
asf = anterior section of dorsal flange of the second valvifer
at cx = acrotergal calyx
bl = basal line of the second valvifer
bulb = bulbous anterior area of the dorsal valve
F1–F8 = flagellar segments 1–8
iva = intervalvifer articulation
LOL = lateral ocellar line
MPMM = metanoto-propodeo-metapecto-mesopectal complex
OOL = ocular ocellar line
POL = posterior ocellar line
res = venom gland reservoir of the second valvifer
S7 = 7th metasomal sternite
T5 = 5th metasomal tergite
T6 = 6th metasomal tergite
ta = tergal apodeme
tva = tergo-valvifer articulation
WIP = wing interference patterns

Institutional abbreviations

SMNS = State Museum of Natural History Stuttgart, Germany
UNHP = University of New Hampshire Collection of Insects and Other Arthropods, USA
ZFMK = Zoological Research Museum Alexander Koenig, Leibniz Institute for the Analysis of Biodiversity Change, Germany
ZSM = Bavarian State Collection of Zoology, Germany

Results

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Ceraphronidae Haliday, 1833
Genus *Aphanogmus* Thomson, 1858

Aphanogmus kretschmanni Moser sp. nov.
urn:lsid:zoobank.org:act:8848B3FB-DC1D-465C-9E67-284EE86BB4CA
Figs 1–3

Diagnosis (female)

The female has seven conspicuous spines in two rows along the ventral edge of the 7th metasomal sternite, with two spines next to each other in the 1st and 5th position.

Etymology

The specific name is a patronym for Winfried Kretschmann, the current Minister-President of the state of Baden-Württemberg (Germany), to honour his scientific curiosity and commitment to preserving biodiversity in his political environment.

Type material

Holotype

GERMANY • ♀ (the holotype is missing the right fore- and mid-tarsus); Baden-Württemberg, Tübingen, Hirschau, Riedweingärten, plot number 4400; 48.504817° N, 8.985067° E; 375 m a.s.l.; 29 Aug.–12 Sep. 2014; Kothe T., Engelhardt M., Bartsch D. leg.; Malaise trap; SMNS SMNS_Hym_Cer_000227.

The 3D model of the holotype, which serves as a cybertype, as well as the original CT image series are available online through MorphoSource (CT image series: https://doi.org/10.17602/M2/M449721; full habitus mesh: https://doi.org/10.17602/M2/M449724; post-edited full habitus mesh https://doi.org/10.17602/M2/M449727).

Paratypes

GERMANY • 1 ♀ (in immaculate condition); Baden-Württemberg, Enzkreis, Königsbach-Stein, NSG 2.119 Beim Steiner Mittelberg; 48.970371° N, 8.659000° E; 181 m a.s.l.; 22 May–5 Jun. 2019; Entomologischer Verein Krefeld e.V. 1905 leg.; Malaise trap; SMNS SMNS_Hym_Hym_027509 • 1 ♀ (in immaculate condition); Baden-Württemberg, Tübingen, Hirschau, Oberes Tal, plot number 4244; 48.505033° N, 8.993467° E; 368 m a.s.l.; 17–31 Jul. 2014; Kothe T., Engelhardt M., Bartsch D. leg.; Malaise trap; ZFMK SMNS_Hym_Cer_000647 • 1 ♀ (in immaculate condition); Baden-Württemberg, Tübingen, Hirschau, Oberes Tal, plot number 4244; 48.505033° N, 8.993467° E; 368 m a.s.l.; 29 Aug.–12 Sep. 2014; Kothe T., Engelhardt M., Bartsch D. leg.; Malaise trap; ZSM SMNS_Hym_Cer_000648.

Additional material examined

GERMANY • 1 ♀; same collection data as for holotype; 6–20 Jun. 2014; SMNS SMNS_Hym_Cer_000408 • 1 ♀; Baden-Württemberg, Tübingen, Hirschau, Oberes Tal, plot number 4244; 48.505033° N, 8.993467° E; 368 m a.s.l.; 17–31 Jul. 2014; Kothe T., Engelhardt M., Bartsch D. leg.; Malaise trap; SMNS SMNS_Hym_Cer_000425 • 1 ♀; same collection data as for preceding; BOLD Sample ID: SMNS_1179430; GenBank: OP722468; SMNS SMNS_Hym_Cer_000467 • 1 ♀; same collection data as for preceding; BOLD Sample ID: SMNS_1179432; GenBank: OP722465; SMNS SMNS_Hym_Cer_000468 • 1 ♀; same collection data as for preceding; BOLD Sample ID: SMNS_1179434, GenBank: OP722466; SMNS SMNS_Hym_Cer_000470 • 1 ♀; same collection data as for preceding; BOLD Sample ID: SMNS_1179433; GenBank: OP722464; UNHP SMNS_Hym_Cer_000469 • 1 ♀; same collection data as for preceding; UNHP SMNS_Hym_Cer_000488 • 2 ♀; same collection data as for preceding; 29 Aug.–12 Sep. 2014; SMNS SMNS_Hym_Cer_000440 • 1 ♀; same collection data as for preceding; SMNS SMNS_Hym_Cer_000464 • 1 ♀; same collection data as for preceding; BOLD Sample ID: SMNS_1179428; GenBank: OP722469; SMNS SMNS_Hym_Cer_000465 • 1 ♀; same collection data as for preceding; BOLD Sample ID: SMNS_1179429; GenBank: OP722462; SMNS SMNS_Hym_Cer_000466 • 1 ♀; same collection data as for preceding; 12–26 Sep. 2014; BOLD Sample ID: SMNS_1177257; GenBank: OP722467; SMNS SMNS_Hym_Cer_000445 • 1 ♀; same collection data as for preceding; SMNS SMNS_Hym_Cer_000446 • 1 ♀; same collection data as for preceding; 26 Sep.–9 Oct. 2014; BOLD Sample ID: SMNS_1177266; GenBank: OP722463; SMNS SMNS_Hym_Cer_000451 • 1 ♀; Baden-Württemberg, Karlsruhe, Östringen, NSG 2.217 Apfelberg, plot number 9836; 49.167541° N, 8.790300° E; 181 m a.s.l.; 16–30 Jul. 2019; Entomologischer Verein Krefeld e.V. 1905 leg.; Malaise trap; SMNS SMNS_Hym_Cer_000543 • 1 ♀; same collection data as for preceding; 27 Aug.–10 Sep. 2019; SMNS SMNS_Hym_Hym_027357 • 1 ♀; same collection data as for preceding; 10–24 Sep. 2019; SMNS SMNS_Hym_Cer_000571 • 1 ♀; same collection data as for preceding; 24 Sep.–8 Oct. 2019; SMNS SMNS_Hym_Cer_000544 • 2 ♀♀; same collection data as for preceding; 8–22 Oct. 2019; SMNS SMNS_Hym_Hym_027358. • 1 ♀; same collection data as for preceding; SMNS SMNS_Hym_Cer_000649 • 4 ♀; Baden-Württemberg, Enzkreis, Königsbach-Stein, NSG 2.119 Beim Steiner Mittelberg; 48.970371° N, 8.659000° E; 181 m a.s.l.; 3–17 Jul. 2019; Entomologischer Verein Krefeld e.V. 1905 leg.; Malaise trap; SMNS SMNS_Hym_Hym_027558. • 2 ♀♀; same collection data as for preceding; 17–31 Jul. 2019; SMNS SMNS_Hym_Hym_027726. • 1 ♀; same collection data as for preceding; 28 Aug.–11 Sep. 2019; SMNS SMNS_Hym_Hym_027685.

For detailed description of localities, habitats and further material see Supp. file 3.

Description

Colouration. Head dark brown, almost black. Mesosoma dorsally concolourous with head, ventrally dark chestnut brown. Metasoma lighter brown. Scape, distal end of pedicel and tibiae light amber brown, tarsi pale ochre, flagellar segments brown, concolourous with femora, distal flagellar segments slightly darker. Wings entirely hyaline. Wing venation light brown, marginal vein darker, light brown stigmal vein with dark margin.

Measurements. Total body length is 0.7–1.1 mm (holotype: 1 mm).

Head. Entire head with imbricate sculpture. Face, frons and eyes covered in short whitish pubescence. Oval in frontal view, 1.1–1.4 (1.3) times as broad as high. Head hypognathous. Truncated in lateral view with preoccipital carina delimiting sharply the deeply concave preoccipital lunula. Preoccipital carina medially interrupted by preoccipital furrow, which fades anteriorly ending inside the ocellar triangle posterior to the median ocellus. Preoccipital furrow as wide anteriorly as posteriorly and crenulate along its entire length. Crenulate occipital carina with continuous median flange. Eyes large, 0.6–0.7 (0.7) times as high as head. Ocellar triangle obtuse, POL:LOL: 1.25; OOL:POL: 0.8. Postocellar carina absent.

Preocellar pit present. Anterior ocellar fovea extended ventrally into short facial sulcus reaching dorsal margin of frontal depression. Antennal scrobe present, ventrally delimited by intertorular carina. Clypeus convex and rectangular (1.5 times as broad as high). Supraclypeal depression, subtorular carina, carina delimiting antennal scrobe, frontal ledge and subantennal groove absent. Mandibles with two distinct teeth, without mandibular lancea. Mandible slender, length along ventral edge 3.3 times as long as height of mandible measured in the middle of its length. Maxillae with four palpomeres.

Fig. 1. *Aphanogmus kretschmanni* Moser sp. nov.; holotype, ♀ (SMNS_Hym_Cer_000227). **a**. Habitus, lateral view. **b**. Habitus, dorsal view. Scale bars = 200 µm.

Antennae. Antennae with eight flagellar segments. Scape distally with flagellar scrobe. Scape 2.1–3.1 (2.5) times as long as pedicel. Pedicel 1.2 times as long as F1. Scape as long as pedicel, F1 and F2 combined. F1 significantly longer than any segments F2–F7 but shorter than F8; F2 to F7 of similar length. F8 significantly longer than other flagellar segments, longer than F6 and F7 combined. Maximum width of scape 1.6 times maximum width of pedicel. Width of flagellar segments F1–F8 increasing steadily, F8 almost as broad as scape. F1 cylindrical, twice as long as broad; F2 subquadrate, 1.3 times longer than broad; F3–F7 subquadrate; F8 cylindrical, twice as long as broad.

Mesosoma. Mesoscutum, mesoscutellar-axillar complex, pronotum and anterior mesopleural area with imbricate sculpture of flat scutes, lower half of mesometapleuron smooth, upper half with roughly strigate sculpture arising anteriorly from the anterior mesopleural sulcus and the mesometapleural sulcus. Mesoscutum and mesoscutellum with numerous short pale setae, axillular carina hemmed with one row of white axillular setae. Mesosoma laterally compressed, 1.2–1.8 (1.6) times as long as broad, 1.4–1.6 (1.5) times as high as broad. Mesoscutum broadest part of mesosoma, maximum mesoscutal width 2.1 times as wide as mesoscutellum. Pronotum triangular in lateral view with transverse pronotal sulcus extending halfway along pronotum. Ventral pronotal pit present. Anterior portion of mesoscutum steeply sloping in lateral view, anteriorly articulating with pronotum at an acute angle. Median mesoscutal sulcus complete

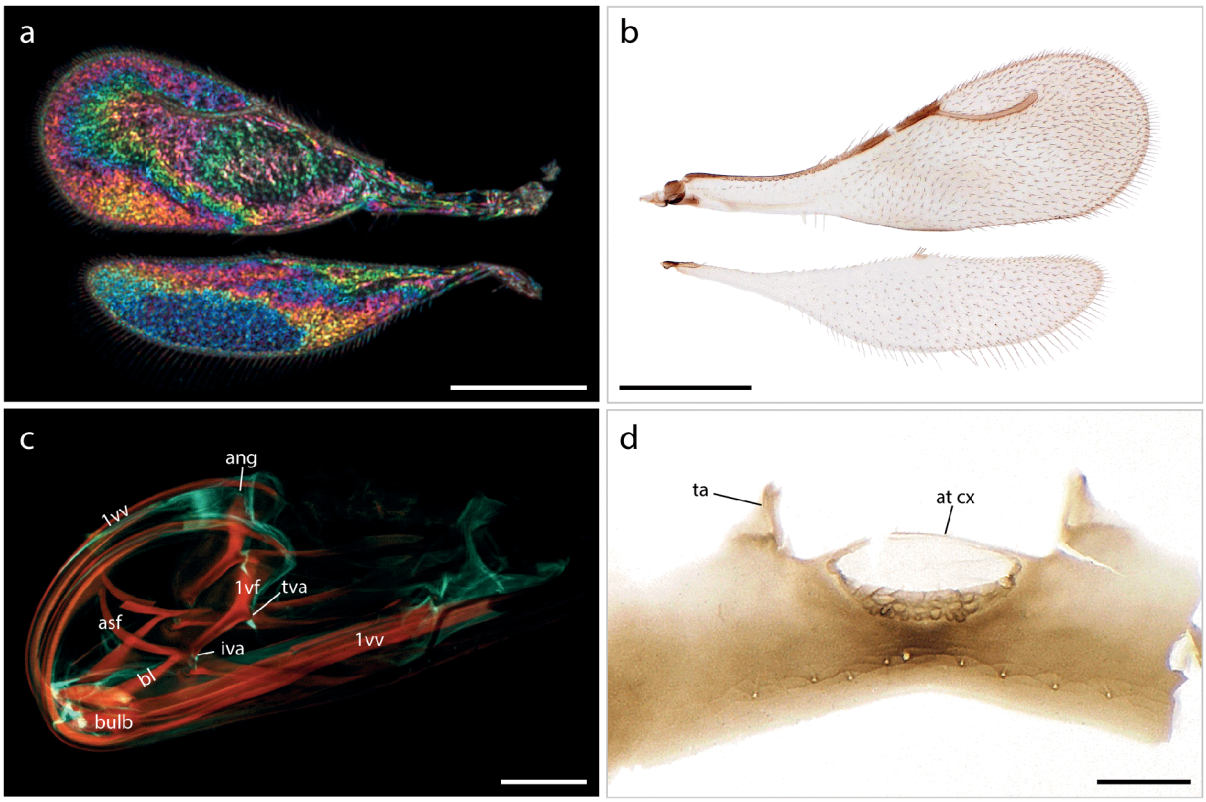

Fig. 2. Detailed images of *A. kretschmanni* Moser sp. nov. (a, d = SMNS_Hym_Cer_000466; b = SMNS_Hym_Cer_000465; c = SMNS_Hym_Cer_000469). **a**. Wing interference patterns of left fore- and hindwing. **b**. Fore- and hindwing. **c**. CLSM image of ovipositor with sclerites in red. Abbreviations: 1vf = 1st valvifer; 1vv = 1st valvulae; ang = anterior angle of the 1st valvifer; asf = anterior section of the dorsal flange of the second valvifer; bl = basal line of the second valvifer; bulb = bulbous anterior area of the dorsal valve; iva = intervalvifer articulation; tva = tergo-valvifer articulation. **d**. Waterston's evaporatorium on T6. Abbreviations: at cx = acrotergal calyx; ta = tergal apodeme. Scale bars: a–b = 200 µm; c–d = 50 µm.

and posteriorly reaching transscutal articulation, notauli absent. Mesoscutum posterolaterally delimited by pronounced parascutal carina. Axillar carina pronounced anteriorly but fading posteriorly. Interaxillar sulcus present, extending medially into scutoscutellar sulcus. Axillae distinct in dorsal view. Scutoscutellar sulcus broad and foveate, angled medially and reaching laterally the ventral margin of mesoscutellum. Circumscutellar carina sharply pronounced, lined with numerous axillular setae. Axillula very steep, almost vertical in relation to scutellar disc. Frenal area very short and separated from mesoscutellum by a steeply plunging ridge. Metanotal-propodeal sulcus foveate. Anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex simple and straight, posteriorly extending the mesonotum. Metanotal-propodeal sulcus distinctly scrobiculate. Mesometapleuron roughly triangular, higher than long in lateral view. Posterior edge of mesometapleuron extends into blunt, down-curved spine at fusion point of metapleural carina and ventral metapleural carina. Dorsal mesometapleural carina along its length slightly undulate, interrupted by propodeal spiracle, posteriorly extending into posterior propodeal projection. Ventral metapleural carina distinctly raised, continuing ventrally into raised ventral mesopleural carina

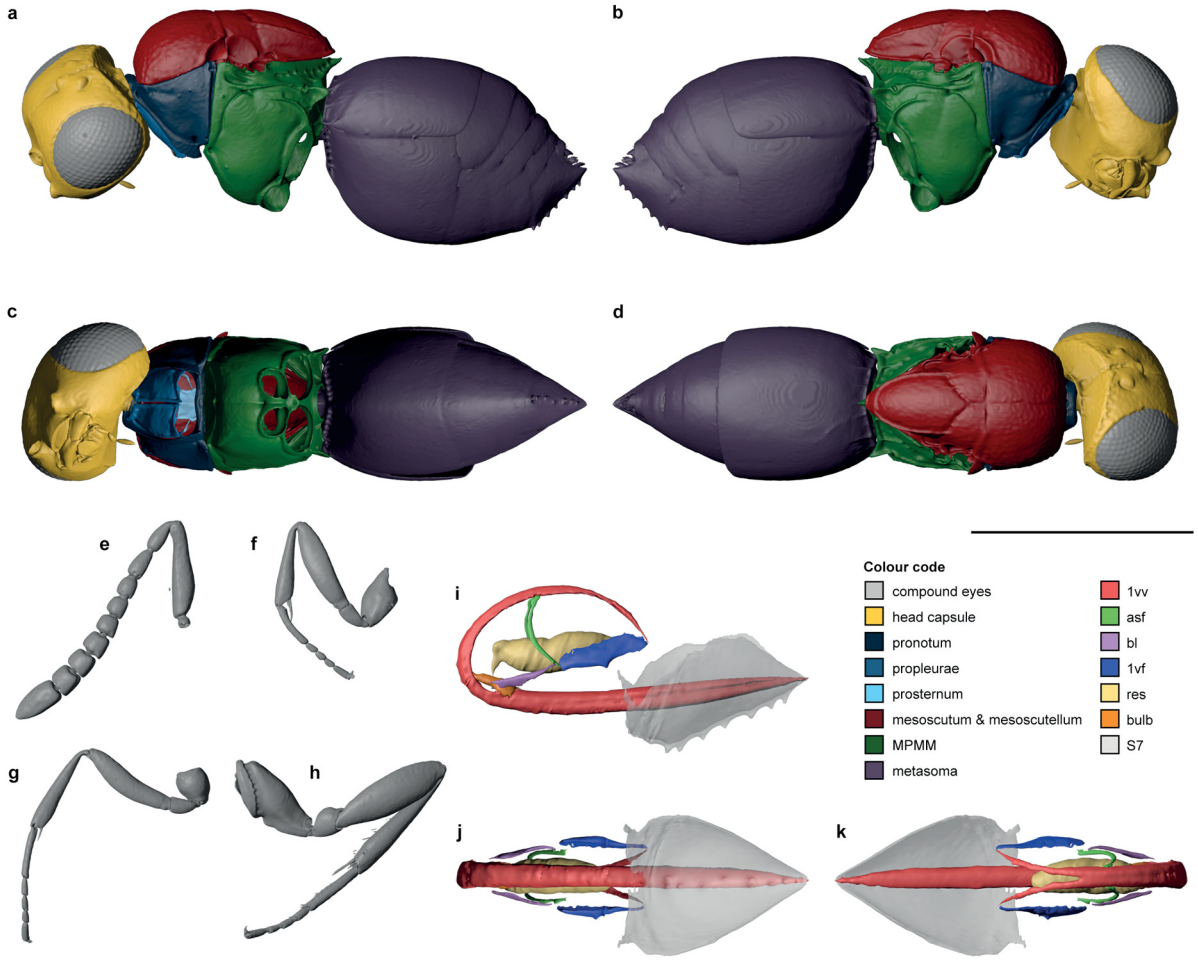

Fig. 3. Digital reconstruction of *A. kretschmanni* Moser sp. nov. based on synchrotron micro-CT; holotype, ♀ (SMNS_Hym_Cer_000227). **a–d**. Habitus in left (a), right (b), ventral (c) and dorsal (d) aspect. **e**. Left antenna. **f**. Left foreleg. **g**. Left midleg. **h**. Left hindleg. **i–k**. Ovipositor in left (i), ventral (j) and dorsal (k) aspect. Abbreviations: 1vf = first valvifer; 1vv = first valvulae; asf = anterior section of dorsal flange of the second valvifer; bl = basal line of the second valvifer; bulb = bulbous anterior area of the dorsal valve; MPMM = metanoto-propodeo-metapecto-mesopectal complex; res = venom gland reservoir of the second valvifer; S7 = 7th metasomal sternite. Scale bars: a–h = 0.5 mm; i–k = 250 µm.

and dorsally into metapleural carina. Anterior mesopleural sulcus distinct, separating anterior mesopleural area from rest of mesopleuron. Mesometapleural sulcus extending halfway across mesometapleuron, fading posteriorly. Lateral propodeal carina distinct, crossing propodeal spiracle. Posterior propodeal projections pronounced and rounded.

Legs. Proximal articulation of metacoxa distinctly foveate. Medial side of hind tibia with dense bristles in distal half, first tarsal segment with two rows of bristles medially. Pro-, meso and metatrochanter of similar length. Femur size increasing from pro- to metafemur, mesofemur 1.1 times, metafemur 1.3 times as long as profemur. Metatibia 1.14 times as long as mesotibia and 1.47 times as long as protibia. 5th tarsomere of hindleg 1.14 times as long as that of midleg and 1.29 times as long as that of foreleg. Tarsi of similar widths. Front and mid tarsal claws are of comparable size, hind tarsal claws slightly larger.

Wings. Forewing very long, 0.73–0.96 mm (0.81 mm), extending distinctly beyond metasoma. Forewing broad, 1.5 times as long as broad. Marginal setae at an acute angle (34.2°) to anterior wing margin. Posterior margin of forewing remarkably straight at level of stigmal vein, slightly sclerotised and without setation proximal to straight part of the wing margin. Marginal vein with triangular elements (sensu Mikó *et al.* 2018). Translucent break between marginal vein and linear stigma. Stigmal vein uniformly bent, slightly increasing in width posteriorly. Anterio-proximal part of marginal vein lined with jutting setae. Hindwing slender, 4.1 times as long as broad. Posterior margin of hind wing lined with setae, setae 0.23 times as long as maximum width of hind wing, these setae significantly longer than setae on forewing. No venation, wing slightly sclerotised below hamuli. Three hamuli present. WIP of forewing indicates highest thickness of wing membrane below distal portion of the marginal vein posterior to the costal notch and lowest thickness on distal posterior wing margin. WIP of hindwing with large elliptical area of low membrane thickness along the setose distal half of the posterior wing margin.

Metasoma. Syntergum margined by transverse carina anteriorly. Syntergum with nine longitudinal striae, present only anteriorly and distributed with subequal distance over width of metasoma. Anterolateral margin of synsternum with distinct foveate carina that converges ventrally in a keel. Ventral edge of 7th metasomal sternite with seven conspicuous spines in two rows, with two spines next to each other in the most ventral and 5th position. Syntergum broadest tergite and slightly longer than all other tergites combined.

Waterston's evaporatorium. On metasomal T6 oblong, acrotergal calyx present, distal crenulate carina on T6 present on caudal setal row, submedian patches absent, campaniform sensillae absent, tergal apodeme with sclerotised ridge along inner margin that also transverses the base of the apodeme, tergal apodemes parallel, at most slightly diverging distally, evaporatorium without basomedial constriction.

Ovipositor. With a large distance between the anterior angle of the first valvifer (ang) and the intervalvifer articulation (iva). First valvifer angled at the tergo-valvifer articulation (tva), therefore appearing convex. First valvifer not subdivided. Tva situated approximately in the middle of the posterior margin of the first valvifer (1vf). Basal line of the second valvifer sharply defined. Dorsal projection of second valvifer shorter than length of anterior area of second valvifer. Anterior and posterior section of the dorsal flange of the second valvifer sharply defined. Venom gland reservoir present, surrounded by second valvifer. First valvula tapers distally in lateral view. Anterior area of the second valvifer more than 2.0 times as high as bulb in lateral view. Apodemes of S7 without apparent modifications.

Variation

The brown colouration of the mesosoma and the anterior part of the metasoma including the synsternum and syntergum of SMNS_Hym_Cer_000446 is considerably brighter than in the holotype and the

anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex is almost clear in this specimen. COI barcodes confirmed that this specimen belongs to *A. kretschmanni* sp. nov.

Discussion

Taxonomic placement of *Aphanogmus kretschmanni* Moser sp. nov.

In the Palearctic, the family Ceraphronidae contains 112 species in 6 genera. *Aphanogmus* Thomson, 1858 is the most species-rich genus with 52 described species (Johnson & Musetti 2004; Buhl *et al.* 2010; Matsuo 2016), whilst four other genera comprise no more than six species. *Aphanogmus* is characterised mainly by a laterally compressed mesosoma, which is taller than broad (Figs 1, 3A–D) as well as trapezoidal flagellar segments on the male antennae with sensillae at least as long as the width of the flagellar segments. Currently, *Aphanogmus* is separated into three species groups (Evans *et al.* 2005). Morphologically, *A. kretschmanni* sp. nov. falls into the *fumipennis* species group based on a complete mesoscutal median sulcus and the presence of a gastral basal carina. In Hellén's key, the new species keys to *A. fumipennis* Thomson, 1858 (Hellén 1966). However, *A. kretschmanni* is easily distinguishable from *A. fumipennis* by the distinct spines on S7 as well as the lack of prominent tufts of dense hairs along the outer margin of the hind coxae that are diagnostic for *A. fumipennis*.

Further, this new species resembles several species within the *Aphanogmus hakonensis* complex, i.e., *A. amoratus* Dessart & Alekseev, 1982; *A. captiosus* Poasszek & Dessart, 1996, *A. goniozi* Dessart, 1988; *A. hakonensis* Ashmead, 1904; *A. jarvensis* (Girault, 1917); *A. manilae* (Ashmead, 1904) and *A. thylax* Polaszek & Dessart, 1996. Shared morphological characters are found mainly on the mesosoma, particularly the sharp circumscutellar carina, the carinate metanotal-propodeal sulcus, the prominent anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex as well as the paired posterior propodeal projections and the lateral striations on the mesopleuron. All species within the *hakonensis* complex have an Indo-Australian distribution with a few occurrences in the westernmost Palearctic. They are hyperparasitoids of Hymenoptera that parasitize Lepidoptera Linnaeus, 1758 and can only be determined to species level through male genitalia (Polaszek & Dessart 1996).

Recently, the Waterston's evaporatorium on the 6th metasomal tergite was discovered to be a taxonomically significant character complex in Ceraphronidae (Ulmer *et al.* 2021). Major differences in the structure of the Waterston's evaporatoria of *Aphanogmus* and *Ceraphron* Jurine, 1807 were found and are supported by a cladistic analysis, which returned a monophyletic *Aphanogmus* group and a paraphyletic *Ceraphron* group (Ulmer *et al.* 2021). Apart from *Aphanogmus* s. str., the *Aphanogmus* group includes the smaller genera *Synarsis* Foerster, 1878, *Gnathoceraphron* Dessart & Bin, 1981 and *Elysoceraphron* Szelényi, 1936 based on striking similarities of the Waterston's evaporatoria of these taxa. The Waterston's evaporatorium of the newly described *A. kretschmanni* sp. nov. lacks campaniform sensilla on T5 and T6 (Fig. 2D), a character that is considered an autapomorphy of *Elysoceraphron* by Ulmer *et al.* (2021). However, there are several differences in external morphology that contradict the placement of the newly described species into *Elysoceraphron*: (1) the mesoscutellum of *A. kretschmanni* is rounded posteriorly rather than subrectangular, which is the diagnostic character for *Elysoceraphron*; (2) the head of *A. kretschmanni* is significantly more transverse, a character shared by most species of *Aphanogmus*, than that of the Palearctic *E. hungaricus* Szelényi, 1936 or of the Oriental *E. aadi* Bijoy & Rajmohana, 2021 with the interocular distance being larger than the eye width (*A. kretschmanni*: 158:146 µm; *E. hungaricus*: 152:228 µm; *E. aadi*: 146:222 µm); (3) the anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex is straight in *A. kretschmanni* whereas it is upcurved in *Elysoceraphron*.

The genus *Elysoceraphron* was first described based on two female specimens of *Elysoceraphron hungaricus* Szelényi, 1936 collected in Hungary (Szelényi 1936). The male was described two decades later from Czechoslovakia (Masner 1957). Since then, the genus has not received much attention. It

appears only briefly in a report adding findings from Sweden and Siberia (Dessart & Alekseev 1980), a few remarks on the taxonomic status of the genus (Masner 1957; Dessart 1975), a short mention in two catalogues (Muesebeck & Walkley 1956; Johnson & Musetti 2004) as well as in keys (Dessart 1962; Alekseev 1978a, 1978b, 1995; Dessart & Cancemi 1987). Recently, a second species, *Elysoceraphron aadi*, was described from India (Bijoy & Rajmohana 2021).

There has been considerable disagreement as to the validity of the genus *Elysoceraphron*. When the genus was established, it was hypothesised that it is closely related to *Aphanogmus* and to some extent also to *Ceraphron* (Masner 1957; Dessart & Alekseev 1980). Masner (1957) bases the validity of *Elysoceraphron* mainly on the unique subrectangular form of the mesoscutellum (Szelényi 1936). In contrast, Dessart (1975) considers *Elysoceraphron* along with a few other genera of Ceraphronidae, most of which are monotypic, as incertae sedis and argues that it is first and foremost for practical reasons that *Elysoceraphron* is classified as a discrete genus. This line of argumentation is reinforced by Dessart & Alekseev (1980) who conclude that *E. hungaricus* is most likely an aberrant species of *Aphanogmus*. One of the most recent keys to the genera of Ceraphronoidea lists *Elysoceraphron* within the satellite group of *Aphanogmus* (Dessart & Cancemi 1987). However, Dessart (1975) explicitly refrained from synonymising *Elysoceraphron* with *Aphanogmus* for practical rather than taxonomic reasons.

The limited number of distinguishing characters in external morphology leads us to agree with previous authors (Dessart 1975; Dessart & Alekseev 1980) who question the validity of *Elysoceraphron*. The fact that *A. kretschmanni* sp. nov. and *Elysoceraphron* share characters of the Waterston's evaporatorium (lack of campaniform sensilla on T5 and T6) further supports this. Based on a subrectangular mesoscutellum, the shape of the head and the straight shape of the anteromedian projection of the metanoto-propodeo-metapecto-mesopectal complex we place the newly described species into *Aphanogmus.*

Host biology and ovipositor mechanisms

From the literature that is available on *Aphanogmus*, species seem to parasitize one of two host types: weakly concealed hosts, which are often quite active, or well-concealed relatively inactive pupae of parasitoid Hymenoptera (Dessart 1995). Free-living predatory larvae of gall midges (Cecidomyiidae Newman, 1835) fall into the category of weakly-concealed hosts and have been reported to be parasitised by various species of *Aphanogmus* (e.g., Bakke 1955; Laborius 1972; Matsuo *et al.* 2016). Cecidomyiids often predate mites (Acari Leach, 1817) or scale insects (Coccidae Fallén, 1814) and are therefore relevant pest control agents in agriculture (Dessart 1963). Hosts of *Aphanogmus* that fall into the second category (well-concealed and inactive) include various hymenopteran parasitoids such as Bethylidae Forster, 1856 (e.g., Buffington & Polaszek 2009), Ichneumonidae Latreille, 1802 (e.g., Yefremova *et al.* 2021), Braconidae Latreille, 1829 (e.g., Austin 1987; Peter & David 1990; Polaszek & LaSalle 1995), Cynipidae Latreille, 1802 (Buhl & O'Connor 2010), and Encyrtidae Walker, 1837 (Ratzeburg 1852). In these hosts, the species of *Aphanogmus* develop as hyperparasitoids. These opposing modes of host concealment are reflected in morphological adaptations in the ovipositor mechanism of their parasitoids (Ernst *et al.* 2013). Host records for *Aphanogmus* from other insect orders include Coleoptera Linnaeus, 1758 (Evans *et al.* 2005), Hemiptera Linnaeus, 1758 (Dessart 1978), Neuroptera Linnaeus, 1758 (Sinacori *et al.* 1992), Thysanoptera Haliday, 1836 (Dessart & Bournier 1971), and Trichoptera Kirby, 1813 (Luhman *et al.* 1999).

For approximately 80% of species of *Aphanogmus*, no host data is available (Matsuo *et al.* 2016). As a lack of solid host information is common in many 'dark taxa' of parasitoid Hymenoptera, a few studies have aimed to infer host data from ovipositor morphology of parasitoids (e.g., Le Ralec *et al.* 1996; Belshaw *et al.* 2003). In a comprehensive study on the ovipositor mechanism of Ceraphronoidea, Ernst *et al.* (2013) found that a larger relative distance between the anterior angle of the first valvifer (ang) and the inter-valvifer articulation (iva) allows for a larger amplitude of sliding motion of the first valvulae. It

is hypothesised that a larger sliding motion of the paired first valvulae represents a rapid but less robust oviposition mechanism that would be suitable for exposed, mobile hosts (Ernst *et al.* 2013). The newly described *Aphanogmus kretschmanni* sp. nov. corresponds to the *Ceraphron* type ovipositor mechanism that is characterised by a relatively large distance between the anterior angle of the first valvifer and the intervalvifer articulation. This would support the potential for a rapid oviposition in *A. kretschmanni*.

However, in *A. kretschmanni* sp. nov., the first valvifer (1vf) is angled at the tergo-valvifer articulation (tva), which is located in the middle of 1vf (Figs 2C, 3I–K). Overall, 1vf has an evenly convex shape in *A. kretschmanni*, a condition unlike any of the Ceraphronidae analysed by Ernst *et al.* (2013). *Creator spissicornis* (Hellén, 1966) is the only other species observed by Ernst *et al.* (2013; therein cited as *Dendrocerus spissicornis* (Hellén) despite having been transferred by Alekseev in 1980) where the first valvifer is convex but its tergo-valvifer articulation is significantly closer to the anterior angle of the first valvifer than that of *A. kretschmanni*. *Creator spissicornis* parasitizes the pupae of two fly species: *Macronychia striginervis* (Zetterstedt, 1844) (Sarcophagidae Macquart, 1834) and *Zabrachia minutissim*a (Zetterstedt, 1838) (Stratiomyiidae Latreille, 1802) (Alekseev 1980). The ovipositor morphology of *A. kretschmanni* does not unequivocally support a host association but it most likely correlated with the unique modification of the 7th metasomal sternite discussed below.

Functional morphology of the distinctive structure on 7th metasomal sternite

The distinctive spines on the 7th metasomal sternite are the distinguishing character that separates this newly described species from all other species of Ceraphronidae. Modifications to the ovipositor are common across Hymenoptera, e.g., the dart-tailed epipygium in *Cameronella* Dalla Torre, 1897 (Wang & Cook 2012), the heavily pubescent ovipositor of *Torymus lasallei* Bubeníková, Pujade-Villar & Janšta, 2020 and serrated ovipositor valvulae occur in several Symphyta Gerstaecker, 1867, Ichneumonoidea Latreille, 1802, Megalyroidea Schletterer, 1890 and Chalcidoidea Latreille, 1817 (Quicke *et al.* 1994). Modifications to metasomal sternites, on the other hand, are less common but have been reported from the following braconids: the females of *Kollasmosoma sentum* (van Achterberg & Góme, 2011), which parasitize adult workers of *Cataglyphis ibericus* (Emery, 1906) (Formicidae Latreille, 1809), have a single apical spine on the penultimate 5th metasomal sternite (Durán & van Achterberg 2011). It is hypothesised that the spine of *K. sentum* fixes the wasp during oviposition and acts as a supporting point for the oviposition movements of the metasoma (Durán & van Achterberg 2011). Further, a few Braconidae have paired or unpaired accessory prongs on the last metasomal sternite: *Metaphidius* Starý & Sedlag, 1959 has a short, unpaired prong at the base of the 7th sternite whereas the paired prongs in *Trioxys* Haliday, 1833 and *Acanthocaudus* Smith, 1944 and the unpaired prong in *Bioxys* Starý & Schlinger, 1967 are variable in shape and size (Starý 1976). These prongs, along with down-curved ovipositor sheaths, were observed to help retain an aphid host in place during oviposition (Starý 1976).

Similarly, the position of the spines along the 7th sternite in *A. kretschmanni* sp. nov. suggests that this modification could play a stabilising role in oviposition. In all Ceraphronoidea, oviposition is initiated by a contraction of the muscles connecting the apical tergites and sternites, which leads to a rotation of the ovipositor and thereby moves it into its active, exposed position (Ernst *et al.* 2013). Along with the ovipositor, which is usually concealed by the 7th metasomal sternite, the 9th sternite is rotated posteriorly and thus the ovipositor is exposed. If the 7th sternite abuts the substrate or surface of the host in the initiating moves of oviposition, the spines could be useful for anchoring the wasp's metasoma. This could allow for the ovipositor to be inserted into the host with significantly greater force or precision. The slight anterior tilt of the spines could be seen as further support for this hypothesis.

Alternatively, the saw-like spines could be used for cutting into harder substrates. This is known from *Drosophila suzukii* (Matsumura, 1931) and *Scaptomyza flava* (Fallén, 1823), both of which have serrated ovipositors (Whiteman *et al.* 2011; Atallah *et al.* 2014). The serrated ovipositor gives these species the

means to cut through the skin of various fruits or the surface of leaves respectively, enabling them to exploit new ecological niches in comparison to species with unserrated ovipositors (Whiteman *et al.* 2011). Similarly, the distinctive spines of S7 of *A. kretschmanni* sp. nov. along with its less robust ovipositor mechanism might enable the wasp to access well-concealed hosts by using the spines to saw through harder substrates.

The somewhat enlarged hind tarsomeres and tarsal claws (Fig. 3F–H), which are slightly broader and longer compared to corresponding structures in the fore and middle legs, might be interpreted as support for either hypothesis. The adaptations in the metatarsus might help anchor the wasp to the substrate. A more extreme form of enlarged tarsal structures of the hind legs has been observed in *Trassedia* Cancemi, 1996 (Ceraphronoidea), where the hind tarsomeres and hind tarsal claws are almost twice as long and wide as these structures in the preceding legs (Mikó *et al.* 2018). It is hypothesised that the enlarged hind tarsomeres and tarsal claws in *Trassedia* are adaptations to anchoring the body while the wasp uses its chisel-shaped tip of the 7th metasomal sternite to cut into hard substrates (Mikó *et al.* 2018). This reasoning is in line with morphological characteristics in the ovipositor of *Trassedia* that set its mechanism apart from the ovipositor systems of all other Ceraphronoidea. In this genus, the first valvifer consists of two articulating sclerites and the tva is located very close to the iva, thus enabling the first valvulae to slide a long distance along the second valvulae (Ernst *et al.* 2013). This particular combination in ovipositor morphology along with the modifications of the metasomal apex allow for accelerated oviposition by enabling the egg to move down the ovipositor extremely quickly whilst still being able to parasitize well-concealed hosts in hard substrates. These exact same conclusions cannot be drawn for *A. kretschmanni* sp. nov. The plesiomorphic division of the first valvifer is a feature unique to *Trassedia* and a few other insect taxa (Ernst *et al.* 2013). Except for *Trassedia*, all ceraphronoids examined by Ernst *et al.* (2013) as well as *A. kretschmanni* described here, have the first valvifer not bi-partitioned into two articulating sclerites. Further, the posterior margin of the first valvifer is slightly concave in *Trassedia*, whereas it is convex in *A. kretschmanni* and the tva is located roughly between the intervalvifer articulation and the anterior angle. These characteristics limit the distance that the first valvulae can slide along the second valvulae in *A. kretschmanni*. Therefore, oviposition in *Trassedia* is expected to be significantly quicker than what is physically possible in the newly described *A. kretschmanni*.

Overall, the functional morphology of the ovipositor of *A. kretschmanni* sp. nov. points to a quick mode of oviposition that is less robust and therefore typically limited to softer substrates. This *Ceraphron* type ovipositor (sensu Ernst *et al.* 2013) is shared by many species of *Aphanogmus* that parasitise weakly-concealed, free-living cecidomyiid larvae. However, the distinctive spines on the 7th sternite of *A. kretschmanni* might enable the wasp to access hosts that are well-concealed by sawing through a hard concealing surface. A potential hypothesis would be that *A. kretschmanni* retained an ovipositor mechanism best suited for quick parasitisation while at the same time overcoming the limitation of this mechanism to softer substrates through the saw-like spines on S7 that could enable the female to access well-concealed hosts. This hypothesis as well as the definitive host organism of *A. kretschmanni* remain yet to be proven by observation or through rearing experiments.

Significance

In 2017, Hallman *et al.* reported a decline in biomass of flying insects of 76% in protected areas in Germany over three decades and hence revealed the magnitude of today's insect decline. In this study, flying insects were sampled indiscriminately with Malaise traps, therefore the results are representative for the flying insect community as a whole (Hallmann *et al.* 2017). These results do not allow for conclusions on the composition of sampled taxa or the decline of individual species but later a correlation was found between insect biomass and the abundance of hover flies (Syrphidae Latreille, 1802): Hallmann *et al.* (2021) found that severe declines of common species and the extirpation of species of intermediate abundance contributed disproportionately to the overall reduction in biomass. Further studies have addressed individual changes in biodiversity and abundance of a few well-studied taxa such as butterflies (Habel *et al.* 2016), carabid beetles (Homburg *et al.* 2019) and solitary bees (Scheuchl &

Schwenninger 2015). At the same time, certain taxa, particularly those termed 'dark taxa' due to their taxonomic inaccessibility, have remained vastly understudied and are still neglected altogether in current conservation efforts. The two largest insect orders, Hymenoptera and Diptera, jointly constitute over half of the German entomofauna (Klausnitzer 2005) and together make up 76.2% of insects caught in Malaise trap samples (Chimeno *et al.* 2022; Srivathsan *et al.* 2022). At the same time, these are the two orders that contain the highest number of dark taxa and that suffer from the most severe gaps in species knowledge (Shaw & Hochberg 2001; Geiger *et al.* 2016; Hausmann *et al.* 2020; Chimeno *et al.* 2022).

At the current rate of decline, many species of insects and other biota will be driven to extinction on both a local and global scale before they can be sufficiently studied or their value realised (Shaw & Hochberg 2001; Wagner *et al.* 2021). The description of *A. kretschmanni* sp. nov. is a prime example of a highly distinctive species within a severely understudied dark taxon. It features a unique morphological character that could possibly be useful in a bionic context as it provides an evolutionary solution to a mechanical challenge.

A neglected aspect of biodiversity decline is that it goes hand in hand with a loss of morphological diversity. This loss could prove detrimental as many modern solutions in engineering and technology are based on biological methods and systems and have been adapted through bionics. One such example is the ovipositor of the wood wasp genus *Sirex* Linnaeus, 1761 (Siricidae Billberg, 1820), which is able to drill into wood with high precision and without transfer of torque. The biomimetic replication of the ovipositor mechanism resulted in a hand-held surgical drilling device that makes drilling cavities in the thigh bones for inserting hip prostheses safer for the patient, easier for the surgeon and improves healing (Nakajima & Schwarz 2014).

Current conservation strategies are traditionally focused almost exclusively on rare or endangered specialist species. Proposals to re-think current conservation strategies and instead apply a more holistic approach would benefit both common taxa (Hallmann *et al.* 2021) and the numerous dark taxa that remain yet to be discovered and whose biology and morphological adaptations remain to be worked out (Shaw 2006). To effectively preserve insect biodiversity, future conservation efforts must be accompanied by long-term biodiversity monitoring and solid integrative taxonomic research that includes also those taxa that show the highest diversity and abundance (Srivathsan *et al.* 2022).

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Supplementary files

Supp. file 1. Machine-readable description of *Aphanogmus kretschmanni* Moser sp. nov.
https://doi.org/10.5852/ejt.2023.864.2095.8787

Supp. file 2. Table of exact measurements of morphological features. Measured in Amira (Thermo Fisher Scientific, Waltham, MA, USA) based on the synchrotron micro-CT reconstruction of the holotype (SMNS_Hym_Cer_000227). All measurements are in µm and decimals were rounded to whole numbers.
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Supp. file 3. Habitat information & Biogeography.
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