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ARTICLE

Revealing the identity of *Mordellistena minima* and *M. pseudorhenana* (Coleoptera: Mordellidae) based on re-examined type material and DNA barcodes, with new distributional records and comments on morphological variability

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Abstract

The current interpretation of two common European species, *Mordellistena minima* Costa, 1854 and *M. pseudorhenana* Ermisch, 1977, is based on misidentification. The confusion regarding the identity of the species is fixed based on the revised type material. Here, the species are redescribed, and diagnostic characters are provided. *Mordellistena pseudorhenana* is revalidated. *Mordellistena emeryi* Schilsky, 1895 is recognised as a **new synonym** of *M. minima*. *Mordellistena sajoi* Ermisch, 1977 is recognised as a **new synonym** of *M. pseudorhenana*. Lectotype and paralectotypes of *M. emeryi* are designated. *Mordellistena pseudorhenana* is reported for the first time from Bosnia and Herzegovina, Slovenia, and Switzerland. Two morphotypes of *M. pseudorhenana* differing in size and shape of the parameres are recognised. Morphological differences are quantified and displayed using principal component analysis. In addition, DNA barcodes have been used for the first time in family Mordellidae to examine the divergences between the species and to interpret the morphological variability observed in *M. pseudorhenana*. Low genetic divergences did not provide the evidence for considering the morphotypes as separate species. The discrepancy between the morphological and molecular evidence raises questions about the efficiency of the *CO1* gene for Mordellidae identification and the stability of morphological traits conventionally used for species separation.

Introduction

The genus *Mordellistena* Costa, 1854 (Coleoptera: Mordellidae) is represented in Europe by approximately 170 species (Horák 2008; Odnosum 2009; Selnekovič and Kodada 2019; Selnekovič and Ruzzier 2019; Selnekovič and Improta 2020). Most of the common and widespread European species were described during the 19th century by Costa (1854), Mulsant (1856), Emery (1876), and Schilsky (1894, 1895, 1898, 1899). Their work was later followed up by specialists and prolific authors such as K. Ermisch, M.E. Franciscolo, and R. Batten, who greatly contributed to the knowledge of the family with descriptions of dozens of new species. Unfortunately, during our recent studies, it became clear that the type material of some previously described taxa remained unstudied, leading to several cases of incorrect species interpretations

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Fig. 1. A, *Mordellistena minima* Costa, 1854, male, body length: 2.4 mm; **B**, *Mordellistena pseudorhenana* Ermisch, 1977, male, body length: 2.5 mm.

and descriptions of taxa that already bore a name (Horák 1990, 1996; Selnekovič and Kodada 2019; Selnekovič and Improta 2020). *Mordellistena minima* Costa, 1854 (Fig. 1A) and *M. pseudorhenana* Ermisch, 1977 (Fig. 1B) discussed in the present paper may serve as examples.

Mordellistena minima was described by Costa (1854) based on a specimen from the island of Ischia, Italy. Later, Emery (1876) considered the type specimen of *M. minima* "just a small

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specimen of *M. micans* (Germar, 1817), which varies greatly in size". His opinion was then followed by all subsequent authors until Ermisch (1954) treated *M. minima* as a valid species but did not provide any description or diagnostic characters to separate it from its allies. Batten (1977), without seeing the type specimen, characterised *M. minima* based on a unique combination of characters: short antennomeres, long and pointed galea, and expanded protibiae in males. Subsequently, Batten (1980) examined the holotype of *M. pseudorhenana* Ermisch, 1977 and considered it to be conspecific with *M. minima*.

The re-examination of the type specimen of *M. minima* surprisingly revealed a unique set of characters that differ significantly from the abovementioned and currently accepted interpretation of the species as presented by Batten (1977). The present paper aims to resolve the confusion regarding the identity of *M. minima* and *M. pseudorhenana* and to provide redescriptions of both species based on the examined type material. We integrated morphometric and DNA barcode analyses to interpret the observed morphological variability in specimens of *M. pseudorhenana*. Furthermore, we have been able to add DNA barcodes for the first time to five species of the *Mordellistena confinis* species group, with recently re-examined and documented type material (Horák 1996; Selnekovič and Kodada 2019; Selnekovič and Improta 2020). This allowed us to examine the interspecific genetic divergences at the species-group level and set the baseline for future studies with the use of DNA markers.

Materials and methods

The present study is based on examination of 242 adult specimens, including a lectotype of *Mordellistena minima* Costa, 1854, a lectotype and paralectotypes of *M. emeryi* Schilsky, 1895, two syntypes of *M. micans* (Germar, 1813), a holotype and paratypes of *M. pseudorhenana* Ermisch, 1977, and a holotype of *M. sajoi* Ermisch, 1977. Freshly collected specimens used for the morphological observations were killed using ethylacetate, dissected, and glued on a cardboard mounting card. Specimens used for the molecular analyses were killed and stored in 96% ethanol. Observations were made using a Leica MZ16 stereomicroscope (Leica Microsystems) with magnification up to 120×, illuminated with diffuse light (neon bulb, 6400 K; Philips, Amsterdam, The Netherlands). Dry specimens were soaked in water with a small amount of acetic acid. Dissected body parts used for drawings were treated with lactic acid for several days, then washed in water or dehydrated in ethanol and mounted on slides in Berlese's fluid (Swan 1936) or Euparal (Paradox Co., Cracow, Poland). Drawings were made using a Leica drawing tube attached to a Leica DM 1000 microscope (Leica Microsystems), then scanned and traced in Adobe Illustrator CC (Adobe, San Jose, California, United States of America). All dissected body parts were glued with 5,5-dimethyl hydantoin formaldehyde on the same card as the respective specimen or put in the microvials filled with glycerine and pinned under the specimen. Digital photographs were made using a Canon EOS 5D mark II camera (Canon, Tokyo, Japan) attached to Zeiss Axio Zoom.V16 stereoscope (Carl Zeiss AG, Oberkochen, Germany). Image stacks were produced manually, combined using the Zerene Stacker 1.4 software (Zerene Systems LLC, Richland, Washington, United States of America), and edited in Adobe Photoshop CC (Adobe). Measurements were taken using a calibrated eyepiece graticule. Morphometric parameters are provided as range and mean ± standard deviation. The following abbreviations are used for the measured characters: BL – body length from anterior margin of pronotum to elytral apices along midline; HL – head length from anterior margin of clypeus to occipital margin along midline; HW – maximum head width; PL – pronotal length along midline; PW – maximum pronotal width; EL – elytral length from apex of scutellar shield to apices of elytra along suture; EW – maximum elytral width combined; PyL – maximum length of pygidium; RPL – maximum length of right paramere; LPL – maximum length of left paramere. Terminology used in morphological descriptions follows Franciscolo (1957), Lu *et al.* (1997), and Lawrence and Ślipiński (2010). All nomenclatorial acts follow regulations of the International Code of Zoological Nomenclature

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(International Trust of Zoological Nomenclature 1999). The examined material is deposited in the following collections: Dávid Selnekovič collection, Bratislava, Slovakia (DSBS), Hungarian Natural History Museum, Budapest, Hungary (HNHM), the Museum für Naturkunde, Humboldt-Universität zu Berlin, Berlin, Germany (MNHU), the Museo Zoologico dell'Università Federico II, Naples, Italy (MZFN), and Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI).

Principal component analysis was performed using PAST 3.12 software (Hammer *et al.* 2001), using log-transformed variables of three morphometric characters: elytral length, right paramere length, and left paramere length (Supplementary material, Table S1). The dataset consisted of 60 male specimens of *M. pseudorhenana* from Bulgaria, Cyprus, Hungary, Israel, Italy, Montenegro, Slovakia, and Turkey, including holotype and all male genetic vouchers. Plots were subsequently edited in Adobe Illustrator CC.

A total of 30 adults were used for the DNA analyses (Table 3). Genomic DNA was extracted from whole individuals using E.Z.N.A.® Tissue DNA kit (OMEGA Bio-tek Inc., Norcross, Georgia, United States of America) according to the manufacturer's protocol. Extracted and purified DNA is stored at –25 °C at the Department of Zoology of Faculty of Natural Sciences, Comenius University, Bratislava, Slovakia. A 568-bp-long fragment of cytochrome oxidase subunit 1 (*CO1*) was amplified with primers LCO1490 and HCO2198 (Folmer *et al.* 1994). Standard polymerase chain reaction was performed using DreamTaq™ Green DNA Polymerase (Thermo Fisher Scientific Inc., Waltham, Massachusetts, United States of America) for a total volume of 25.0 μL, comprising 100–200 ng genomic DNA, 2.5 μL DreamTaq™ Buffer, 2.5 μL 25 mM $MgCl_2$, 2.0 μL of dNTP (deoxynucleotide triphosphohydrolase) mix, 1.0 μL of 3.0 pmol/mL each primer, 0.4 μL (5 U/ μL) DreamTaq™ DNA polymerase and nuclease-free water to 25.0 μL. Polymerase chain reaction was carried out on an Eppendorf thermal cycler (Eppendorf, Hamburg, Germany), with initial denaturation at 94 °C for 1 minute, followed by 35 cycles of 94 °C for 30 seconds, 52 °C for 40 seconds, and 72 °C for 1 minute, and 10 minutes of final extension at 72 °C. All polymerase chain reaction products were detected on 1% agarose gel stained with GoldView (SBS Genetech, Beijing, China). Purification and Sanger sequencing were done in the commercial laboratory of Macrogen Europe Inc. (Amsterdam, The Netherlands) using both amplification primers. Consensus sequences, alignment, and final matrix were produced in Geneious 6.1.8 software (Kearse *et al.* 2012). *Mordella aculeata* Linnaeus, 1758 and *Mordellistena variegata* (Fabricius, 1798) were used as outgroups. Estimates of evolutionary divergence between *CO1* sequences were calculated using the Kimura two-parameter model (Kimura 1980). The dendrogram was based on the maximum likelihood method, and bootstrap support values were calculated in MEGA X software (Kumar *et al.* 2018). The best-fitted substitution model (GTR + I + G) was selected by jModelTest 2 (Darriba *et al.* 2012) using 1000 replicates. Voucher identifiers and GenBank and BOLD accession numbers are listed in Table 3.

Results

Morphology and systematics

Examination of the male lectotype of *Mordellistena minima* Costa, 1854 deposited in the Museo Zoologico dell'Università Federico II revealed a unique set of characters separating the species from other congeners (see differential diagnosis). The presence of yellow metatibial spurs, in combination with an entirely black body and short antennomeres, observed in the lectotype of *M. minima* is a rather unique condition that appears only in two other taxa from the *M. confinis* group: *M. emeryi* Schilsky, 1895 and *M. lindbergi* Ermisch, 1963. Re-examination of the lectotype of *M. emeryi* and comparison of the male genitalia with the lectotype of *M. minima* (Fig. 5F,G) revealed that the specimens are conspecific, and therefore we propose *M. emeryi* as a new junior

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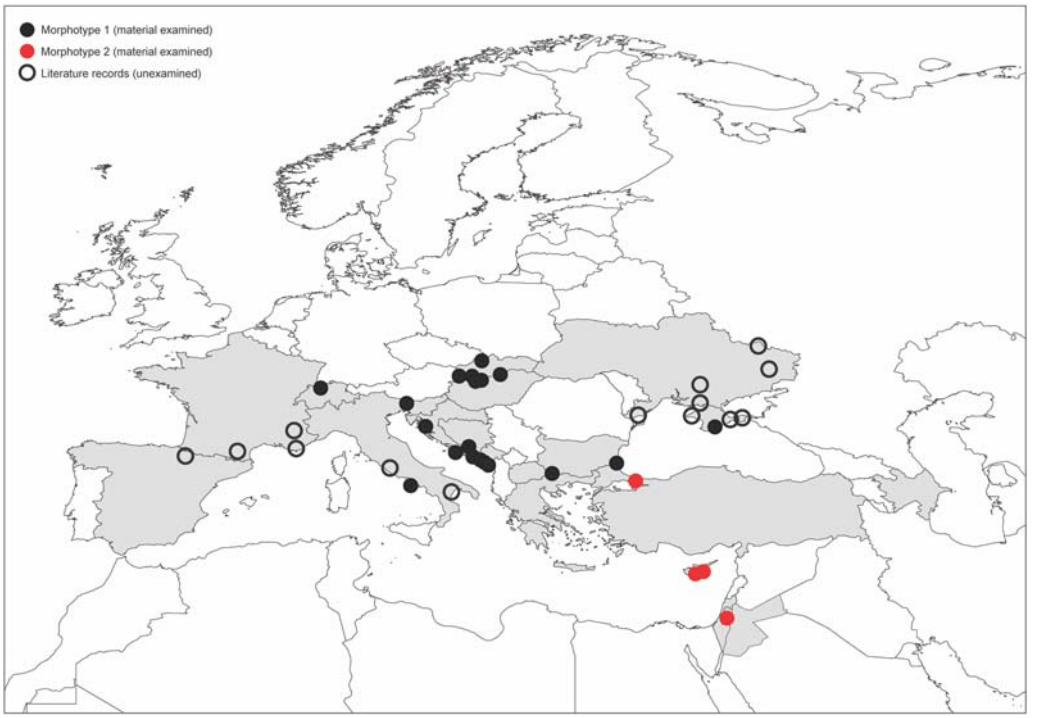

Fig. 2. Distribution of *Mordellistena pseudorhenana* Ermisch, 1977. Countries with reported occurrence are highlighted in grey. Black-filled circles represent the examined specimens of morphotype 1, red-filled circles those of morphotype 2. Black open circles represent the published records that have not been re-examined for the present study.

subjective synonym of the latter. The redescription of the species provided below is based on a lectotype of *M. minima*, the type series of *M. emeryi*, and a series of specimens recently collected in the type locality, Ischia, Italy.

The identity of *M. minima* is not consistent with a previously accepted interpretation of the species presented by Ermisch (1963) and Batten (1977) and followed by subsequent authors (Odnosum 1992, 1993, 2003, 2005, 2010; Horák 2008; Ruzzier 2013). The definition of *M. minima* as a species, with long apically pointed galea, expanded protibiae in males with distinct clusters of extended setae, and short antennomeres 5–10, was based on a misidentification. The aforementioned species interpretation was found to correspond with the holotype of *M. pseudorhenana* Ermisch, 1977 previously synonymised with *M. minima* by Batten (1980). After a re-examination of the holotype, we consider *M. pseudorhenana* to be a valid species, which can be separated from other members of *M. confinis* species group by the presence of long and pointed galea (Fig. 6A) and the combination of characters listed in the differential diagnosis section. The holotype of *M. sajoi* Ermisch, 1977 shares the important diagnostic characters with the holotype of *M. pseudorhenana*, and we consider *M. sajoi* a new junior subjective synonym of the latter species.

Among the material examined for the present study, we were able to identify two morphotypes of *M. pseudorhenana* that differ in the size and shape of the parameres. Morphotype 1 is represented here by a holotype and 88 additional male specimens from several localities in Europe (Fig. 2), while morphotype 2 is represented by 27 male specimens from Cyprus, Israel, and Turkey. The two morphotypes differ in the size and shape of the parameres: morphotype 1's parameres are shorter and smaller in proportion to the elytral length than they are in morphotype

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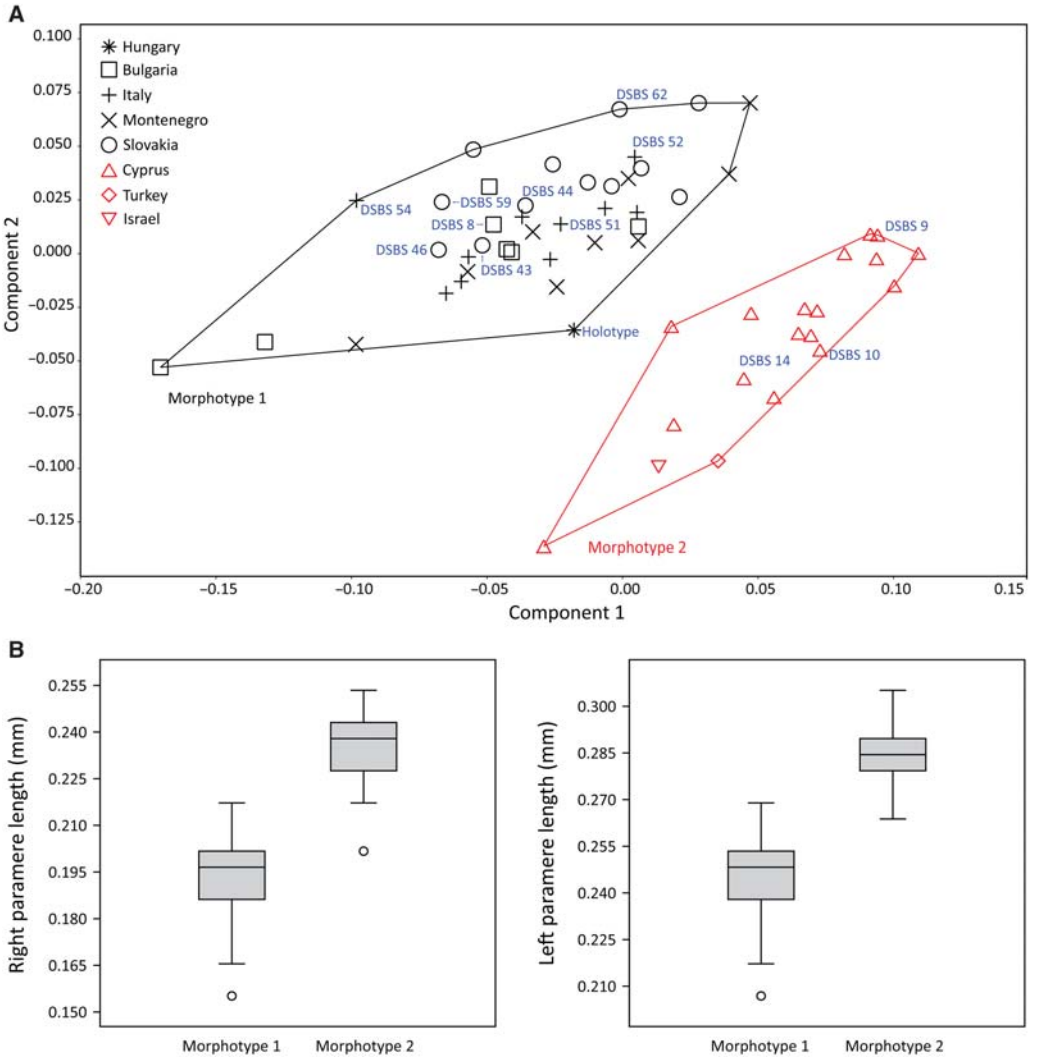

Fig. 3. **A**, Ordination of 58 male specimens of *Mordellistena pseudorhenana* Ermisch, 1977 along the first two components of the principal component analysis. The analysis is based on three morphometric characters: elytral length, right paramere length, and left paramere length. The black cluster represents the specimens from central and southern Europe, the red cluster represents specimens from Cyprus. Entire dataset used for the analysis is provided in Supplementary material, Table S1; **B**, differences in the length of parameres between the specimens of *M. pseudorhenana* from southern and central Europe *versus* the specimens from Cyprus.

2 (Figs. 3B, 6E, F; Table 1); basal portions of the parameres in morphotype 1 are shorter in proportion to the distal processes than they are in morphotype 2 (Fig. 6E,F); and the dorsal process of the left paramere in morphotype 1 is shorter and wider than it is in morphotype 2 (Fig. 6E, F). The differences in dimensions are also shown by the results of the principal component analysis (Fig. 3A). Despite the morphological differences, the genetic divergence in *CO1* fragment between the representatives of the two morphotypes is very low (Table 5; discussed in the Molecular Analyses section).

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Table 1. Dimensions of parameres in *Mordellistena minima* Costa, 1854 and two morphotypes of *M. pseudorhenana* Ermisch, 1977. The ranges are followed by arithmetic mean ± standard deviation.

		Mordellistena pseudorhenana	
	Mordellistena minima	Morphotype 1	Morphotype 2
N	14	39	21
RPL	0.19–0.27 (0.23 ± 0.02)	0.16–0.22 (0.19 ± 0.01)	0.20–0.25 (0.23 ± 0.01)
LPL	0.24–0.30 (0.28 ± 0.02)	0.21–0.27 (0.25 ± 0.01)	0.26–0.31 (0.28 ± 0.01)
EL/RPL	7.54–9.10 (8.30 ± 0.46)	9.10–12.10 (10.48 ± 0.61)	7.04–8.77 (8.14 ± 0.52)
EL/LPL	5.90–7.35 (6.73 ± 0.33)	7.05–9.32 (8.24 ± 0.48)	5.52–7.49 (6.73 ± 0.49)

EL, elytral length from apex of scutellar shield to apices of elytra along suture; RPL, maximum length of right paramere; LPL, maximum length of left paramere.

Table 2. Principal component loadings and percentage of explained variance from principal component (PC) analysis of 60 male specimens of *Mordellistena pseudorhenana* Ermisch, 1977. The highest values are highlighted in bold.

	PC 1	PC 2	PC 3
Explained variance (%)	68.45	29.84	1.71
Loadings of variables			
EL	0.196	**0.981**	0.008
RPL	0.578	−0.122	**0.807**
LPL	**0.792**	−0.153	−0.590

EL, elytral length from apex of scutellar shield to apices of elytra along suture; RPL, maximum length of right paramere; LPL, maximum length of left paramere.

Morphometric analysis

For the principal component analysis, we focused on two morphotypes of *M. pseudorhenana* that can be distinguished based on the shape and size of the parameres. The first group representing morphotype 1 consisted of 39 male specimens from Bulgaria, Hungary, Italy, Montenegro, and Slovakia, including the holotype and voucher specimens used for the molecular analyses. The second group consisted of 21 male specimens from Cyprus, Israel, and Turkey, also including the genetic vouchers. The principal component analysis was based on a set of three characters (elytral length, right paramere length, and left paramere length) that best reflect the differences in morphology. The analysis revealed two separate clusters that represent the two morphotypes (Fig. 3 A). The first principal component explained 68.5% of the variance and correlated strongly with the length of the right paramere (Table 2). The second principal component explained 29.8% of the variance and correlated strongly with elytral length (Table 2). Results of the principal component analysis are congruent with differences in the actual measurements (Fig. 3B; Table 1; Supplementary material, Table S1).

Molecular analyses

The sequences of *CO1* gene fragment were obtained from 30 out of 35 amplified samples representing five species of *M. confinis* group, plus two outgroup species (Table 3). The analysed *CO1* fragment was 568 bp long, with no indels and stop codons. The maximum likelihood analysis revealed all five presumed ingroup species as distinctly separate clades, each with bootstrap value of 100 (Fig. 4). The Kimura two-parameter genetic divergences between species were high and ranged from 13.9%

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Table 3. Samples used in the molecular analyses with voucher IDs, GenBank, and Barcode of Life Database (BOLD) BIN accession numbers, haplotypes, and countries of origin.

Species	Voucher	GenBank	BOLD BIN	Haplotype	Country
Mordellistena pseudorhenana	DSBS 6	MT232528	BOLD:AEA3479	Ht_1	Bulgaria
Mordellistena pseudorhenana	DSBS 7	MT232529	BOLD:AEA3479	Ht_1	Bulgaria
Mordellistena pseudorhenana	DSBS 8	MT232530	BOLD:AEA3479	Ht_1	Bulgaria
Mordellistena pseudorhenana	DSBS 9	MT232531	BOLD:AEA3479	Ht_2	Cyprus
Mordellistena pseudorhenana	DSBS 12	MT232533	BOLD:AEA3479	Ht_2	Cyprus
Mordellistena pseudorhenana	DSBS 13	MT232534	BOLD:AEA3479	Ht_2	Cyprus
Mordellistena pseudorhenana	DSBS 10	MT232532	BOLD:AEA3479	Ht_3	Cyprus
Mordellistena pseudorhenana	DSBS 14	MT232535	BOLD:AEA3479	Ht_3	Cyprus
Mordellistena pseudorhenana	DSBS 51	MT232544	BOLD:AEA3479	Ht_4	Italy
Mordellistena pseudorhenana	DSBS 52	MT232545	BOLD:AEA3479	Ht_4	Italy
Mordellistena pseudorhenana	DSBS 53	MT232546	BOLD:AEA3479	Ht_4	Italy
Mordellistena pseudorhenana	DSBS 54	MT232547	BOLD:AEA3479	Ht_4	Italy
Mordellistena pseudorhenana	DSBS 46	MT232542	BOLD:AEA3479	Ht_5	Slovakia
Mordellistena pseudorhenana	DSBS 43	MT232539	BOLD:AEA3479	Ht_6	Slovakia
Mordellistena pseudorhenana	DSBS 44	MT232540	BOLD:AEA3479	Ht_6	Slovakia
Mordellistena pseudorhenana	DSBS 45	MT232541	BOLD:AEA3479	Ht_6	Slovakia
Mordellistena pseudorhenana	DSBS 59	MT232548	BOLD:AEA3479	Ht_6	Slovakia
Mordellistena pseudorhenana	DSBS 62	MT232549	BOLD:AEA3479	Ht_6	Slovakia
Mordellistena minima	DSBS 79	MT232550	BOLD:AED6814	Ht_7	Italy
Mordellistena minima	DSBS 81	MT232551	BOLD:AED6814	Ht_7	Italy
Mordellistena lindbergi	DSBS 86	MT232553	BOLD:AED2412	Ht_8	Spain
Mordellistena hirtipes	DSBS 18	MT232537	BOLD:AED9694	Ht_9	Cyprus
Mordellistena hirtipes	DSBS 17	MT232536	BOLD:AED9694	Ht_10	Cyprus
Mordellistena hirtipes	DSBS 19	MT232538	BOLD:AED9694	Ht_10	Cyprus
Mordellistena hirtipes	DSBS 50	MT232543	BOLD:AED9695	Ht_11	Italy
Mordellistena purpurascens	DSBS 82	MT232552	BOLD:AED6443	Ht_12	Italy
Mordellistena purpurascens	DSBS 117	MT232555	BOLD:AED6443	Ht_12	Italy
Mordellistena purpurascens	DSBS 111	MT232554	BOLD:AED6443	Ht_13	Spain
Outgroup					
Mordella aculeata	DSBS 78	MT232556	BOLD:AED3319	Ht_14	Slovakia
Mordellistena variegata	DSBS 89	MT232557	BOLD:ADW7498	Ht_15	Germany

DSBS, Dávid Selnekovič collection, Bratislava, Slovakia.

between *M. hirtipes* Schilsky, 1895 and *M. purpurascens* Costa, 1854 to 22.4% between *M. minima* and *M. hirtipes* (Table 4; Supplementary material, Table S2). The mean interspecific distance between the five analysed species from the *M. confinis* species group was 18.5%. The mean intraspecific distances ranged from 0% in *M. minima* to 1.9% in *M. hirtipes* (Table 4).

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Table 4. Pairwise genetic distances between and within five species of the *Mordellistena confinis* Costa, 1854 species group, plus two outgroup species, based on 568-bp fragment of the *CO1* mitochondrial gene calculated by the Kimura 2-parameter model. The intraspecific divergences are highlighted in bold.

	1.	2.	3.	4.	5.	6.	7.
1. *Mordellistena pseudorhenana*	**0.0066**						
2. *Mordellistena hirtipes*	0.1764	**0.0192**					
3. *Mordellistena minima*	0.1999	0.2244	**0.0000**				
4. *Mordellistena purpurascens*	0.1944	0.1386	0.2177	**0.0035**			
5. *Mordellistena lindbergi*	0.1670	0.1498	0.1929	0.1884	**n/a**		
6. *Mordella aculeata*	0.2836	0.2907	0.3101	0.3406	0.3260	**n/a**	
7. *Mordellistena variegata*	0.3154	0.2938	0.2198	0.3185	0.3077	0.3120	**n/a**

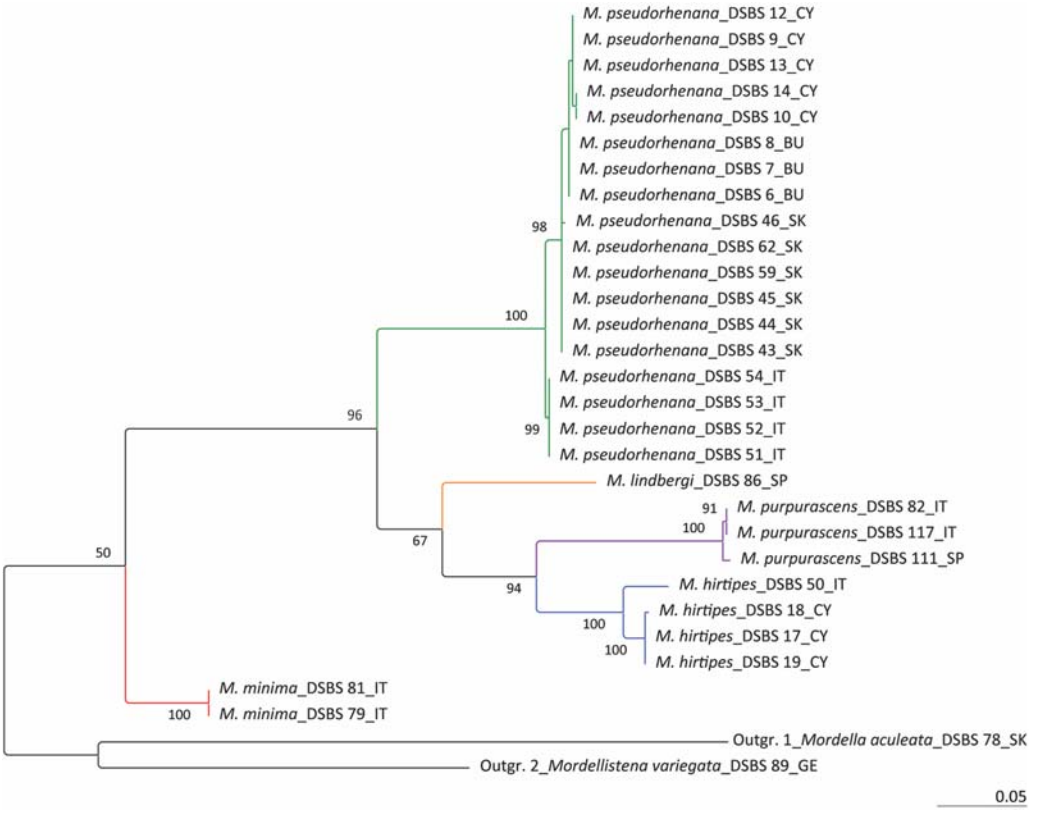

Fig. 4. Maximum likelihood tree based on 568-bp fragment of *CO1* mitochondrial gene sampled from five species of *Mordellistena confinis* Costa, 1854 species group.

The *M. pseudorhenana* morphotype 1 was represented in the analyses by 13 specimens from Bulgaria, Italy, and Slovakia. Morphotype 2 was represented by five specimens from Cyprus. The analyses revealed four haplotypes in the morphotype 1 and two haplotypes in morphotype 2 (Tables 3 and 5). Based on the Kimura two-parameter distances, *M. lindbergi* was recovered as the closest neighbour of *M. pseudorhenana*, with the smallest interspecific distance (16.5%)

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Table 5. Pairwise genetic distances between detected haplotypes of *Mordellistena pseudorhenana* Ermisch, 1977, based on a 568-bp fragment of *CO1* gene calculated by the Kimura 2-parameter model.

Haplotype	1.	2.	3.	4.	5.
1. Ht_1 (Bulgaria)					
2. Ht_2 (Cyprus)	0.0018				
3. Ht_3 (Cyprus)	0.0035	0.0018			
4. Ht_6 (Slovakia)	0.0035	0.0053	0.0071		
5. Ht_5 (Slovakia)	0.0053	0.0071	0.0089	0.0018	
6. Ht_4 (Italy)	0.0142	0.0125	0.0143	0.0107	0.0125

(Supplementary material, Table S2). The divergences between the two *M. pseudorhenana* morphotypes ranged from 0.2% between haplotypes from Cyprus and Bulgaria to 1.4% between haplotype 3 from Cyprus and haplotype 4 from Italy (Table 5). The highest intraspecific Kimura two-parameter distance between the two morphotypes is 11.8 times less than the smallest interspecific distance between *M. pseudorhenana* and *M. lindbergi.* The analysed *CO1* fragment did not provide any evidence to consider the two morphotypes separate species.

Distribution

Distributional records for *M. minima* that were published by Ermisch (1963), Batten (1976), Odnosum (1993, 2003, 2010), and Horák (2008, 2020) were identified to refer to *M. pseudorhenana*, based on the revised material and the illustrations of male genitalia presented in the publications. The large series of examined material revealed new distributional records for *M. pseudorhenana* from Bosnia and Herzegovina, Slovenia, and Switzerland. The range of *M. pseudorhenana* reaches from Spain in the west, across the whole Mediterranean basin to Turkey, from Israel and Jordan in the south, across the Pannonian basin to Hungary and Slovakia in the north, and along the Black and Caspian seas to Ukraine, Azerbaijan, and Kyrgyzstan in the east (Fig. 2). A new record from Rajecké Teplice, Slovakia marks the northernmost known extent of the species' distribution (Fig. 2).

Mordellistena (*s. str.*) *minima* Costa, 1854

(Figs. 1A, 2, 4, 5, 7A)

Mordellistena (*s. str.*) *minima* Costa, 1854: 18–19, Pl. XXII, Fig. 1 [original description, figures, type locality: Ischia, Italy]; Mulsant (1856: 383–385) [description]; Gemminger and Harold (1870: 2112) [catalogue, first report from France].

Mordellistena (*s. str.*) *micans*: Emery (1876: 96) [as syn. of *M. micans*]; Heyden *et al.* (1883: 142) [catalogue, as var. of *M. micans*]; Heyden *et al.* (1906: 456) [catalogue, as syn. of *M. micans*]; Winkler (1928: 885) [catalogue, as syn. of *M. micans*].

Mordellistena (*s. str.*) *confinis* var. *emeryi* Schilsky, 1895: 53 **new synonymy** [original description, type locality: Oesterreich [Austria]]; Heyden *et al.* (1906: 456) [catalogue]; Schaufuss (1916: 766) [catalogue, first report from Germany]; Roubal (1934: 5) [first report from Morocco]; Franciscolo (1942: 7) [localities], Franciscolo (1956: 4) [localities].

Mordellistena (*s. str.*) *emeryi*: Ermisch (1956: 286, 308–309) [new status, key, first report from Albania, Algeria, Croatia, Spain, Switzerland]; Ermisch (1969a: 847, 853) [localities]; Ermisch (1969b: 181) [key]; Köstlin and Vogt (1971: 51) [localities]; Batten (1976: 167) [localities]; Ermisch (1977: 167) [localities]; Kaszab (1979: 69–70) [key, figures]; Compte (1985: 66) [localities]; Angelini (1986: 87) [localities]; Franciscolo (1991: 168) [localities, first report from Tunisia];

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Horák (1996: 178) [key]; Horák (2008: 97) [catalogue, first report from Greece]; Ruzzier (2013: 107) [localities]; Horák (2020: 93) [catalogue].

Type locality. Ischia, Italy.

Type material examined. Lectotype of *M. minima* (Fig. 5 A,F) by designation of Selnekovič and Improta (2020), male, MZFN, labelled: "45.194 | *Mordellistena minima*, n. Ischia [original Costa's label] | LECTOTYPUS *Mordellistena minima* Costa, 1854 D. Selnekovič des. 2019 [red label]"; in bad condition, pinned between elytra, right antenna, right maxillary palpus, and left metatarsus missing; left antenna, left maxilla, left elytron, abdomen, and genitalia stored in micro-vial with glycerine. **Lectotype of *M. emeryi*** by present designation (Fig. 5G), MNHU, male, labelled: "Austria Schuster [handwritten] | ♂ | Type [red label] | Zool. Mus. Berlin | [card with dissected genitalia] | LECTOTYPUS Mordellistena (*s. str.*) emeryi Schilsky J. Horák design. 2006 [red label]". **Paralectotypes of *M. emeryi*** by present designation, MNHU, 5 males, 4 females, 2 sex undetermined, labelled: "Austria Schuster [handwritten] | Type [red label] | Zool. Mus. Berlin | PARALECTOTYPUS *Mordellistena* (*s. str.*) *emeryi* Schilsky J. Horák design. 2006 [red label]".

Additional material examined. Italy: 9 ♂♂, 3 ♀♀, Ischia Island, Serrara env., 40° 43′ 17″ N, 13° 52′ 59″ E, 550 m a.s.l., 30.vi.2019, D. Selnekovič *leg*., dry grassland (DSBS DSBS_79, DSBS_81, DS-138 to DS-140, DS-154 to DS-158); 10 ♂♂, 7 ♀♀, Ischia Island, Serrara env., 40° 42′ 60″ N, 13° 53′ 11″ E, 517 m a.s.l., 29.vi.2019, D. Selnekovič *leg*., ruderal vegetation, on flowers of *Daucus* (DSBS DS-141 to DS-147, DS-151 to DS-153, DS-159 to DS-168).

Differential diagnosis. The species is characterised by the following combination of characters: (1) body black, metatibial spurs yellowish (Fig. 1A); (2) pubescence on most body surfaces yellowish to light-brownish with purple sheen; (3) antennomeres 5–10 *ca*. 1.20–1.30 times longer than wide; (4) galea short, apically rounded (Fig. 5A); (5) protibiae in males slightly expanded, sometimes with several extended setae; (6) metatibiae with 3–5 short lateral ridges, metatarsomere 1 with 3–5 ridges, metatarsomere 2 with two ridges; (7) abdominal sternite VIII in males *ca*. 2.00 times longer than wide, rounded at apex (Fig. 5C); in females *ca*. 1.60 times longer than wide, with speculum ventrale narrowly clavate (Fig. 5D); and (8) parameres as in Figure 5F,G; ovipositor rather short, with paraprocts distinctly shorter than gonocoxites, as in Figure 5E.

Mordellistena minima may be assigned to the *M. confinis* species group as defined by Ermisch (1956). Within this group, the combination of yellowish metatibial spurs and completely black body, including legs and antennae, is shared by three other species: *M. lindbergi* Ermisch, 1963, *M. eversi* Ermisch, 1965, and *M. canariensis* Ermisch, 1965. The species most closely resembles *M. lindbergi* and can be distinguished by the following characters: (1) the pubescence on elytra in *M. minima* has a distinct purple sheen, whereas that of *M. lindbergi* has a distinct greenish sheen; (2) protibiae are, in males of *M. minima*, slightly expanded, sometimes with several extended setae, compared to those of *M. lindbergi*, which are not expanded and are without extended setae; (3) the metatibiae in *M. minima* usually possess 4–5 lateral ridges, whereas those of *M. lindbergi* usually possess three lateral ridges, the last of which is very short; (4) abdominal sternite VIII in males of *M. minima* is *ca*. 2.00 times longer than wide with a rounded apex (Fig. 5C), whereas that of *M. lindbergi* is approximately 1.60 times longer than wide, with lateral margins distinctly convergent and a slightly emarginated apex; (5) the parameres of *M. minima* are as illustrated in Figure 5F,G, and those of *M. lindbergi* are as shown in Horák (1996); (6) the species are separated by *ca*. 19% divergence in the barcoding fragment of the *CO1* gene (Table 3). Both *M. eversi* and *M. canariensis* are known only from the Canary Islands and differ from *M. minima* by having distinctly longer antennae, with antennomeres 5–10 almost twice as long as wide.

Redescription. Body slender (Fig. 1A), wedge-shaped, widest before middle of elytra, dorsum moderately convex, venter strongly so. Basic metric characters are listed in Tables 1 and 6. Colour of almost entire integument black, with very fine bluish sheen; maxillary palpi and four basal antennomeres sometimes dark reddish-brown; metatibial spurs yellowish with black apices. Vestiture consisting of dense, decumbent, dorso-ventrally flattened setae; colour uniformly

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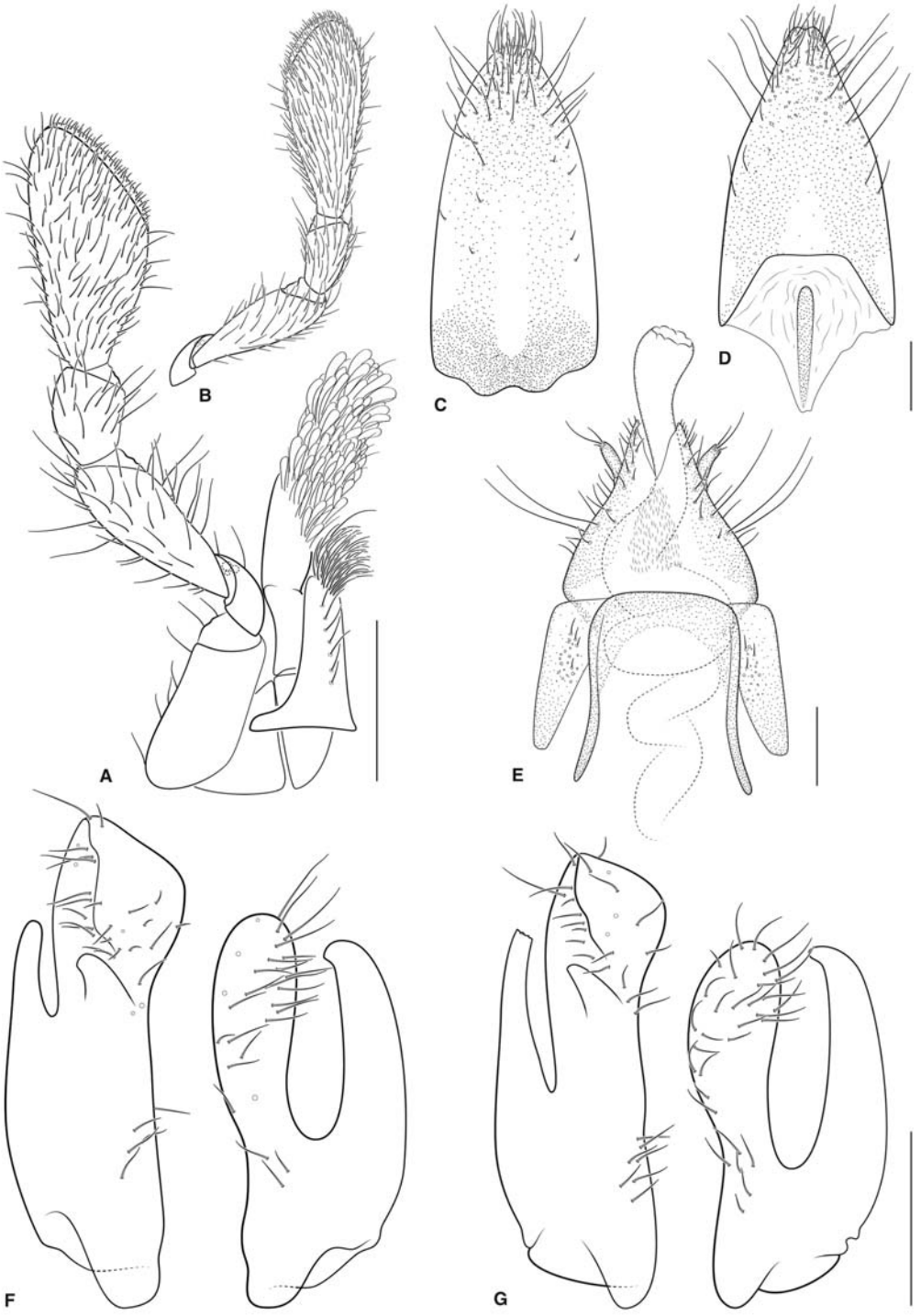

Fig. 5. *Mordellistena minima* Costa, 1854. **A**, male maxilla (lectotype); **B**, female maxillary palp; **C**, male abdominal sternite VIII; **D**, female abdominal sternite VIII; **E**, ovipositor; **F**, parameres (lectotype); and **G**, parameres (*M. emeryi* Schilsky, 1895 lectotype).

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yellowish on head and sternal thoracic parts; in anterior portions of pronotum yellowish, somewhat darkened posteriorly; in anterior portions of elytra yellowish, gradually darkened posteriorly to completely black at apices; on first to abdominal ventrites yellowish, on following ventrites gradually darkened to completely black on ventrite 5 and pygidium; on legs yellowish, somewhat darkened towards apices; vestiture on pronotum and elytra with distinct purple sheen.

Head on dorsum moderately convex; surface finely microreticulated with minute, round, setiferous punctures; frontoclypeus with anterior margin straight; occipital carina evenly rounded in dorsal aspect, straight to slightly concave in posterior aspect; tempora absent. Labrum with antero-lateral angles broadly rounded, transverse with exposed portion *ca*. 1.30 times wider than long, microreticulate, bearing setiferous punctures. Eyes broadly oval, *ca*. 1.30 times longer than wide, finely faceted with distinct interfacetal setae. Antennae moderately long, feebly serrate (Fig. 1A); scapus and pedicel cylindrical, subequal; antennomeres 3–4 subequal, slightly shorter than pedicel, distinctly shorter than following segments; antennomeres 5–10 subequal, in males *ca*. 1.30 times and in females *ca*. 1.20 times longer than wide; antennomere 11 elongate oval, *ca*. 2.00 times longer than wide. Mandibles slightly asymmetrical in molar parts, bidentate, with exposed lateral portion setose; mola denticulate; prostheca with thin, medially oriented trichoid sensilla. Maxilla as in Figure 5 A,B, galea distinctly shorter than maxillary palpus, rounded or subtruncate at apex, densely covered with trichoid and apically widened, spoon-like sensilla; lacinia with trichoid sensilla arranged in longitudinal row and scattered in apical portion; palpifer cylindrical, setose laterally; maxillary palpomere 1 short, setose ventrally; palpomere 2 moderately widened apically, in males not expanded and with few extended setae; palpomere 3 *ca*. 0.50 times as long as previous one; terminal palpomere narrowly securiform, *ca*. 2.50 times longer than wide, with inner angle situated behind middle. Terminal labial palpomere broadly fusiform.

Pronotum moderately convex, slightly wider than long (Table 6), widest behind middle, finely microreticulate with dense rasp-like punctures; anterior margin slightly produced in middle, margination complete, anterior angles rounded; lateral carinae rounded in dorsal aspect and very slightly concave in lateral aspect, margination inapparent but complete; posterior angles obtuse and rounded in lateral aspect. Prosternal process obliterated. Scutellar shield triangular, with rasp-like setiferous punctures. Mesoventral process truncate at apex, as wide as mesotibia. Metaventral discrimen distinct, reaching shortly before middle. Metanepisternite rather wide, with lateral margin concave and mesal margin straight.

Elytra moderately convex, about twice as long as combined width (Table 6), widest around end of anterior one-third, moderately narrowed, with lateral carinae convergent behind middle (Fig. 1A); apices separately rounded; surface with rasp-like, setiferous punctures, and with fine microreticulation consisting of transverse, undulate lines.

Protibiae straight, in males expanded basally and sometimes with few extended setae; mesotibiae slightly bent medially; metatibiae with short apical ridge and 3–5 short lateral ridges parallel to apical tibial margin, reaching *ca*. one-quarter of tibial width, subequal in length except the last one usually shorter, sometimes inapparent; metatibial spurs yellowish with black apices, outer one *ca*. 0.60 times as long as inner one. Protarsi slightly longer than protibiae, first protarsomere slightly longer than following two segments combined, penultimate protarsomere distinctly longer than wide, with anterior margin slightly concave, claws tridentate; mesotarsi *ca*. 1.30 times as long as mesotibiae; metatarsomere 1 with 3–5 ridges, metatarsomere 2 with two ridges, metatarsomere 3 without ridges.

Pygidium moderately long, conical, narrowly truncate at apex (Fig. 1A), about half as long as elytra (Table 6) and about twice as long as ventrite 5. Ventrite 5 with apical margin convex. Sternite VIII in males *ca*. twice as long as wide, setose apically, with lateral margins convergent and evenly rounded, apex rounded (Fig. 5C); in females *ca*. 1.60 times longer than wide, setose apico-laterally, with apex shallowly concave, spiculum ventrale narrowly clavate (Fig. 5D). Sternite IX in males slender, arrow shaped. Phallobase moderately long, *ca*. 0.40 times as long as elytra, with distal arms *ca*. 2.80 times as long as tubular part. Median lobe long and slender, almost as

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Table 6. Metric characters of *Mordellistena minima* Costa, 1854 and *M. pseudorhenana* Ermisch, 1977. Measurements are provided as range followed by mean ± standard deviation.

	Mordellistena minima		*Mordellistena pseudorhenana*	
	Males	Females	Males	Females
N	14	7	20	20
BL (mm)	1.82–2.73 2.44 ± 0.26	2.60–3.19 2.84 ± 0.23	1.89–2.99 2.58 ± 0.32	2.24–3.45 2.76 ± 0.37
HL (mm)	0.44–0.65 0.59 ± 0.05	0.60–0.75 0.68 ± 0.05	0.51–0.73 0.64 ± 0.06	0.56–0.84 0.68 ± 0.08
HW (mm)	0.48–0.75 0.68 ± 0.07	0.70–0.82 0.76 ± 0.04	0.53–0.82 0.70 ± 0.08	0.59–0.91 0.74 ± 0.09
HW/HL	1.08–1.20 1.14 ± 0.04	1.07–1.17 1.11 ± 0.03	1.04–1.17 1.09 ± 0.03	1.04–1.16 1.09 ± 0.03
PL (mm)	0.52–0.84 0.75 ± 0.08	0.81–0.96 0.88 ± 0.06	0.58–0.93 0.78 ± 0.11	0.70–1.11 0.87 ± 0.13
PW (mm)	0.57–0.98 0.83 ± 0.09	0.91–1.12 1.01 ± 0.07	0.60–0.99 0.82 ± 0.11	0.73–1.16 0.91 ± 0.14
PW/PL	1.05–1.16 1.11 ± 0.03	1.11–1.18 1.15 ± 0.02	1.00–1.09 1.05 ± 0.02	1.00–1.14 1.05 ± 0.04
EL (mm)	1.40–2.08 1.89 ± 0.18	1.98–2.42 2.16 ± 0.17	1.50–2.32 2.02 ± 0.24	1.73–2.68 2.16 ± 0.27
EW (mm)	0.64–1.01 0.89 ± 0.09	0.94–1.20 1.06 ± 0.09	0.67–1.05 0.88 ± 0.11	0.82–1.23 1.00 ± 0.14
EL/EW	2.03–2.31 2.13 ± 0.08	1.98–2.11 2.03 ± 0.04	2.13–2.59 2.30 ± 0.10	2.02–2.27 2.15 ± 0.08
PyL (mm)	0.78–1.18 1.05 ± 0.10	1.00–1.17 1.07 ± 0.05	0.82–1.48 1.20 ± 0.17	0.84–1.50 1.18 ± 0.16
EL/PyL	1.66–1.98 1.80 ± 0.07	1.88–2.25 2.01 ± 0.12	1.52–2.00 1.70 ± 0.13	1.65–2.16 1.83 ± 0.13

BL, body length from anterior margin of pronotum to elytral apices along midline; HL, head length from anterior margin of clypeus to occipital margin along midline; HW, maximum head width; PL, pronotal length along midline; PW, maximum pronotal width; EL, elytral length from apex of scutellar shield to apices of elytra along suture; EW, maximum elytral width combined; PyL, maximum length of pygidium; RPL, maximum length of right paramere; LPL, maximum length of left paramere.

long as elytra, with apex slightly expanded and pointed. Dimensions of parameres are provided in Table 1. Right paramere (Fig. 5F,G) with basal part distinctly shorter than distal processes; ventral process subequal in length to dorsal process and curved dorsally with pointed apex; dorsal process rather narrow, expanded, and rounded apically, setose. Left paramere (Fig. 5F,G) with basal part slightly shorter to slightly longer than dorsal process and setose dorso-medially; ventral process narrowly rounded at apex; dorsal process wide, obliquely truncate, and setose apically; medial process small. Ovipositor short and wide (Fig. 5E), slightly sclerotised except for baculi; paraprocts distinctly shorter than gonocoxites, with heavily sclerotised baculi and several trichoid sensilla dorso-laterally; proctiger short, truncate at apex, with sclerotised baculi; gonocoxite entire, with sclerotised, oblique baculi, setose apico-laterally; gonostyli cylindrical, attached before apices of gonocoxites, with three trichoid sensilla at apex. Proximal portion of vagina spirally twisted (Fig. 5E).

Sexual dimorphism. Females generally larger than males, with elytra somewhat wider in proportion to length (Table 6). Protibiae in males slightly expanded basally, sometimes with several extended setae; in females not expanded and without longer setae. Terminal maxillary palpomere in males wider than in females (Fig. 5A,B).

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Variability. The individual variability is, besides the dimensions (Table 6), most strongly pronounced in the colouration of the pubescence, which may be pale yellowish on most of the dorsal surfaces or darkened to various extent in posterior portions of pronotum and elytra or entirely brownish. The number of lateral ridges on metatibiae varies from three to five and those on metatarsomere 1 also from three to five.

DNA sequences. Two DNA sequences of 568-bp *CO1*-gene fragment are deposited in GenBank and BOLD databases with accession numbers listed in Table 3.

Distribution. Albania, Algeria, Austria, Croatia, Italy, France, Germany, Greece, Morocco, Spain, Switzerland, and Tunisia.

Natural history. The adults were collected on the xeric Mediterranean grasslands (Fig. 7A) and ruderal vegetation on the flowers of Apiaceae plants. The larva is not known.

Mordellistena (*s. str.*) *pseudorhenana* Ermisch, 1977, status restituted

(Figs. 1B, 2, 3, 4, 6, 7)

Mordellistena (*s. str.*) *pseudorhenana* Ermisch, 1977: 164 [original description as part of identification key, type locality: Érd, Hungary, first report from Hungary, Croatia, Bulgaria, and Macedonia]; Kaszab (1979: 41–42, Fig. 21C) [identification key, figures]; Batten (1980: 43) [synonymised with *M. minima*, description of *M. nessebarica* Batten, 1980 based on paratypes of *M. pseudorhenana* from Bulgaria].

Mordellistena (*s. str.*) *minima*: Ermisch (1963: 61–62) [first report from Cyprus]; Batten (1976: 167, 169, Fig. 5) [localities, first report from France and Spain, figure]; Batten (1977: 172–175, Figs. 20, 26) [figures, identification key, localities]; Odnosum (1992: 523, Pl. 251, Figs. 5–6) [identification key, figures, first report from Russian Far East]; Odnosum (1993: 24–26, Pl. 3, Fig. 26) [identification key, figure, first report from Ukraine]; Odnosum (2003: 36, 40, 46, Pl. 4, Fig. 5) [identification key, figures, first report from Kyrgyzstan]; Odnosum (2005: 95–108, Figs. 19, 45, 110) [identification key, figures, localities]; Horák (2008: 99) [catalogue, first report from Azerbaijan, Bulgaria, Greece, Israel, Turkey]; Odnosum (2010: 154, 195–197, Fig. 76) [identification key, description, figure, first report from Jordan]; Ruzzier (2013: 108) [localities]; Horák (2020: 96) [catalogue, first report from Slovakia].

Mordellistena sajoi Ermisch, 1977: 165 **new synonymy** [original description as part of identification key, type locality: Őrszentmiklós, Nyáras [Őrbottyán, Hungary]]; Kaszab (1979: 45) [identification key].

Type locality. Érd, Hungary.

Type material examined: Holotype of *M. pseudorhenana*, HNHM, male, labelled: "♂ | Genitalpräparat | Érd Csiki | Coll. E. Csiki | *Mordellistena nana* Motsch. [handwritten] | Typus [red label] | pseudorhenana [handwritten] | Holotypus 1978 *Mordellistena pseudorhenana* Ermisch [handwritten, white label with red margins] | *Mordellistena minima* Costa det R. Batten 1977". A photograph of the holotype is available on Flickr (Selnekovič 2020). **Paratype of *M. pseudorhenana***, HNHM, female, labelled: "Lesina [Hvar island] 1914 Horváth". **Holotype of *M. sajoi***, HNHM, female, labelled: "Örszentmiklós Nyáras, Sajó | Holotypus 1978 *Mordellistena sajoi* Ermisch [handwritten; white label with red margins] | Staatl. Museum für Tierkunde. Dresden | *MORDELLISTENA* (*s. str.*) *MINIMA* Costa J. Horák det. 2017 | *Mordellistena* (*s. str.*) *pseudorhenana* Ermisch, 1977 D. Selnekovič det. 2020". A photograph of the holotype is available on Flickr (Selnekovič 2020).

Additional material examined: Bosnia and Herzegovina: 1 ♂, Mostar env., in collection as *M. minima* (HNHM). **Bulgaria:** 3 ♂♂, 3 ♀♀, Kiten, 42° 13′ 47″ N, 27° 46′ 20″ E, 10 m a.s.l., 26.vii.2014, D. Selnekovič *leg.*, ruderal vegetation, on flowers of *Daucus carota* (DSBS DS-37 to DS-42); 5 ♂♂, 1 ♀, Lilyanovo env., 41° 36′ 39″ N, 23° 18′ 36″ E, 460 m a.s.l., 26.vi.2015, D. Selnekovič, dry grassland (DSBS DS-51 to DS-56); 2 ♂♂, 1 ♀, Lilyanovo env., 41° 37′ 23″ N, 23° 19′ 41″ E, 570 m a.s.l., 26.vi.2015, D. Selnekovič (DSBS DS-57 to DS-59); 6 ♂♂, 2 ♀♀,

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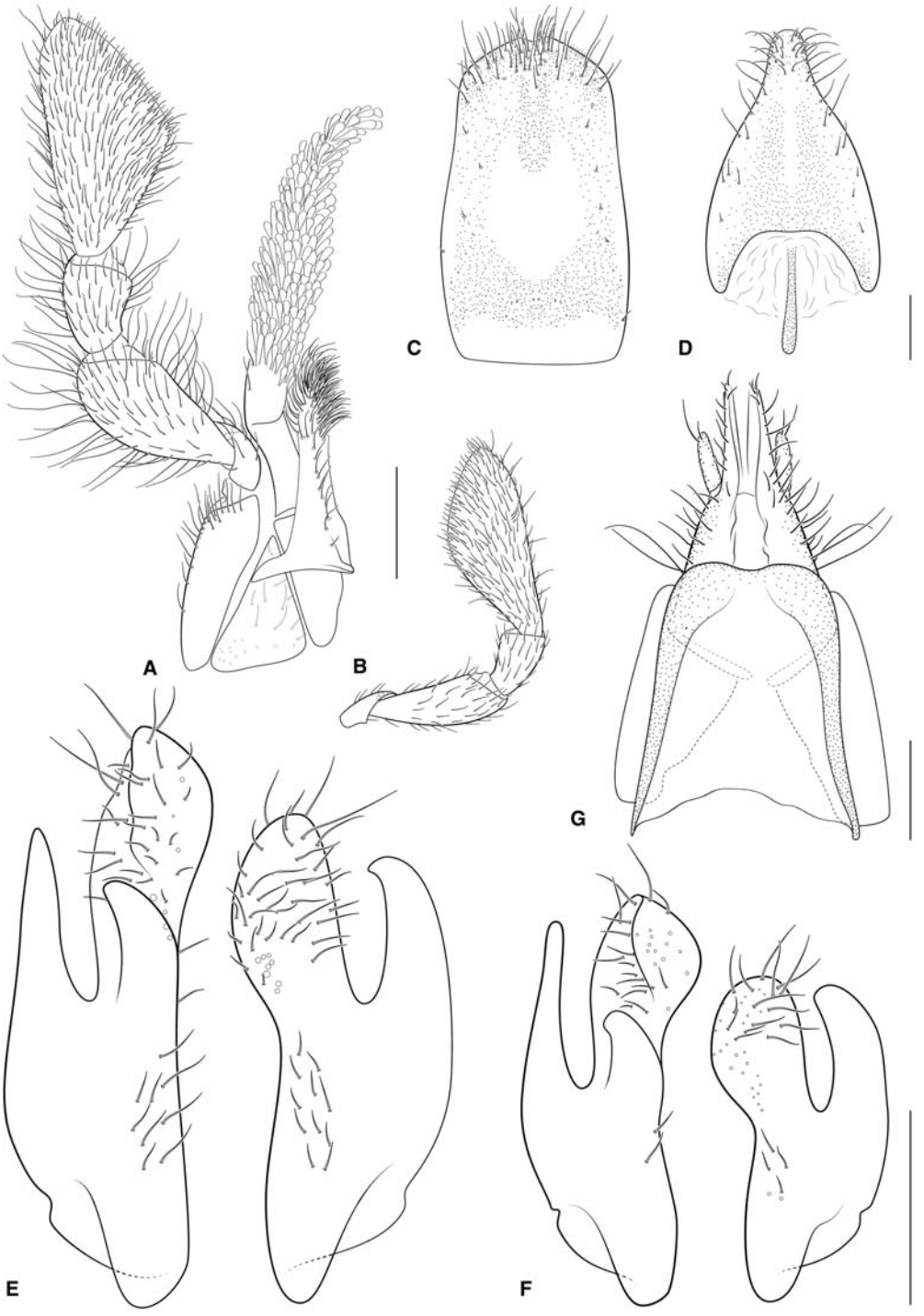

Fig. 6. *Mordellistena pseudorhenana* Ermisch, 1977. **A**, male maxilla; **B**, female maxillary palp; **C**, male abdominal sternite VIII; **D**, female abdominal sternite VIII; **E**, parameres (Cyprus, morphotype 2); **F**, parameres (holotype, morphotype 1); and **G**, ovipositor.

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Fig. 7. Habitats of *Mordellistena minima* Costa, 1854 and *M. pseudorhenana* Ermisch, 1977. **A**, xeric grasslands near Serrara village, Ischia, Italy (40°43′17″ N, 13°52′59″ E), with the presence of *M. minima* and *M. pseudorhenana*; **B**, xeric grasslands near Rozhen village, Pirin Mountains, Bulgaria (41° 31′ 51″ N, 23° 25′ 23″ E), with the presence of *M. pseudorhenana*; and **C**, ruderal habitat near Chotín village, Slovakia (47° 48′ 28″ N, 18° 11′ 53″ E), with the presence of *M. pseudorhenana*.

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Melnik env., 41° 30′ 43″ N, 23° 22′ 46″ E, 335 m a.s.l., 27.vi.2015, D. Selnekovič, dry grassland, on flowers of *Daucus carota* (DSBS DS-43 to DS-50); 5 ♂♂, 1 ♀, Rozhen env., 41° 31′ 51″ N, 23° 25′ 23″ E, 630 m a.s.l., 25.vii.2018, D. Selnekovič & Z. Peczová *leg*., xeric sandy steppe (DSBS DSBS_6 to DSBS_8 and DS-148 to DS-150). **Croatia:** 1 ♂, "Curzola" [Korčula island], 1914, Horváth *leg*., in collection as *M. minima* (HNHM); 2 ♂♂, Dubrovnik, Lokrum island, 2.viii.1958, Endrödy-Younga *leg*., in collection as *M. minima* (HNHM); 2 ♂♂, Dubrovnik, 16.viii.1967, S. Horvatovich *leg*., "Meeresküste" [seashore], in collection as *M. minima* (HNHM); 1 ♂, 3 ♀♀, Jablanac, 27–28.vii.1969, S. Horvatovich *leg*., in collection as *M. minima* (HNHM). **Cyprus:** 1 ♂, 1 ♀, Larnaka, Glaszner *leg*., R. Batten identified as *M. grisea* Mulsant, 1856 in 1979 (HNHM); 24 ♂♂, 7 ♀♀; Limassol, Germasogeia reservoir, 34° 45′ 19″ N, 33° 05′ 36″ E, 80 m a.s.l., 27.iv.2018, D. Selnekovič *leg*., dry grassland, on flowers of Apiaceae (DSBS DS-73 to DS-84, DS-112 to DS-113, DS-170 to DS-180, DSBS_9, DSBS_10, DSBS_12 to DSBS_14). **Israel:** 1 ♂, Jerusalem, Reitter *leg*., in collection as *M. minima* (HNHM DS-187). **Italy:** 4 ♂♂, 1 ♀, Ischia Island, Serrara env., 40° 42′ 60″ N, 13° 53′ 11″ E, 517 m a.s.l., 29.vi.2019, D. Selnekovič *leg*., ruderal vegetation, on flowers of *Daucus* (DSBS DS-169, DSBS_51 to DSBS_54); 6 ♂♂, 2 ♀♀, Ischia Island, Serrara env., 40° 43′ 17″ N, 13° 52′ 59″ E, 550 m a.s.l., 30.vi.2019, D. Selnekovič *leg*., dry grassland, on flowers of *Daucus* (DSBS DS-116 to DS-118, DS-181 to DS-185). **Montenegro:** 1 ♂, 1 ♀, Sutorman, Apfelbeck *leg*., in collection as *M. minima* (HNHM); 1 ♀, Zelenika, viii.1906, Horváth *leg*. (HNHM); 1 ♂, 1 ♀, Budva, 9.vii.1958, Kaszab & Székessy *leg*. (HNHM); 2 ♂♂, 3 ♀♀, Bar, 42° 06′ N, 19° 06′ E, 19.vii.2011, D. Selnekovič *leg*., ruderal vegetation, on flowers of *Daucus carota* (DSBS DS-12 to DS-16); 2 ♂♂, 2 ♀♀, Bar, Stari Bar, 42° 05′ 31″ N, 19° 07′ 58″ E, 120 m a.s.l., 19.vi.2011, D. Selnekovič *leg*. (DSBS DS-22 to DS-25); 2 ♂♂, 1 ♀, Bar, Volujica hill, 42° 04′ 16″ N, 19° 06′ 10″ E, 110 m a.s.l., 20.vi.2011, D. Selnekovič *leg*., dry grassland (DSBS DS-26 to DS-28); 3 ♂♂, 3 ♀♀, Virpazar env., 42° 14′ 40″ N, 19° 05′ 36″ E, 30 m a.s.l., 21.vi.2011, D. Selnekovič *leg*. (DSBS DS-29 to DS-34); 3 ♂♂, 2 ♀♀, Bar, Ribnyak monastery env., 42.13222° N, 19.12583° E, 215 m a.s.l., 22.vi.2011, D. Selnekovič *leg*., dry grassland, on flowers of *Helichrysum* (DSBS DS-17 to DS-21). **Slovakia:** 6 ♂♂, 3 ♀♀, Bratislava, Lamač, 48° 11′ 20″ N, 17° 03′ 30″ E, *ca*. 280 m a.s.l., 15.vii.2008, O. Šauša *leg*. (DSBS DS-02 to DS-10); 1 ♂, Rajecké Teplice env., 4.vii.2009, O. Šauša *leg*. (DSBS DS-01); 1 ♀, Štúrovo env., Vŕšok NR, 47° 49′ 10.0″ N, 18° 39′ 28.4″ E, 190 m a.s.l., 10.vi.2011, D. Selnekovič *leg*., Pannonian steppe (DSBS DS-11); 1 ♀, Bratislava, Ostrov Kopáč NR, 48° 06′ 04″ N, 17° 09′ 34″ E, 130 m a.s.l., 7.viii.2011, D. Selnekovič *leg*., Pannonian steppe (DSBS DS-35); 1 ♀, Hajnačka env., Tilič hill, 48° 12′ 28″ N, 19° 55′ 53″ E, 450 m a.s.l., 13.vii.2013, D. Selnekovič *leg*., dry steppe (DSBS DS-36); 1 ♀, Tvrdošovce env., 48° 05′ 30″ N, 18° 02′ 03″ E, 110 m a.s.l., 23.vii.2015, D. Selnekovič *leg*., ruderal vegetation along field margin (DSBS DS-60); 6 ♂♂, 5 ♀♀, Tvrdošovce env., 48° 06′ 01″ N, 18° 01′ 59″ E, 110 m a.s.l., 26.vii.2016, D. Selnekovič *leg*., salt marsh (DSBS DS-61 to DS-71); 24 ♂♂, 18 ♀♀, Chotín env., 47° 48′ 28″ N, 18° 11′ 53″ E, 106 m a.s.l., 12–18.vii.2017, D. Selnekovič *leg*., ruderal vegetation (DSBS DS-85 to DS-111, DS-123 to DS-137); 3 ♂♂, 1 ♀, Chotín env., 47° 48′ 28″ N, 18° 11′ 53″ E, 106 m a.s.l., 20.vi.2019, D. Selnekovič *leg*., ruderal vegetation (DSBS DSBS_43 to DSBS_46); 1 ♀, Virt env., 47° 45′ 35″ N, 18° 20′ 21″ E, 115 m a.s.l., 10.viii.2017, D. Selnekovič *leg*., ruderal vegetation along field margin, on flowers of *Daucus carota* (DSBS DS-72); 2 ♂♂, Virt env., 47° 45′ 36″ N, 18° 20′ 26″ E, 110 m a.s.l., 9.vii.2019, D. Selnekovič *leg*., ruderal vegetation along field margin, on flowers of *Daucus carota* (DSBS DSBS_59, DSBS_62); 1 ♀, Virt env., Mašan NR, 47° 46′ 10″ N, 18° 19′ 09″ E, 120 m a.s.l., 30.vii.2019, D. Selnekovič *leg*., sandy steppe, on flowers of *Seseli* (DSBS DS-122); 1 ♂, Iža env., Bokroš salt marsh NR, 47° 44′ 53″ N, 18° 15′ 38″ E, 107 m a.s.l., 29.vii.2019, D. Selnekovič *leg*., grazed salt marsh, on flowers of *Daucus carota* (DSBS DS-120). **Slovenia:** 3 ♂♂, Drežnica, Apfelbeck *leg*., in collection as *M. minima* (HNHM). **Switzerland:** 1 ♀, "Helvetia", in collection as *M. perroudi* (SDEI Col-11369). **Turkey:** 1 ♂, 1 ♀, Istanbul, 20.vi.1925, Biró *leg*., in collection as *M. minima* (HNHM DS-186). **Ukraine:** 2 ♀♀, Krim, Alusta, 18.vi.1956, L. Horváth *leg*., in collection as *M. minima* (HNHM).

Differential diagnosis. *Mordellistena pseudorhenana* can be characterised by the following combination of characters: (1) body including mouthparts, antennae, and legs black (Fig. 1B); (2) pubescence on dorsal surfaces yellowish or pale brownish with purple sheen; (3) galea long, apically pointed (Fig. 6A); (4) antennomeres 5–10 *ca*. 1.20–1.30 times longer than wide; (5) protibiae in males expanded basally, with distinct clusters of extended setae; (6) metatibiae with three lateral ridges, the second one being the longest and the third one usually the shortest; (7) abdominal sternite VIII in males 1.50–1.60 times longer than wide, with *ca*. parallel lateral margins (Fig. 6C); in females, apically produced and rounded, with spiculum ventrale narrowly clavate (Fig. 6C); and (8) parameres and ovipositor as in Figure 6E,F,G.

Based on the morphology, the species can be assigned to the *M. confinis* species group as defined by Ermisch (1956). From other members of the group, it can be differentiated based on the long and pointed galea (Fig. 6A), in combination with short antennomeres 5–10, expanded protibiae with distinct clusters of extended setae in males, and completely black-coloured body. Such form of galea is also present in *M. grisea* Mulsant, 1856 (*sensu* Batten 1977), but it can be differentiated from *M. pseudorhenana* by its protibiae not being expanded in males and by parameres of different shape.

Redescription. Body slender, wedge-shaped, widest at proximal one-half of elytra, dorsum moderately convex, venter strongly so (Fig. 1B). Metric characters are provided in Tables 1 and 6. Colour of almost all surfaces uniformly black with fine bluish sheen; anterior margin of frontoclypeus, mandibles, lacinia, galea, and labium, including palpi, brownish. Vestiture consisting of dense, decumbent, dorso-ventrally flattened setae; colour uniformly light-yellowish on head and sternal thoracic parts; in anterior one-half of pronotum light-yellowish and slightly darkened postero-medially; in antero-lateral portions of elytra light-yellowish and gradually darkened postero-medially to completely black in apical portions; on femora and proximal portions of tibiae light-yellowish and gradually darkened distally; on abdominal ventrites 1–2 light-yellowish, gradually darkened on following ventrites to entirely black on ventrite 5 and pygidium; vestiture on elytra with strong purple sheen.

Head moderately convex dorsally; anterior margin of frontoclypeus straight; occipital carina evenly rounded in dorsal view, straight to slightly concave in posterior view; tempora absent; dorsal surface very finely microreticulated, with minute, round setiferous punctures. Labrum transverse, microreticulate, with setiferous punctures, exposed portion *ca*. 2.50 times wider than long, anterior margin and antero-lateral angles rounded. Eyes broadly oval, *ca*. 1.40 times longer than wide, not extending onto ventral surfaces, finely faceted with distinctly apparent interfacetal setae. Antennae moderately long, feebly serrate (Fig. 1B); scapus and pedicel cylindrical, subequal; antennomeres 3–4 slightly shorter than previous and distinctly shorter than following, subequal; antennomeres 5–10 subequal, in males *ca*. 1.20–1.30 times and in females *ca*. 1.10 times longer than wide; antennomere 11 oval, *ca*. 1.80 times longer than wide. Mandibles symmetrical except in molar parts, bidentate, with lateral exposed portion setose; mola denticulate; prostheca with thin, medially oriented setae. Maxilla as in Figure 6A,B; galea almost as long as maxillary palp, pointed at apex, densely covered with trichoid and distally expanded, spoon-like sensilla; lacinia with trichoid sensilla arranged in longitudinal row and scattered in apical portions; palpifer subcylindrical, setose antero-laterally; maxillary palpomere 1 short, setose ventrally; maxillary palpomere 2 cylindrical, widened apically, in males wider than in females; maxillary palpomere 3 short, widened apically; maxillary palpomere 4 securiform, *ca*. 2.40 times longer than wide, with inner angle situated behind middle; maxillary palpomeres 2–3 in males with very long setae on ventral surfaces. Terminal labial palpomere broadly fusiform.

Pronotum convex, slightly transverse (Table 6), widest around middle; anterior margin slightly produced in middle, anterior margination complete, anterior angles rounded; lateral carinae rounded in dorsal aspect, slightly concave in lateral aspect, lateral margination inapparent but complete; posterior angles slightly obtuse, narrowly rounded; surface finely microreticulate, with rasp-like setiferous punctures. Hypomeron with large concavity for reception of procoxae. Prosternal

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process obliterated. Scutellar shield triangular, punctuate, and setose. Mesoventral process as wide at apex as mesotibia, truncate. Metaventral discrimen inapparent. Metanepisternite with exposed portion rather wide, distally narrowed; lateral margin concave, mesal margin straight.

Elytra moderately convex, evenly and strongly narrowed posteriorly, widest at end of first one-quarter, EL/EW ratio in Table 6; lateral carinae rounded, strongly convergent behind first one-quarter (Fig. 1B); apices separately rounded; surface with fine microreticulation formed by transverse, undulate lines and with rasp-like setiferous punctures.

Protibiae straight, distinctly dilated basally and with fringe of long, medially oriented setae in males; mesotibiae slightly bent medially; metatibiae with one apical and three lateral ridges parallel to apical tibial margin; second lateral ridge is usually distinctly longer than first one, not reaching beyond one-half of tibial width; third lateral ridge often short and inapparent; metatibial spurs black, outer one *ca*. 0.70 times as long as inner one. Protarsi about as long as protibiae, protarsomere 1 as long as following two tarsomeres combined; protarsomere 4 distinctly longer than wide with anterior margin slightly concave; protarsal claws tridentate; mesotarsi *ca*. 1.30 times as long as mesotibiae; metatarsomere 1 with three ridges, metatarsomere 2 with two ridges, metatarsomere 3 without ridges.

Pygidium moderately long (Table 6), slightly bent ventrally in lateral aspect, about twice as long as ventrite 5. Ventrite 5 with apical margin rounded. Sternite VIII in males *ca*. 1.50–1.60 times longer than wide, setose apically, with lateral margins slightly convergent, postero-lateral angles distinct, rounded, apical margin slightly sinuated in middle (Fig. 6C); in females, *ca*. 1.50–1.60 times longer than wide, setose apico-laterally, strongly produced and narrowly rounded apically, with basal margin broadly concave, spiculum ventrale narrowly clavate (Fig. 6D). Sternite IX in males slender, arrow-shaped. Phallobase long, *ca*. 0.60 times as long as elytra, with distal arms *ca*. 4.00 times as long as tubular part. Median lobe very long and narrow, *ca*. 1.20 times as long as elytra, slightly expanded, and pointed apically. Dimensions of parameres as in Table 1. Right paramere (Fig. 6E,F) with basal part subequal to distinctly longer than the branches, setose dorso-medially; ventral branch shorter than dorsal one, slightly bent dorsally; dorsal branch wide, setose, rounded apically. Left paramere (Fig. 6E,G) with basal part about as long as dorsal branch, setose dorso-medially; ventral branch rather long, narrowly rounded apically; dorsal branch setose, moderately expanded, and obliquely truncate apically; medial process large, bent ventrally. Ovipositor (Fig. 6G) slightly sclerotised except for baculi; paraprocts slightly shorter than gonocoxites, with narrow, heavily sclerotised baculi; proctiger rather long with heavily sclerotised baculi, with apical margin sinuate; gonocoxites rather long and narrow, not divided, setose, with heavily sclerotised, oblique baculi; gonostyli cylindrical, attached well before apices of gonocoxites, bearing three trichoid sensilla at apices.

Sexual dimorphism. Antennomeres 5–10 in males slightly longer, *ca*. 1.20–1.30 times longer than wide, whereas in females they are *ca*. 1.10 times longer than wide. Maxillary palpomeres 1–3 in males bearing very long setae on the ventral surface; palpomeres 2 and 4 in males wider than in females (Fig. 6 A,B). Protibiae in males basally expanded, with group of longer, medially oriented setae; in females, simple, without extended setae.

Variability. The colour of pubescence on the dorsal surfaces varies from pale yellowish to darkened to various extents in posterior portions of pronotum and elytra to completely brownish. Rather distinct differences can be found in the shape and dimensions of the parameres between the morphotype 1 represented by holotype plus all the examined male specimens from Europe and the morphotype 2 represented by male specimens from Cyprus, Israel, and Turkey (Figs. 2, 3, 6 E,F; Table 1; Supplementary material, Table S1). The specimens of morphotype 2 have their parameres longer (Table 1), with the basal part of the right paramere longer and the dorsal process of the left paramere longer and narrower than in the morphotype 1 (Fig. 6 E,F). The barcoding region of *CO1* gene shows very small differences between the representatives of the two morphotypes (0.18–1.43%; Table 5).

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DNA sequences. Eighteen DNA sequences of the 568-bp *CO1* gene fragment are deposited in GenBank and BOLD databases, with accession numbers listed in Table 3.

Distribution. Azerbaijan, Bosnia and Herzegovina (**first record**), Bulgaria, Croatia, Cyprus, France, Greece, Hungary, Italy, Israel, Jordan, Kyrgyzstan, Macedonia, Montenegro (**first record**), Slovakia, Slovenia (**first record**), Spain, Switzerland (**first record**), Turkey, and Ukraine. Horák (2008, 2020) reports this species from the former Yugoslavia (present Serbia and Montenegro) without specifying the country. The report from Russian Far East by Odnosum (1992) is probably based on misidentification. *Mordellistena pseudorhenana* is reported here for the first time from Bosnia and Herzegovina, Montenegro, Slovenia, and Switzerland.

Natural history. The adults were found on the flowers of herbaceous plants, for example, *Daucus carota* Linnaeus, *Seseli* sp. (Apiaceae), *Galium* sp. (Rubiaceae), and *Helichrysum* sp. Miller (Asteraceae), in various grassland and ruderal habitats (Fig. 7) from June to August in altitudes 10–630 m above sea level. The larva of *M. pseudorhenana* is not known. The first author's efforts to obtain and rear larvae from the stems of *Cirsium arvense* (Linnaeus), *Centaurea* sp. (Asteraceae), and *Daucus carota* Linnaeus (Apiaceae) collected from two localities – Chotín (Fig. 7C) and Tvrdošovce, Slovakia – with abundant populations of the species were unsuccessful.

Remarks. *Mordellistena sajoi* Ermisch, 1977 was briefly described in the identification key based on a single female specimen. The re-examination of the holotype revealed it is conspecific with *M. pseudorhenana*, and we consider it a new junior subjective synonym of the latter.

Discussion

Revision of the type material is of great importance for future research in the European Mordellidae. Results of our recent studies show that re-examination of type material can reveal surprising findings regarding the identity and status of the taxa, including the common and widespread species (Horák 1990, 1996; Selnekovič and Kodada 2019; Selnekovič and Improta 2020). Naturally, searching for and obtaining the type material from museum collections can complicate the taxonomic work, especially when specimens cannot be found – for example, much of E. Mulsant's material. However, once the type specimens are documented and the species are redescribed and properly delimited based on morphological and molecular markers, modern identification methods such as DNA barcoding allow easier recognition of the species and can provide the basis for further studies in different fields, such as ecology, phylogeography, or development.

We used DNA barcodes for the first time to examine the genetic divergences between European Mordellidae species and to interpret the morphological variability observed in *M. pseudorhenana*. We were able to provide the DNA barcodes of *CO1* gene fragments conventionally used for species identification from five species of the *Mordellistena confinis* species group with revised and documented type material (Horák 1996; Selnekovič and Kodada 2019). The species showed wide genetic divergence even between morphologically similar species – for example, *M. minima* and *M. lindbergi* (19.3%), and *M. hirtipes* and *M. purpurascens* (13.8%; Table 4) – corresponding to results in other beetle groups (*e.g.*, Raupach *et al.* 2010; Pentinsaari *et al.* 2014). In contrast to high divergence between species, the mean intraspecific divergences were considerably less, up to 1.9% in *M. hirtipes*. The incongruence between morphological and molecular evidence appeared in *M. pseudorhenana*. Based on the differences in the shape and dimensions of parameres, we were able to identify two distinct morphotypes (Figs. 2, 3A, 6E,F; Table 1). To help us with the interpretation of such differences in morphology, we compared the intra- and interspecific Kimura 2-parameter divergences. Although no universal threshold exists for separating species based on the genetic divergences, the comparison of intra- and interspecific distances with the presence of a distinct genetic gap proved to be useful for species separation in beetles (*e.g.*, Raupach *et al.* 2010; Woodcock *et al.* 2013; Pentinsaari *et al.* 2014). The highest intraspecific Kimura 2-parameter distance within *M. pseudorhenana* (1.4%) was 11.8 times less than the smallest interspecific distance

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between *M. pseudorhenana* and *M. lindbergi* (16.8%). Furthermore, the intraspecific Kimura 2-parameter distances within *M. pseudorhenana* ranged from 0.2 to 1.4%, with no distinct gap. Such low genetic divergence between the two morphotypes does not provide evidence for establishing the morphotypes as separate species.

The discrepancy between the morphological and molecular evidence opens the discussion about the efficiency of using the conventional DNA barcoding marker (*CO1*) for testing the taxonomic boundaries and verifying the status of the species within the family Mordellidae. It also raises questions about the validity of species that have been defined by rather weak morphological differences. The broader datasets, a combination of multiple genes, and the use of more advanced tools in molecular taxonomy such as character-based DNA barcoding should yield more insights into the taxonomy of this problematic group.

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