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Detection and description of four *Vespa mandarinia* (Hymenoptera, Vespidae) nests in western North America

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Abstract

Vespa mandarinia Smith 1852 is a semi-specialized predator of other social Hymenoptera and one of the two largest species of *Vespa*. Several individuals of this predatory wasp were detected in Canada and the United States in 2019, including an entire nest that was located and destroyed on Vancouver Island, British Columbia. The Washington State Department of Agriculture and the United States Department of Agriculture's Animal and Plant Health Inspection Service have collaborated to survey Washington State for *V. mandarinia* since 2020, using traps staffed by agency personnel, collaborators from local governments and nongovernmental organizations, and the general public. Trap data and public reports were used to select sites for live-trapping or net surveys, and live hornets captured in these efforts were subsequently collected and fitted with radio tags to locate nests. The survey ultimately led to the discovery of a *V. mandarinia* nest in October 2020, and three nests in August and September 2021. All of the nests were located within in red alder trees (*Alnus rubra*), with one just above the ground in a standing dead tree, and the other three in cavities ~2 to 5 meters above the ground in living trees. The number of combs in each nest varied between four and ten, cells between 418 and 1,329, and total hornets per nest between 449 and 1,474 (including immature and mature stages). Together, the four nests indicate an incipient population of *V. mandarinia* in the Cascadia region, and ongoing action by local, state, provincial, and federal governments, and residents of both countries is required to avoid the establishment of this exotic species in the region.

Keywords
community science, Eradication, radio-tracking, social Hymenoptera

Introduction

Vespa mandarinia Smith, 1855, is one of the 22 species of hornet (Vespidae: *Vespa*) (Smith-Pardo et al. 2020). Like all hornets, *V. mandarinia* is a eusocial predaceous wasp that feeds on many different types of insects. One aspect of its behavior (shared by the closely related *V. soror*) is the ability to mount group attacks on other social Hymenoptera, including honey bees (*Apis* spp.), resulting in rapid destruction of entire colonies of their prey (Matsuura and Sakagami 1973). This behavior makes it a perennial pest of apiaries throughout its native range, and it is a notable predator of *Apis mellifera*, which lacks effective defensive behaviors against *V. mandarinia* (Matsuura and Sakagami 1973; Arca et al. 2014; Mattila et al. 2020).

The first verified North American specimens of *V. mandarinia* outside of ports of entry were collected in British Columbia in 2019. Several wasps were observed that year on Vancouver Island, British Columbia, culminating in the location and eradication of an entire nest in the city of Nanaimo in September 2019 (Bérubé 2020). In December 2019, *V. mandarinia* workers were found approximately 90 km SW in Blaine, WA. The first confirmed specimen in the United States was a single dead worker that was collected on a porch (Wilson et al. 2020). Two additional specimens that had been collected earlier in the year were subsequently provided to the Washington State Department of Agriculture (WSDA), both of which were associated with beehive attacks – one hornet that had been "hawking" at a hive, and two specimens which were collected from a killed colony. Two colony losses that strongly resembled descriptions of *V. mandarinia* attacks in Japan (see Matsuura and Sakagami 1973) were also recorded in fall 2019 in the same region, although wasp specimens were not collected at either event. Based on the available evidence, WSDA, the United States Department of Agriculture's Animal and Plant Health Inspection Service (USDA APHIS), and the British Columbia Ministry of Agriculture implemented a robust trapping program in 2020, with the goal of early detection and eradication of any nascent *V. mandarinia* populations. The program included trapping by agency personnel and the general public and continuous public outreach to locate hornet populations. Because trapping hornet workers will not lead to eradication, WSDA also developed a protocol for capturing live hornets and tracking them to their nest, which could then be eliminated.

Public reporting

Washington State used active outreach to inform the public about *V. mandarinia* and encourage residents to report sightings. Potential hornet sightings were received via email, social media, phone calls, and through a purpose-built web application. All sightings were reviewed and positive/probable reports were used to inform trapping activities or initiate a site visit.

Lethal trapping

The basic survey approach was to use lethal traps and public reports to locate centers of hornet activity, and then shift to capturing live hornets that could be tracked back to nests. A variety of trapping approaches were identified from the literature and the experiences of beekeepers in the hornet's native range (Tatsuta and Makino 2003; Choi et al. 2012; Paschapur et al. 2022). Although there is considerable diversity in trapping approaches reported in the literature, many utilize a blend of fruit juices and ethanol. WSDA used bottle traps armed with orange juice and rice cooking wine (Makino and Sayama 2005; Okuda et al. 2011) because both components were available at grocery stores and promoted consistency across our collaborator and community science trapping programs. In 2020, traps were constructed from 1.65L (56 oz) clear plastic bottles with 2 cm square openings on 3 sides (Fig. 1). Each bottle contained a bait/killing solution comprising approximately 120 ml (4 oz) of orange juice and 120 ml (4 oz) of rice wine of at least 10% ABV. Captured hornets would subsequently drown in the bait. This approach was repeated in 2021, with the exception that the square-shaped openings were replaced by star-shaped openings due to concerns that the hornets might escape from the traps. This concern was raised when late-season captures of other insects in 2020 were so massive that they formed a solid surface inside the traps, allowing hornets to avoid the killing solution.

Traps maintained by WSDA were mostly placed in Whatcom County in northwestern Washington State and maintained from June through November, covering the entire presumed area of potential hornet occupancy. In 2020, three traps were placed per square km, within a 2 km radius from any detection made through May 2020. Trap density was decreased to two traps/km^2 at a 4 km radius, and to one trap/km^2 at an 8 km radius. The maximum distance for the 2020 trapping areas was based on the maximum foraging distance of 8 km reported by Matsuura and Sakagami (1973). Traps were placed on branches in trees at ca. 2-2.2 meters high, depending on site characteristics and trapper height. In 2021, the trap density was reduced to 1/km^2 throughout the trapping area, but the geographic area of trap coverage was expanded. A series of traps testing alternative lures (e.g., isobutanol, 2-methyl butanol, and acetic acid; Landolt and Zhang 2016) was also maintained at eight sites in 2020 during the trapping season. Those results are not analyzed in this paper, but hornets caught using experimental lures are included in the results reported here.

Figure 1. A bottle trap used to survey for *V. mandarinia* by the Washington State Department of Agriculture, collaborating agencies, and community scientists.

Traps maintained by WSDA were inspected every 7 to 10 days, and each trap action (e.g., trap placement, service, specimen collected) was recorded using a smartphone. A short trap check interval was selected in part because the traps lacked a preservative, with longer trap return intervals potentially compromising DNA and morphological analysis of trap contents, in addition to being unpleasant to service. The short interval also allowed the agency to rapidly respond to captures and begin attempts to collect live specimens to track to a nest. In 2020, all trap contents were strained, sorted for field detection of *V. mandarinia*, and all bycatch collected into a sample bottle for further analysis. In 2021, contents were sorted in the field to detect *V. mandarinia*, with one trap randomly selected daily by each trapper for analysis of bycatch. Because trap contents were not returned to the lab in 2021, the agency initiated a quality control program by placing a preserved hornet in a random trap in each trapper's field area once a week to ensure suspect hornets were reported.

WSDA also recruited other agencies, nongovernmental organizations, and private residents (i.e., community scientists) to employ the same trapping protocol and expand the program more broadly in the state. This approach was also used in British Columbia, with community scientists staffing most traps. Instructions for constructing and servicing traps were provided on the WSDA website, and trap locations were logged by participants via an ArcGIS web app. These traps were located opportunistically and at the convenience of the participants, who were asked to check traps weekly. In 2020 the agency requested participants to send all trap contents to the WSDA Entomology Laboratory for analysis, in part to ensure hornets were not missed, and in part to analyze bycatch for impacts on non-hornet species. In 2021 the agency only requested trap contents from captures of potential hornets. In all, 1,681 traps were deployed in 2020 (797 WSDA, 263 collaborating agencies, 621 community science), and 1,648 total traps were deployed in 2021 (868 WSDA, 370 collaborating agencies, 410 community science) (Fig. 2).

Live trapping

An array of live traps was deployed near any hornet detections. Two live trap designs were used. One was based on a modified bottle trap incorporating a screen to separate the hornets from the attractant/kill solution. We also used translucent unitraps, again with a screen to isolate hornets from the killing solution. The unitraps were further modified by adding additional screened holes to the upper section to reduce heat and fumes inside of the trap, and potentially increase the chemical plume released from the baits (Fig. 3). Once deployed, live traps were checked daily, six days a week.

Tracking

Live hornets captured in traps or by net were chilled on ice and affixed with a radio tag for tracking back to a nest. Bluetooth tags constructed at the University of Washington, modified from tags developed to monitor bumble bee activity, were used for the first two tracking attempts. Subsequent tracking efforts employed VHF radio tags produced by Lotek (in 2020) or Advanced Telemetry Systems (in 2021). The initial attempt to glue a tag to a captive hornet, following the approach used by Iyer et al. (2019, 2020) was not successful. Bluetooth and VHF tags were subsequently attached by gluing them to dental floss or Teflon thread, and then looping this around the petiole of the insect and tightening it against the body (Fig. 4). After affixing the tag to a captive hornet, it was provided with commercially-produced jam or jelly, allowed to feed, and then followed with antenna-enhanced cell phones (for the Bluetooth tags) or commercially-produced receivers and Yagi antennas (for VHF tags) once the hornet commenced flying (Fig. 4).

Nest removal

Upon locating a nest, an electric vacuum with an in-line collection chamber was used to capture as many worker hornets as possible, followed by physical removal of the nests. The vacuum approach was preferred to insecticides to avoid contaminating sites and to

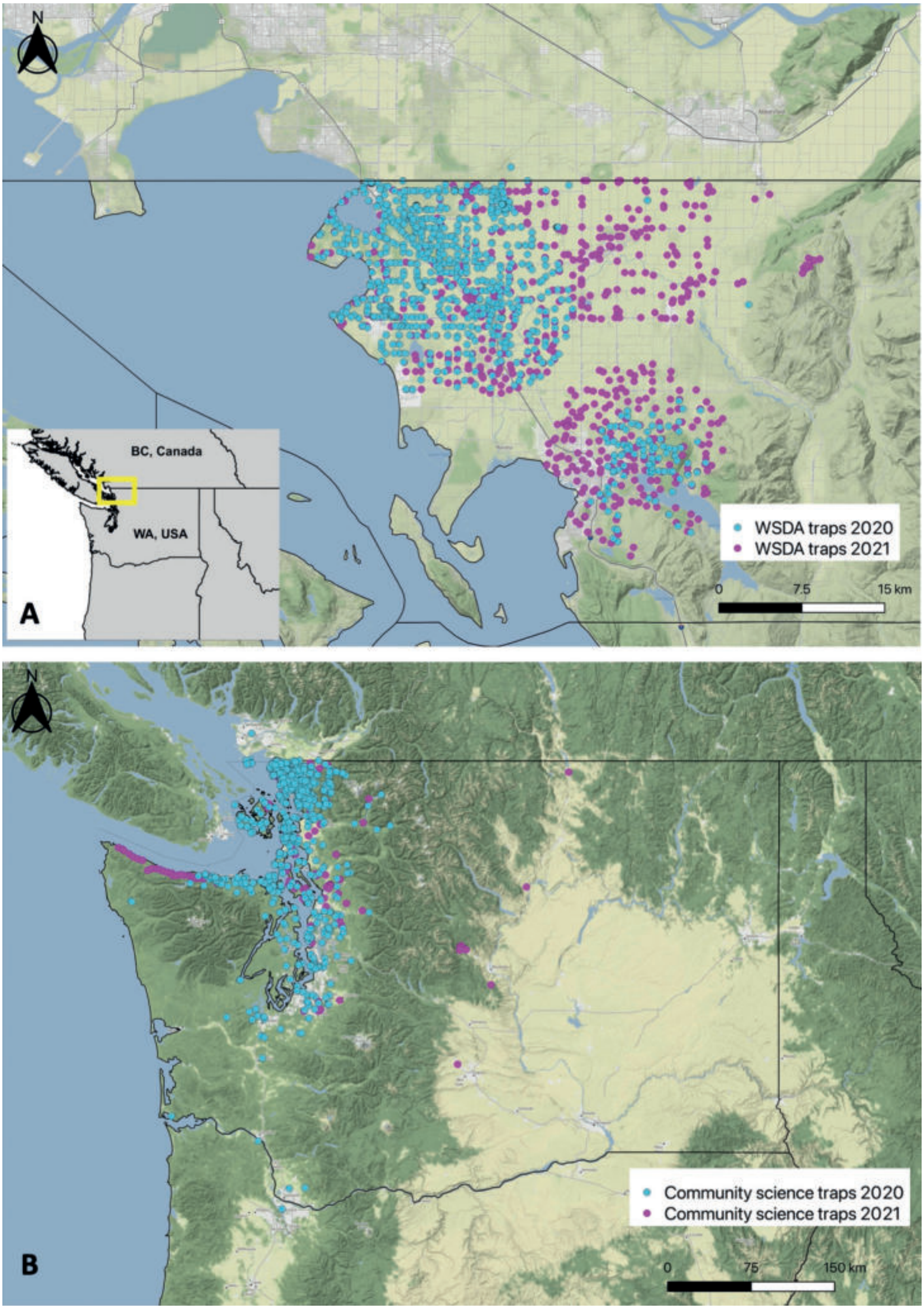

Figure 2. A map of bottle traps maintained by WSDA **B** map of bottle traps maintained by private residents and collaborating agencies. (Trap sites in British Columbia were not typically logged on the website and are thus underrepresented in these maps.) Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

Figure 3. Two styles of live traps used to collect *V. mandarinia* specimens for subsequent tracking back to an active nest.

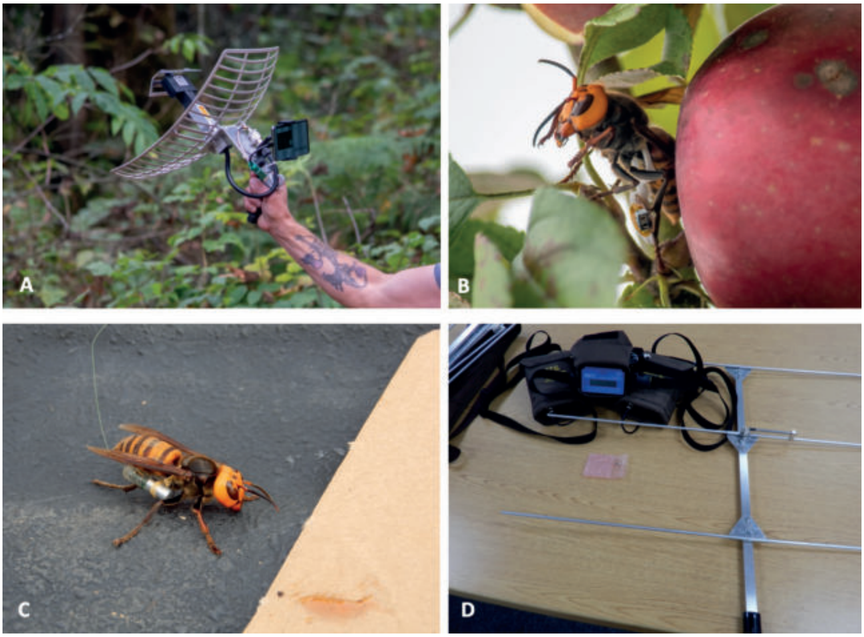

Figure 4. A antenna for Bluetooth tracking tag after Iyer et al. (2019) **B** *V. mandarinia* with affixed Bluetooth tag **C** *V. mandarinia* with ATS T-15 tag affixed **D** VHF receiver and Yagi antenna (Advanced Telemetry Systems).

facilitate safe study of nests following extraction. A 1% cyfluthrin dust was on hand for any situations where the vacuum was impractical, but was never required. Once located, hornets were vacuumed from the nest opening early in the morning, typically just before or at dawn. After the majority of workers were captured using the vacuum, carbon dioxide was used to anesthetize any hornets remaining in the nest. Nest openings were sealed with foam or plastic wrap and the entire structure removed from the site for study, or, if hornet activity was low, partially studied in situ. Live adult hornets collected with the vacuum or found within the nests were placed on ice and transported to the laboratory for study. Protective suits constructed from a thick mesh were worn during all nest extraction activities.

Nest analysis

Nest cavities were measured in the laboratory or on site. Combs were separated, and the depth and width of each cell was measured in the laboratory using a digital caliper, with the exception of two combs from nest 4 that were provided to landowners before they could be measured. The caste of each adult hornet collected was recorded (queens and workers were distinguished by size), and immature stages were counted as egg, larva, or capped cell. Capped cells were opened for nest 4 and the sex of all pupae was recorded. We did not distinguish between pupae and prepupae for the other three. Two nests had abundant litter beneath the combs, which was retained and placed in Berlese funnels to collect other insects living within the nest cavity.

A subset of hornets was collected alive at each eradication event, chilled, weighed, and body length and mesosomal width measured with digital calipers. Length was measured by pressing the chilled hornet gently onto a flat surface, positioning the head so that it was vertical, and measuring between the frons and the tip of the metasoma. Care was taken to ensure that the metasoma was not artificially extended by pushing on it nor shortened by compressing it with the caliper. Mesosomal width was measured at the wing hinge. Most hornets were well-chilled throughout the measurements; any that showed signs of activity were chilled again and remeasured.

Results

Four hornets were found and one photograph was submitted by the public in 2019. In 2020, 15 hornets were captured in WSDA or community science traps, one was collected in a net by a WSDA entomologist, one was collected in a net by a community member, and 17 confirmed hornet reports were received through photographs or dead specimens. In 2021, four hornets were collected in traps, three were captured by WSDA entomologists, one was captured by a community member, and three were reported or found dead by community members (Table 1, Fig. 5).

Only a small amount of these detections led to opportunities to find nests. A homeowner report in late September 2020 was followed by a site visit by a WSDA entomologist, who was able to capture a foraging hornet with a net. The following day a Bluetooth tag was glued to the mesosoma of the hornet, but it failed to fly. It was initially supposed

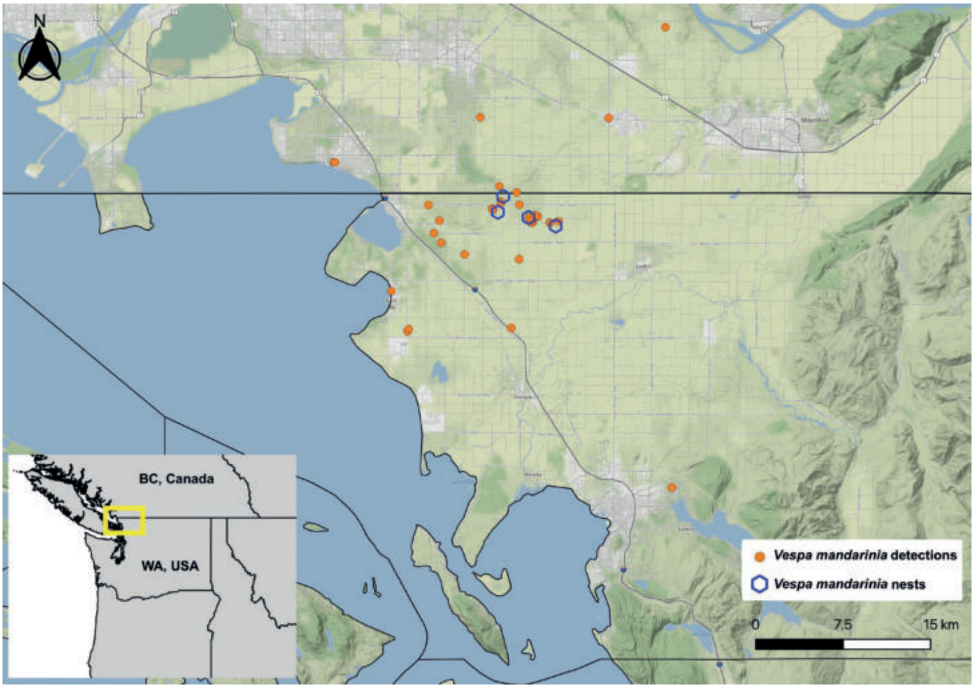

Figure 5. Map of confirmed *Vespa mandarinia* specimens and nests recorded from British Columbia and Washington State in 2020–2021. Details on the nest collected in British Columbia (not shown) in 2019 can be found in Bérubé, 2020. A single male specimen found in 2021 further south in Washington State was unrelated to these sightings and is also not included here. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

that the wings were glued together while affixing the tag, but later examination showed that the wings were intact. We suspect instead that the hornet may have been chilled for too long. The homeowner captured another hornet the following week, which was successfully affixed with a Bluetooth tag by gluing it to floss and tying it around the hornet's petiole. The hornet successfully recovered and flew, but left the range of the antennas within an hour and was not detected again. Four hornets were collected alive in nearby traps the following week, two of which were affixed with VHF tags (NanoPin, Lotek Inc.). One of these was subsequently tracked for approximately 240 m from the release site to the first *V. mandarinia* nest located in the United States, and the second in North America. The nest was found in a cavity within a living red alder (*Alnus rubra* Bong.), approximately 2.4 m above the ground (Fig. 6a). A few more hornets were subsequently found in the vicinity of that nest after the nest was removed, but no more hornet nests were detected in 2020.

In 2021, several reports of hornets were received from a site located near the US/Canada border. Upon intensive trap placement and survey of the area, WSDA entomologists captured two hornets, which were subsequently tagged with VHF tags (T15, Advanced Telemetry Systems). One of these was successfully followed for about 625 m to the second nest detected in the US. Nest 2 was found within a completely dead alder tree, with the entrance at roughly ground level and combs extending both into the tree and below

Table 1. *Vespa mandarinia* specimens and confirmed sightings in British Columbia and Washington State, 2019–2021.

Date	State/ province	County (US)/ regional district (BC)	Caste	Method	Number	Notes
Aug-Sep 2019	BC	Vancouver Island	W, Q	found	many	Nanaimo nest; see Bérubé 2020 for more details
19-Oct-2019	WA	Whatcom	W	found	2	workers collected from killed *A. mellifera* colonies
22-Oct-2019	WA	Whatcom	W	found	1	dead worker, hornets observed hawking at apiary
13-Nov-2019	BC	Fraser Valley	Unk	photo only	1	
8-Dec-2019	WA	Whatcom	W	found	1	dead worker found on porch
10-May-2020	BC	Fraser Valley	W	hand capt.	1	
13-May-2020	BC	Fraser Valley	Q	found	1	queen found dead in garden
27-May-2020	WA	Whatcom	Q	found	1	queen found dead in driveway
6-Jun-2020	WA	Whatcom	Q	found	1	queen dead on porch
14-Jul-2020	WA	Whatcom	Q	trap	1	orange juice/rice wine trap, WSDA
29-Jul-2020	WA	Whatcom	M	trap	1	orange juice/rice wine trap, WSDA
17-Aug-2020	WA	Whatcom	Unk	photo only	1	
19-Aug-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, citizen science survey
21-Sep-2020	WA	Whatcom	W	hand capt.	1	sprayed with pesticide
25-Sep-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, citizen science survey
29-Sep-2020	WA	Whatcom	Unk	photo only	1	
29-Sep-2020	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
30-Sep-2020	WA	Whatcom	W	found	1	dead worker found in porch light
2-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
5-Oct-2020	WA	Whatcom	W	hand capt.	1	collected by private citizen
9-Oct-2020	BC	Fraser Valley	W	trap	1	orange juice/rice wine trap
9-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
15-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine/honey bee comb, WSDA
15-Oct-2020	WA	Whatcom	W	trap	1	isobutanol-acetic acid, WSDA
20-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine/honey bee comb, WSDA
20-Oct-2020	WA	Whatcom	W	trap	2	isobutanol-acetic acid, WSDA
21-Oct-2020	WA	Whatcom	W	trap	2	orange juice/rice wine/honey bee comb/ isobutanol, WSDA
24-Oct-2020	WA	Whatcom	W	nest erad.	many	US nest 1
27-Oct-2020	BC	Fraser Valley	M	hand capt.	1	feeding on pumpkin
29-Oct-2020	WA	Whatcom	M	found	1	sticky trap
29-Oct-2020	WA	Whatcom	W	found	1	found dead in water bowl
29-Oct-2020	WA	Whatcom	Q	found	3	found dead in water bowl
30-Oct-2020	WA	Whatcom	M	trap	1	orange juice/rice wine trap, WSDA
1-Nov-2020	WA	Whatcom	M	hand capt.	1	crawling in garage
4-Nov-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
7-Nov-2020	BC	Fraser Valley	Q	hand capt.	1	crawling in house
12-Nov-2020	WA	Whatcom	M	hand capt.	1	crawling in driveway
4-Jun-2021	WA	Snohomish	M	found	1	found dead in yard
12-Aug-2021	WA	Whatcom	W	photo only	1	internet report
12-Aug-2021	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
13-Aug-2021	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
17-Aug-2021	WA	Whatcom	W	hand capt.	1	collected by private citizen
8-Sep-2021	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
8-Sep-2021	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
9-Sep-2021	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
25-Aug-2021	WA	Whatcom	W	nest erad.	many	US nest 2
10-Sep-2021	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
21-Sep-2021	WA	Whatcom	W	nest erad.	many	US nest 3
12-Sep-2021	WA	Whatcom	W	hand capt.	1	crawling in yard
23-Sep-2021	WA	Whatcom	W	nest erad.	many	US nest 4
22-Oct-2021	BC	Fraser Valley	W	trap	1	dead in Japanese beetle trap

Figure 6. A nest 1 (23 October 2020) **B** nest 2 (25 August 2021) **C** nest 3 (11 September 2021) **D** nest 4 (23 September 2021). Arrows indicate location of nest entrance.

ground (Fig. 6b). Soon after the detection and removal of the second nest, a homeowner captured a hornet using a makeshift trap, which was subsequently tagged and tracked 490 m from the release point to the third nest in the US, and fourth in North America. A public report also led to the capture of a fifth living hornet in 2021, which was tagged and tracked for 650 m to the fourth nest. Nests 3 and 4 were, like the first nest in 2020, located within red alder trees well above ground (nest 3 – ~2.2 m, and nest 4 – ~ 5.5 m; Fig. 6c, d).

All nest measurements and life stages are presented in Tables 2–6. The nests varied in the number of combs and total cells, ranging from 4 to 10 combs (Figs 7–8; Tables 2–4), and 418 to 1,329 cells (Tables 2–6). Nest 1, found late in 2020, contained 76 queens, and another 25 emerged while the nest was being studied. It was not possible to identify the foundress, which may have already died. Nine males were also recovered from nest 1. Only a single queen was found in each of the other nests. In each of these, the queen was not found until the nest was extracted, and in each case was the last adult hornet to be collected in the nest. The only other nest that contained adult males was nest 3 (the smallest), of which approximately 37% of adult hornets were males (Table 4). All capped cells from nest 4 were opened, and found to contain 23 male pupae, 112 female pupae, and 126 pre-pupae.

Table 2. Characteristics of *V. mandarinia* nest 1, collected 23 Oct 2020.

Comb	Total cells	Mean cell depth	Mean cell width	Eggs	Larvae[1]	Capped cells
1	238	21.82	10.34	0	0	0
2	212	44.49	11.52	0	6	9
3	177	34.74	12.53	0	8	41
4	137	32.8	12.08	0	30	58
5	98	29.20	12.81	0	12	0
6	31	18.91	11.22	6	7	0

[1] Only larvae still in the combs are represented here. Many larvae fell from the combs when CO2 was applied to the nest while it was still in the tree.

Table 3. Characteristics of *V. mandarinia* nest 2, collected 25 Aug 2021.

Comb	Total cells[1]	Mean cell depth	Mean cell width	Eggs	Larvae	Capped cells
1[*#]	79	21.66	9.65	18	12	28
2	86	24.40	10.56	12	9	62
3	129	26.47	10.78	25	52	47
4[+]	168	24.16	10.81	48	17	97
5	200	25.71	11.23	0	45	150
6	207	26.29	11.26	16	59	128
7	236	23.66	11.38	53	104	52
8[*]	170	27.39	11.75	66	104	0
9	54	22.06	11.53	54	0	0

[*] One cell with 2 eggs.

[#] One cell with a larva and an egg.

[+] Two cells with 2 eggs.

Table 4. Characteristics of *V. mandarinia* nest 3, collected 11 Sep 2021.

Comb	Total cells	Mean cell depth	Mean cell width	Eggs	Larvae	Capped cells
1*	178	25.79	10.12	28	24	88
2	143	26.32	10.89	16	44	79
3	92	23.46	11.70	42	33	12
4	5	10.97	9.35	5	0	0

* One cell with 2 eggs.

Table 5. Characteristics of *V. mandarinia* nest 4, collected 23 Sep 2021.

Comb	Total cells	Mean cell depth	Mean cell width	Eggs	Larvae	Capped cells
1	93	22.75	9.80	6	20	31
2	91	23.89	10.28	2	15	52
3	88	25.75	11.08	2	16	56
4*	77	unmeasured	unmeasured	17	37	17
5	57	31.99	12.50	1	2	49
6	62	unmeasured	unmeasured	4	17	40
7	59	30.47	12.35	6	44	16
8	59	27.40	11.75	15	40	0
9	53	24.43	12.04	40	11	0
10	35	24.52	11.76	35	0	0

* One cell with 2 larvae, both appeared to be 2nd instar.

Table 6. Overview of *Vespa mandarinia* nests found in the United States, 2020–202021.

Nest	Collection date	Combs	Total cells	Eggs	Larvae	Capped cells	Workers	Males	Queens
1	23 Oct 2020	6	893	6	190[3]	108	112	9	76
2	25 Aug 2021	9	1329	292	422	564	195	0	1
3	11 Sep 2021	4	418	91	101	179	49	28	1
4	23 Sep 2021	10	674	128	202	261*	185	0	1

*23 of the capped cells contained male pupae, 112 contained female pupae, and 126 were prepupae.

A subsample of 366 hornets comprising 15 males, 249 workers, and 102 queens was measured from the four nests. Worker mass ranged from 0.36 g to 1.41 g, and males from 0.82 g to 1.3 g. Queens ranged between 1.84 g and 2.88 g (Fig. 9). The three foundress queens massed 2.7 g (nest 2), and 2.16 g (nests 3 and 4). Length of males ranged from 27.8 to 35.19 mm, workers from 21.83 to 37.08 mm, and queens from 36.93 to 44.15 mm. Mesosomal width of males was between 7.3 to 8.99 mm, workers from 6.2 to 9.1 mm, and queens from 8.94 to 10.96 mm. While queen mass was always appreciably larger than workers and males, there was slight overlap at the extremes of length and mesosomal width for a few individuals.

Other insects located in the nest included species of Staphylinidae, Elateridae, and Cantharidae commonly associated with decaying tree environments. Two species of flies were common in two nests, and have been recorded in other Vespidae nests (Table 7). Other invertebrates (e.g., Acari, Collembola, Annelida) were also collected in the Berlese funnels but were not enumerated.

Discussion

The nests located in the Pacific Northwest were generally somewhat smaller than those described by Matsuura and Sakagami (1973). The nest removed on Vancouver Island in mid-September 2019 contained approximately 400 cells and 200 adult hornets and was located in a subterranean burrow (Bérubé 2020). The largest nest reported here, collected in late August 2021, contained 1,329 cells, which is close to the size of the

Figure 7. Top – combs from nest 1, 23 Oct 2020; Bottom – combs from nest 2, 25 August 2021. Numbers next to the combs indicate the position in the nest (smaller numbers are older and higher in the nest). Comb characteristics are recorded in Tables 2–5.

Figure 8. Top – combs from nest 3, 11 September 2021; Bottom – combs from nest 4, 23 September 2021. Numbers next to the combs indicate the position in the nest (smaller numbers are older and higher in the nest). Comb characteristics are recorded in Tables 2–5.

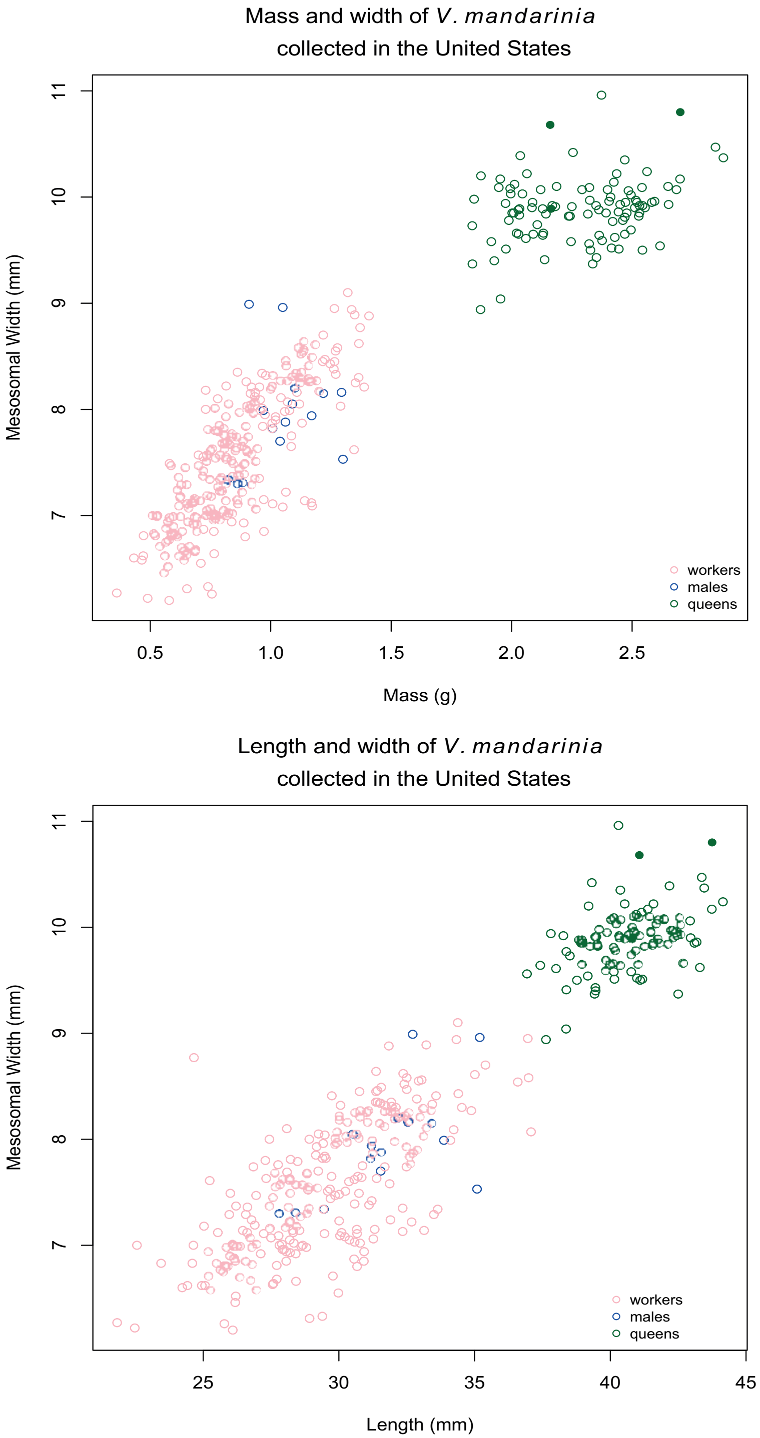

Figure 9. Body measurements of *V. mandarinia* collected from four nests in North America. The three foundress queens are represented with solid circles.

Table 7. Insects collected from litter below three *V. mandarinia* nests in Washington State, USA.

Order	Family	Species	Nest
Diptera	Scatopsidae	*Coboldia fuscipes* (Meigen, 1830)	1, 4
		Scatopse notata (Linnaeus, 1758)	1
	Phoridae	*Dohrniphora cornuta* (Bigot, 1857)	1
		Triphleba lugubris (Meigen, 1830)	1, 3, 4
		Megaselia sp.	4
	Sphaeroceridae	*Minilimosina parva* (Malloch, 1913)	1
	Milichiidae	*Leptometopa latipes* (Meigen, 1830)	1
	Fanniidae	*Fannia incisurata* (Zetterstedt, 1838)	1
Coleoptera	Staphylinidae	*Quedius* sp.	1
		Hylota ochracea Casey, 1906	1
		Phloeopora oregona Casey, 1906	1
		Crataraea suturalis (Mannerheim, 1830)	3
		Silusa californica (Bernhauer, 1905)	1, 4
		Scydmaenus ovipennis Casey, 1897	1
		Euplectus confluens LeConte, 1849	4
		Lobrathium subseriatum LeConte 1880	4
		Medon pugetense Hatch, 1957	4
	Elateridae	*Limoniscus* sp.	1
	Leiodidae	*Ptomaphagus nevadicus* Horn 1880	1
	Cantharidae	*Silis lutea* LeConte, 1853	1
	Corylophidae	*Sericoderus lateralis* (Gyllenhal, 1827)	3
	Histeridae	*Bacanius hatchi* Wenzel, 1960	3

smallest nest (collected in December) reported by Matsuura and Sakagami (1973). It is possible that the August nest would have continued to grow and may have approached the more typical size reported for nests in Japan. However, nests described by Matsuura and Sakagami (1973) were collected from south-central Japan, and more southerly nests may be able to expand more quickly to large sizes. Although details about nests from northern parts of the hornet's range are sparse, two nests collected on Hokkaido (Yamane and Makino 1977) each comprised five combs, with 675 cells (col. Aug 26, 1973) and 1141 cells (col. Sep 15, 1976). The nests removed in Washington State and British Columbia seem to be in accord with these northern records, so it is also possible that the nests we removed were typically sized for this latitude and climate.

One factor that may have impacted nest size and shape, particularly for nests 1, 3, and 4, was the constraining geometry of the tree cavity they were located within. The shape of the combs mirrored the internal shape of the cavities, and it is possible that workers could not use the space as efficiently as a nest in excavated soil. Indeed, the nest with the greatest number of cells reported here was nest 2, collected in August and the only one of the Washington nests not wholly confined to a tree cavity. Nest 3 seemed exceptionally small and contained a high proportion of males early in the season. The high number of males so early in the season is suggestive of inbreeding effects causing the production of diploid males (Van Wilgenburg et al. 2006; Darrouzet et al. 2015), which may have contributed to the very small nest size. Body measurements of all castes indicate that the largest workers and smallest queens could be confused if mesosomal width or body length is the only characteristic available for distinguishing between them, a phenomenon observed in other Vespidae (O'Donnell 1998).

It is interesting that all of the nests we located were in tree cavities in alder trees, with three of them high above the ground in still-living trees. Even though this is a small sample size, it is unexpected based on the most comprehensive reports of other nest sites (Matsuura and Sakagami 1973), where less than 16% of nests were reported from any sort of tree cavity. However, other data suggests that nests in cavities are somewhat more frequent (Choi et al. unpublished), and two of the three *V. mandarinia* nests reported by Yamane and Makino (1977) from Hokkaido were in tree hollows, although no further description is provided. Even so, the proportion of tree cavity nests in our results seems unusual. This could be a result of heavily saturated ground in the study area at the time queens are establishing nests, with more than 650 mm of total precipitation typical during the winter and spring months. Alternatively, nests from 2021 could have been established by queens that successfully dispersed from the 2020 nest after imprinting on the cues of their natal home, biasing nest selection towards alders.

No hornets were detected in British Columbia or Washington State in 2022. It is too early to feel confident that the species has been prevented from establishing, and several years of survey remain to be conducted. Some of the findings described in this paper suggest that small population effects may be impeding establishment, i.e., the unseasonably high number of males observed in nest 3. However, the characteristics of the other three nests, and our observations of foraging behavior and analysis of the local prey base (unpublished) concur with climate modeling (Alaniz et al. 2020; Zhu et al. 2020; Nuñez-Penichet et al. 2021) in suggesting that the region provides viable habitat for this species. Those results, and the recent spread of other hornet species outside of their range in multiple countries, are evidence that Vespidae require further study to either prevent, or mitigate the effects of, future introductions.

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RESEARCH ARTICLE

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The *taeniaticornis*-group of genus *Apanteles* Foerster (Hymenoptera, Braconidae, Microgastrinae) from China with one new species

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Abstract

The *taeniaticornis*-group of genus *Apanteles* Foerster from China is revised, in which a total of 3 species are recorded and illustrated. One new species, named, *A. parectangular* Liu & Chen, **sp. nov.** is described and illustrated, and a key to Chinese species of the *taeniaticornis*-group, is provided.

Keywords

China, Microgastrinae, new taxon, *taeniaticornis*

Introduction

The *taeniaticornis*-group was erected by Nixon (1965) along with other 43 species groups of *Apanteles* s. l. Six species were originally included in this group, which were largely characterized by the long metacarp and wedge shape of tergite I. Mason (1981) kept this group in the genus *Apanteles* s. str in his comprehensive reclassification of Microgastrinae which is preferred and used by most researchers worldwide (Fernandez-Triana et al. 2020). No other references had mentioned this group till one new species, *A. cuneiformis* Song et Chen, 2004, was reported from China and was defined as a member of the *taeniaticornis*-group by Chen and Song (2004). All members of this group are distributed in the Oriental region except for *A. conon* Nixon, 1965 which also occurs in Eastern Palaearctic (Papp, 1974).

The *taeniaticornis*-group is easily confused with other species-groups of the genus *Apanteles*, especially the *ater*-group, for their well-defined, sharp areolation of propodeum and setoseless and more or less concave vannal lobe beyond its widest part of hind wing, but it may be distinguished from other similar species-groups by characters combining the following: metacarp (vein 1-R1) rather long, often many times longer than its distance from the apex of marginal cell (from six times to nearly touching the apex of marginal cell); hind wing moderately broad, the length of the 1-M hardly shorter than the distance between its distal extremity and the apex of the vannal lobe; median and submedian cell densely setose all over; T1 narrowly wedge-shaped, its horizontal surface at least twice as long as wide across the hump; propodeum with complete, sharply defined areolation; ovipositor sheath same length of the hind tibia.

Before this study, there were two species belonging to *taeniaticornis*-group reported from China (Chen & Song, 2004). Here, we describe one new species of this group from China as a part of an on-going project on the revision of the Chinese Microgastrinae (Zeng et al. 2011a, b; Liu et al. 2014, 2015, 2016, 2018, 2019, 2020; Song et al. 2014).

Materials and methods

Specimens studied are deposited in the Parasitic Hymenoptera Collection of Zhejiang University, Hangzhou, China (**ZJUH**) and Hunan University of Arts and Science (**HUAS**). Each dried specimen is tagged with a unique voucher code.

Descriptions and measurements were made using a stereomicroscope (Zeiss Stereo Discovery V8). All photographs of the wasps were taken and processed using a digital camera KEYENCE VHX-2000C. The images were further processed using Adobe Photoshop CS6. Morphological terms for body structures and measurements follow Nixon (1965) and Mason (1981). The veins follow the modified Comstock-Needham system (van Achterberg 1993). The terminology of the cuticular sculpture follows Harris (1979). Abbreviations used in this research are as follows: POL = postocellar line, OOL = ocular-ocellar line, OD = ocellar diameter; T1 = 1st tergite of metasoma, T2 = 2nd tergite of metasoma, T3 = 3rd tergite of metasoma.

Taxonomy

Key to species of the *taeniaticornis*-group of the genus *Apanteles* Foerster from China

1 T1 not strongly constricted apically (Fig. 3g); interspaces of punctures on mesoscutum obviously bigger than their diameter, largely polished at middle and posterior parts (Fig. 3i); hind coxa entirely yellow (Fig. 3c) .... ***A. parectangular*** **Liu & Chen, sp. nov.**

– T1 strongly constricted apically (eg. Fig. 1h); interspaces of punctures on mesoscutum at most indistinctly bigger than their diameter, at most polished at posterior part (eg. Fig. 2g); hind coxa largely brown (Fig. 1f).................. **2**

2 Scutellar sulcus broad and deep (Fig. 2g); vein r of fore wing 1.3× longer than 2-SR (Fig. 2b)...................................... ***A. cuneiformis*** **Song & Chen, 2004**

– Scutellar sulcus narrower and shallower (Fig. 1d); vein r of fore wing 1.9× longer than 2-SR (Fig. 1g) .... ***A. conon*** **Nixon, 1965**

Chinese species of the *taeniaticornis*-group of *Apanteles*

Apanteles conon **Nixon, 1965**

Fig. 1

Apanteles conon Nixon, 1965: 124. Type in Natural History Museum, London. Chen et Song 2004: 38.

Diagnosis. Vertex between the eye and the posterior ocellus shiny with superficial fine punctures; ocelli big, posterior imaginary tangent to fore ocellus transecting the posterior pair; antenna slightly longer than body length, with penultimate antennomere 1.4× longer than wide; punctures on mesoscutum coarse, interspaces not bigger than their diameter, punctures indistinctly confluent above the hind polished area; areola on propodeum open anteriorly, V-shaped apically, with strong costulae, three posterior fields smooth without carinae; pterostigma big, 2.3× as long as its widest part, vein 1-R1 1.5× longer than pterostigma, 7.5× as long as its distance from the apex of the marginal cell, r 2.4× longer than 2-SR, angled at their meeting; T1 strongly wedged-shaped, 4.6× longer than hind width, turned-over part with rugose punctures laterally, T3 2× as long as T2; legs mostly yellow, hind coxa brown; ovipositor sheath about as long as hind tibia.

Variation. Body length 3.0–3.2 mm.

Male. Similar to female, except for antenna distinctly longer than body length, penultimate antennomere 2× longer than wide, and T2 higher.

Host. Unknown.

Material examined. ZJUH: 1♀, Shaxian, **Fujian**, 1980.XII, Gong Weili, No. 810003; 4♀♀, Mt. Wuyi, Fujian, 1988.IX.7, Lin Changfu, Nos. 20005691, 20005687, 20005692, 20005700; 1♀, Mt. Wuyi, Fujian, 1989.XI.1, Wang Jiashe, No. 964568; 1♀, Chibi, Yongqin, Fujian, 2002.IX.17, Liu Jinxian, No. 20023635; 2♀♀, Dazhulan, Fujian, 1991.X.6, Chen Xuexin, Nos. 920343, 920354; 2♀♀, Qingliu, Fujian, 1986.VI.20, Qi Shicheng, Nos. 965199, 9651200; 1♀, Antongmu, Fujian, 1981.IX.29, Fei Juyi, No. 20004167; 2♀♀, Mt. Longxi, Jiangle, Fujian, 1991.VII.16/IX.30, Liu Changming, Nos. 20007164, 20007209; 3♀♀2♂♂, Mt. Wuyi (Tongmucun), Fujian, 2009.IV.17/15, Wang Manman, Nos. 200900409, 200900398, 200900411, 200900408, 200900545; 6♂♂, Mt. Wuyi (Qili), Fujian, 2009.IV.18, Zeng Jie, Nos. 200900618, 200900650, 200900639, 200900647, 200900646, 200900642; 1♂, Mt. Wuyi (Sangang), Fujian, 2009.IV.17, Zeng Jie, No. 200900481; 1♂, Mt. Wuyi (Pikeng), Fujian, 2009.IV.21, Zeng Jie, No. 200900503; 1♂, Sangang, Fujian, 1981.V.6, Han Ying, No. 20003920; 1♂, Guanxian, **Sichuan**, 1980.VIII.1, He Junhua, No. 803037; 1♀, Hangzhou, **Zhejiang**, 1981, Lou Xiaoming, No. 930324; 1♀, Mt. Tianmu, Zhejiang, 1987.VII.21, Lou Xiaoming, No. 874572; 2♀♀, Mt. Fengyang, Longquan, Zhejiang, 2003.VIII.7/10, Liu Jingxian, Nos. 20055581, 20048319; 1♀, Mt. Jiulong, Suichang, Zhejiang, 1994.VIII.18, Can Ping, No. 944261; 2♀♀, Mt. Longwang, Anji, Zhejiang, 1996.VI.26, Zhao Weichun, Nos. 963915, 963916; 1♀, Mt. Jiulong, Suichang, Zhejiang, 1993.VIII.31, Chen Xuexin, No. 939685; 1♀, Mt. Tianmu (Jinshanmen), Zhejiang, 1999.VIII.6, Zhao Mingshui, No. 20002876; 4♀♀, Hangzhou, Zhejiang, 1989.VI.24/XI.10, He Junhua, Nos. 893118, 893108, 893311, 896960; 2♀♀, Liuheta, Hangzhou, Zhejiang, 2001.V.19, Piao Meihua, Nos. 200702186, 200702187; 1♀, Songyang, Zhejiang, 1992.XI.1–XII.9, Chen Hanlin, No. 934062; 1♀, Hangzhou, Zhejiang, 1991.V.28, He Junhua, No. 911118; 1♂, Mt. Tianmu (Xianrending), Zhejiang, 2011.VII.25–29, Liu Zhen, No. 201102651; 1♀, Mt. Tai, Taian, **Shandong**, 1997.VII.17, Chen Xuexin, No. 974014; 1♀, Yuexi, **Anhui**, 1981.V.16, Yang Fuan, No. 820593; 1♀, Shenlongjia (Honghua, 900m), **Hubei**, 1982.VIII.25, He Junhua, No. 825390; 1♀, Mengxiu, Ruili, **Yunnan**, 1981.V.2–6, He Junhua, No. 812956; 1♀, Jianfengling, **Hainan**, 2007.VI.7, Liu Jinxian, No. 200702381; 1♀, Meitan, **Guizhou**, 1982.VI.2, Xia Huaien, No. 824620; 1♀, Fengxi, Meizhou, **Guangdong**, 2003.VII.29, Chen Jujian, No. 20048632; 1♀, Mt, Yunji, Xinfeng, Guangdong, 2003.VII.20, Li Ping, No. 20053969; 1♀, Fengkai, Guangdong, 1992.V.16, Ma Yun, No. 921135; 3♀♀, Nanling, Fuyuan, Guangdong, 2004.V.8/2003.VII.23, Xu Zaifu, Nos. 20049641, 20049592, 20049143; 2♂♂, Dianba (900m), Wenxian, **Gansu**, 1998.VI.16, Ma Yun, Nos. 984241, 984332; 1♂, Yingtaogou, Xiangshan, **Beijing**, 1992.VII.6, Lin Naiquan, No. 20004394; 5♂♂, Shouka, **Taiwan**, 2011.V.30, Tang Pu, Nos. 201105461, 201105456, 201105455, 201105483, 201105454; 1♂, Mt. Dongmao, Taiwan, 2011.VI.4, Tangpu, No. 201104500; 1♂, Mt. Beishou, Gaoxiong, Taiwan, 2011.V.29, Tang Pu, No. 201104487; 2♂♂, Duonalindao, Taiwan, 2011.VI.13, Tang Pu, Nos. 201104994, 201104953; 9♂♂, Mt. Wugong, Gaoxiong, Taiwan, 2011.VI.15, Tang Pu, Nos. 201104826, 201104837, 201104838, 201104844, 201104846, 201104847, 201104855, 201104821, 201104827; 1♂, Mt. Nantou, Taiwan, 2011.VI.19, Tang Pu, No. 201104794;

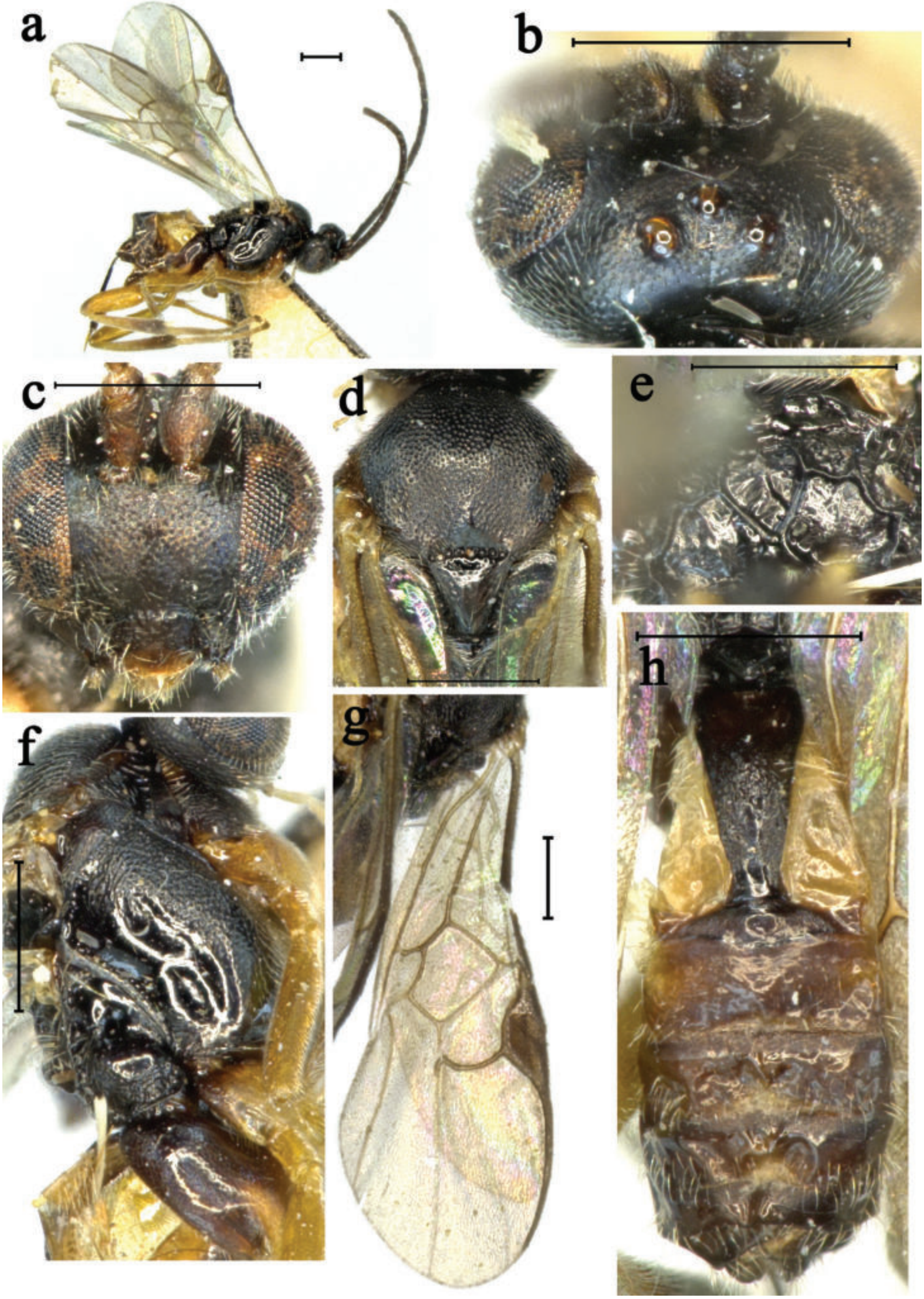

Figure 1. *Apanteles conon* Nixon, 1965 **a** habitus, lateral view **b** head, dorsal view **c** head, frontal view **d** mesosoma, dorsal view **e** propodeum **f** mesopleuron **g** fore wing **h** abdomen, dorsal view. Scale bars: 0.5 mm.

HUAS: 1♀, Bawangling, **Hainan** (malaise trap), 2020.IX.30–X.30, Chen Longlong, No. 202203542; 1♀, Mt. Limu, Qiongzhong, Hainan (malaise trap), 2020.IX.30–X.31, Chen Longlong, No. 202201705; 1♀, Haizhu Wetland, Guangzhou, **Guangdong** (malaise trap), 2021.III.20–IV.5, Liu Jingxian, No. 202200412; 8♀♀, Haizhu Wetland, Guangzhou, Guangdong (malaise trap), 2021.IV.26–V.11, Liu Jingxian, Nos. 202200200, 202200204, 202200226, 202200237, 202200263, 202200269, 202200274, 202200290.

Distribution. China (Anhui, Beijing, Fujian, Gansu, Guangdong, Guizhou, Hainan, Hubei, Hunan, Shandong, Sichuan, Taiwan, Yunnan, Zhejiang); Indonesia; Korea; Philippines.

Notes. Fernandez et al. (2020) examined the holotype in Natural History Museum, noting *A. conon* is possible a *Dolichogenidea* species because the punctures near the scutellar sulcus on mesoscutum do not fuse, but they kept it in *Apanteles* because other characters were invisible (such as setae beyond the widest part of vannal lobe). We had no opportunity to check the type, but checked the original description (Nixon, 1965), detailed examination from Chen and Song (2004) and Papp (1974) and characters from Chinese specimens (the typical wedged shaped T1). We also favor its placement in the genus *Apanteles*.

Apanteles cuneiformis Song & Chen, 2004

Fig. 2

Apanteles cuneiformis Song & Chen, 2004: 42.

Diagnosis. Vertex between the eye and the posterior ocellus shiny with superficial fine punctures; ocelli big, posterior imaginary tangent to fore ocellus transecting the posterior pair; antenna slightly longer than body length, with penultimate antennomere 2× longer than wide; interspaces of punctures on mesoscutum obviously bigger than their diameter, without striations at posterior end of the imaginary course of the notaulices; areola on propodeum closed anteriorly, V-shaped apically, with strong costulae, three posterior fields somewhat uneven; pterostigma big, 2.8× as long as its widest part, vein 1-R1 1.3× longer than pterostigma, 6.2× as long as its distance from the apex of the marginal cell, r 1.7× longer than 2-SR, angled at their meeting; T1 strongly wedged-shaped, 5× longer than hind width, turned-over part with rugose punctures laterally and deep concavity medially, T3 2.1× as long as T2; legs mostly yellow, hind coxa brown to black; ovipositor sheath slightly shorter than hind tibia.

Variation. Body length 2.4–2.6 mm.

Male. Similar to female, except for antenna distinctly longer than body length, penultimate antennomere 2.1× longer than wide and T2 higher.

Host. Unknown.

Material examined. ZJUH: 3♀♀, Letu, Nanjing, **Fujian**, 1991.V.23, Liu Changming, Nos. 20006107, 20006047, 20006130; 1♀, Nanjing, Fujian, 1991.VI.6, Pan Shen, No. 969562; 3♀♀3♂♂, Mt. Baxian, **Taiwan**, 2011.VI.4–5, Tang Pu, Nos. 201105226, 201105239, 201105277, 201105318, 201105273, 201105254; 2♂♂, Gaozhonglindao, Taiwan, 2011.VI.8, Tang Pu, Nos. 201105433, 201105437; 1♀,

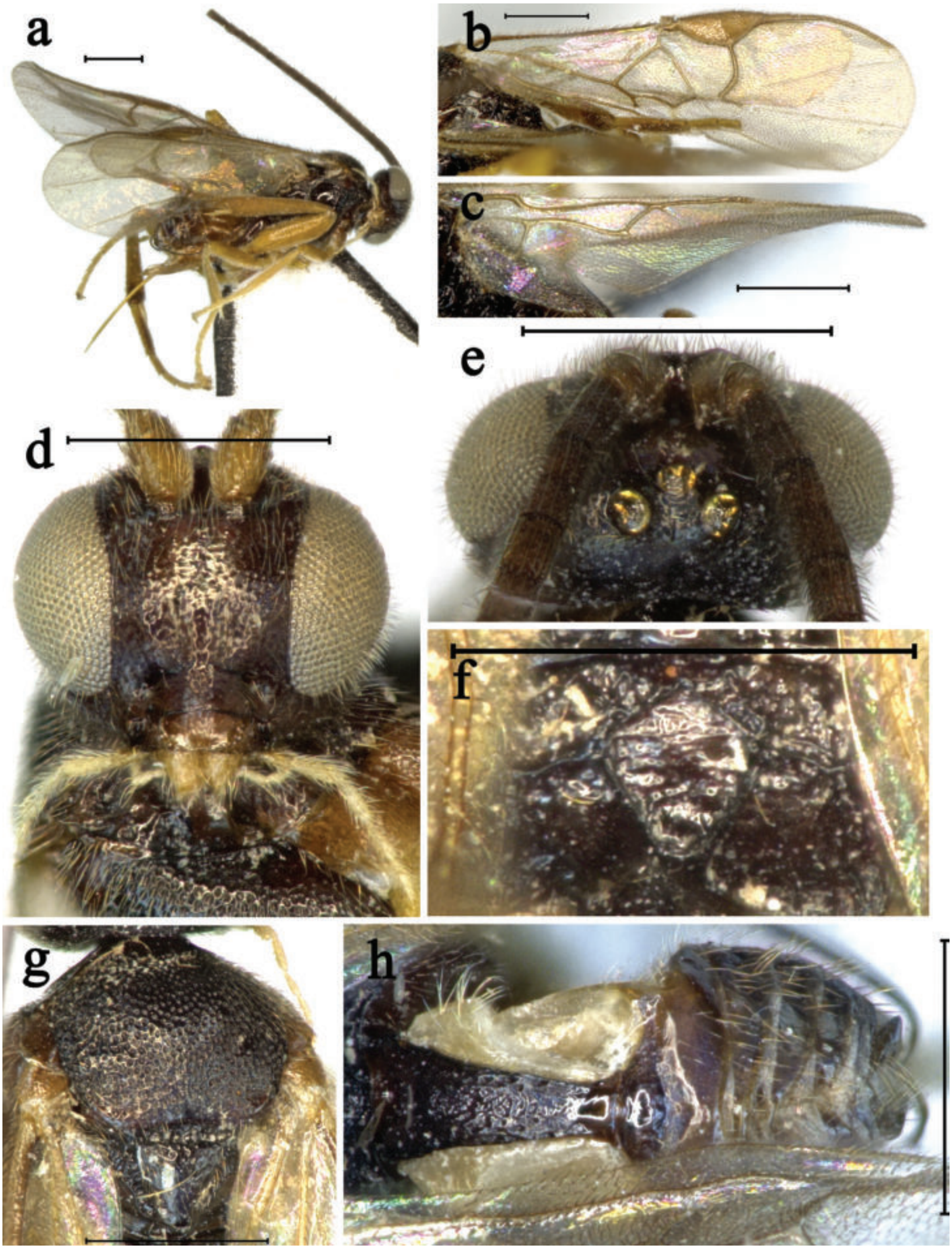

Figure 2. *Apanteles cuneiformis* Song & Chen, 2004 **a** habitus, lateral view **b** fore wing **c** hind wing **d** head, frontal view **e** head, dorsal view **f** propodeum **g** mesosoma, dorsal view **h** abdomen, dorsal view. Scale bars: 0.5 mm.

Sanchahe, Xishui, **Guizhou**, 2000.IX.22, Li Guiren, No. 200102301; 1♀, Changqiangou, Xishui, Guizhou, 2000.IX.29, Ma Yun, No. 200102730.

Distribution. China (Fujian, Guangdong, Guizhou, Taiwan, Yunnan).

Apanteles parectangular Liu & Chen, sp. nov.

https://zoobank.org/033C1CE0-A0CE-4F27-8F85-3C63525E7220
Fig. 3

Description. Female. Body length 2.5 mm, fore wing length 3.0 mm (Fig. 3a).

Head. Transverse in dorsal view, 2× as wide as long, 1.2× wider than mesoscutum. Vertex between the eye and the posterior ocellus shiny with undefined punctures (Fig. 3d). Temple slightly shiny with superficial, indistinct puncture, strongly constricted behind eyes from dorsal view. Face (Fig. 3h) shiny with shallow punctures, transverse, 0.8× as high as wide, inner margin of eyes parallel-sided. Ocelli big, posterior tangent to anterior ocellus hardly touching posterior pair of ocelli, distance between anterior and a posterior ocelli distinctly shorter than diameter of a posterior ocellus, POL:OD:OOL = 3.5:2.5:4.5 (Fig. 3d). Antenna distinctly longer than body length, penultimate antennomere 1.5× longer than wide (Fig. 3e).

Mesosoma. Length:width:height = 48.0:36.0:27.5. Mesoscutum (Fig. 3i) slightly shiny with strong, sparse punctures, interspaces obviously bigger than diameter of puncture, punctures largely disappeared at middle and posterior parts where it is shinier and smoother than elsewhere. Scutellar sulcus straight, broad with carinae in between. Scutellum highly shiny, smooth without punctuation except for some undefined small punctures laterally. Lateral polished field of scutellum reaching half-length of scutellum, carinae obsolescent anteriorly. Propodeum (Fig. 3f) highly shiny, smooth, areolation strongly, well defined, V-shaped apically and closed basally, costulae strongly, well defined. Mesopleuron (Fig. 3c) highly polished, anterior part shallowly, finely punctate except for slightly rugose on top, sternaulus smooth, broad and concave.

Legs. Hind coxa shiny and smooth, impunctate basally. Spines on outer side of hind tibia not dense. Inner spurs of hind tibia 2/5 length of hind basitarsus, outer spur 1/3. Basitarsus of hind leg distinctly longer than tarsomeres 2–4 (24.0: 19.0), claws of moderate size.

Wings. Pterostigma 2.9× as long as its widest part. Vein 1-R1 1.4× longer than pterostigma, nearly touching apex of marginal cell (Fig. 3b). Vein r arising from middle of pterostigma, distinctly inclined outwards, 1.1× longer than width of pterostigma, r 1.4× longer than 2-SR, indistinctly angled at meeting, 2-M half-length of 2-SR and slightly shorter than 1-SR, 2-SR+M shorter than m-cu, the latter about the length of r. First discal cell of fore wing 1.3× wider than high. Second submarginal cell of hind wing 1.3× wider than high. Vein cu-a of hind wing slightly curved. Hind wing not broad, the length of the 1-M as long as the distance between its distal extremity and the apex of the vannal lobe. Vannal lobe beyond its widest part somewhat concave without obvious setae.

Metasoma. 0.7 length of mesosoma. T1 narrowly wedged-shaped, not strongly constricted apically, basal width to apical width 1.4:1.0, basal 1/3 concave, turned-over part 2.1× longer than wide across the hump, obscure with obsolescent punctures laterally, longitudinal channel obvious with transversal carinae inside, apical tubercle highly polished and smooth (Fig. 3g). T2 shiny and polished, transverse, 4× wider than long in middle, slightly curved apically. T3 as long as T2. Tergites posterior to T2 polished,

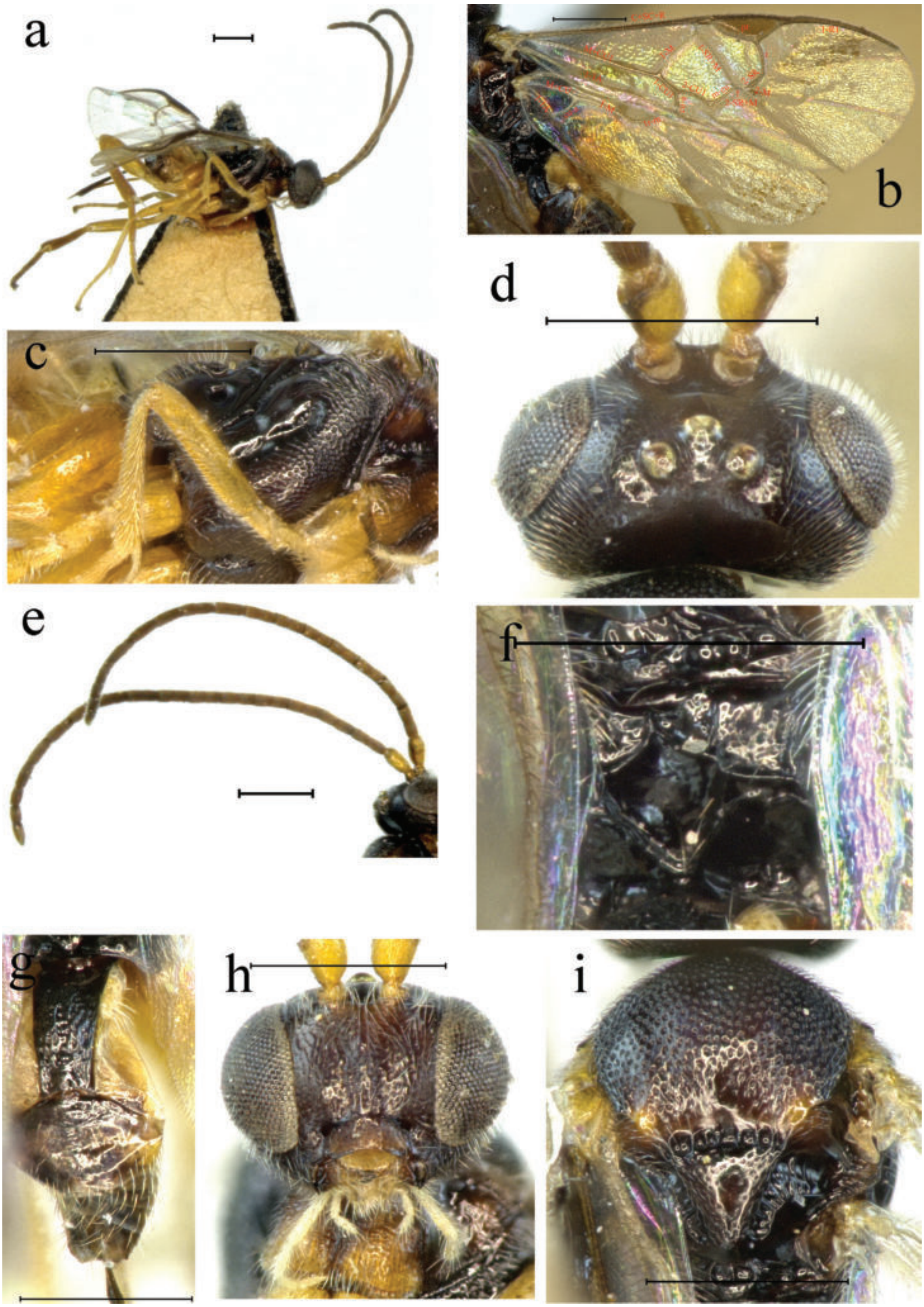

Figure 3. *Apanteles parectangular* Liu & Chen, sp. nov. **a** habitus, lateral view **b** fore and hind wings **c** mesopleuron **d** head, dorsal view **e** antenna **f** propodeum **g** abdomen, dorsal view **h** head, frontal view **i** mesosoma, dorsal view. Scale bars: 0.5 mm.

shiny, and densely pubescent. Hypopygium shorter than apex of metasoma. Ovipositor sheath slightly longer than hind tibia, narrow, evenly widened towards apex.

Colour. Reddish brown to black (Fig. 3a). Tegula yellow. Palpi and spurs pale yellow. Labrum and mandible light reddish-yellow. Flagellum of antenna yellowish-brown basally, darkened towards apex, pedicel and scape bright yellow. Ovipositor sheath brown. Legs bright yellow except hind tibia and tarsus somewhat reddish-yellow. Wing membrane hyaline, slightly brownish, vein C+SC+R, 1-R1 and pterostigma brown, other veins light brown.

Variation. Body length 2.0–2.7 mm.

Male. Unknown.

Host. Unknown.

Material examined. ZJUH: *Holotype*: ♀, Linghou, **Zhejiang**, 1985.VIII.6, Chen Xuexin, No. 852530. ***Paratypes*:** 1♀, Hangzhou, Zhejiang, 1989.VI.24, Chen Xuexin, No. 893296; 1♀, Mt. Jigong, **Henan**, 1997.VII.12, Chen Xuexin, No. 975015; 1♀, Kuankuoshui Natrure Reserve (Xiangshuwan), **Guizhou**, 2010.VI.4, Chai Hongfei, No. 201004049; 1♀, Mt. Diaoluo, **Hainan**, 2006.VII.16–17, Liu Jingxian, No. 200802283; 1♀, Jianfengling (Tianchi), Hainan, 2008.XI.25, Tan Jiangli, No. 200805125; 1♀, Jianfengling, Hainan, 2008.XI.22, Tan Jiangli, No. 200805327.

HUAS: 2♀♀, Haizhu Wetland, Guangzhou, **Guangdong** (malaise trap), 2021.IV.26–V.11, Liu Jingxian, Nos. 202200268, 202200214.

Distribution. China (Guangdong, Guizhou, Hainan, Henan, Zhejiang)

Etymology. The specific name "*parectangular*" derives from the Latin, referring to the shape of T1 (indistinctly constricted apex, nearly rectangular-shaped).

Remarks. This species is similar to *A. conon* Nixon, but differs in the following: T1 not strongly constricted apically (strongly constricted in latter); punctures sparser, largely disappeared on mesoscutum (punctures more denser in latter); and hind coxa entirely yellow (largely brown in latter).

Acknowledgements

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RESEARCH ARTICLE

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New and little-known bees of the genus *Colletes* Latreille, 1802 (Hymenoptera, Colletidae) from Siberia

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Abstract

An annotated list of seven species of rarely collected and little-known bees of the genus *Colletes* from Siberia is given, including five species whose ranges within the region are enlarged. *Colletes ravuloides* Kuhlmann & Proshchalykin, **sp. nov.** is described from Tyva Republic (Russia). An updated checklist of the 27 species of *Colletes* so far known from Siberia is provided.

Keywords

Anthophila, Apiformes, fauna, new records, new species, Palaearctic

Introduction

Siberia is a major geographical region (total area about 13,100,000 km^2) extends eastwards from the Ural Mountains to the Pacific Ocean, and includes most of the drainage basin of the Arctic Ocean. The river Yenisey divides Siberia into two parts: Western and Eastern (Fig. 1).

There are currently about 490 species of bees known from Siberia (Lelej et al. 2017), although this is undoubtedly a gross underrepresentation due to sparse sampling that has been done on the fauna, and new records and species are frequently discovered (Byvaltsev et al. 2018, 2021; Byvaltsev and Proshchalykin 2019; Proshchalykin and Müller 2019; Sidorov et al. 2020; Litman et al. 2021; Astafurova and Proshchalykin 2022; Sidorov and Proshchalykin 2022).

The genus *Colletes* Latreille, 1802 currently includes roughly 520 described species with an estimated total of about 700 species (Kuhlmann and Proshchalykin 2011) from all continents except Antarctica and Oceania (Michener 2007; Kuhlmann 2014). In recent years significant progress has been made towards a better knowledge of species of *Colletes* in Russia (Kuhlmann and Proshchalykin 2011, 2014; Proshchalykin and Kuhlmann 2012, 2015, 2019, 2020). Currently 53 species are known from this country (Proshchalykin and Kuhlmann 2020). Considering our latest data, the genus *Colletes* is one of the best studied genera among the bees of Siberia.

Based on a study of recently collected specimens we here provide additional geographical data for seven rarely collected and little-known species of *Colletes*, with one species described as new and five species recorded from certain regions of Siberia for the first time. Including published records, a total of 27 species are now known from this region (Western Siberia – 18; Eastern Siberia – 26) (Table 1). The number of *Colletes* species in the fauna of Russia is now increased to 54.

Materials and methods

The results presented in this paper are based on 115 specimens newly collected in Siberia and currently housed in the Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia, **ZISP**); Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences (Vladivostok, Russia, **FSCV**) and the research collection of M. Kuhlmann at the Zoological Museum of Kiel University (Kiel, Germany, **RCMK**).

Notes on the general distribution of species follow Proshchalykin (2017) and Proshchalykin and Kuhlmann (2018).

Morphological terminology as well as measurements used in the descriptions follow those of Michener (2007). Puncture density is expressed as the relationship between puncture diameter (d) and the space between them (i), such as $i = 1.5d$ or $i < d$. The letters T and S are used as abbreviations of metasomal tergum and sternum, respectively. Body length is measured from the vertex to the tip of the metasoma in profile.

Images were taken with a digital microscope (Keyence VHX-5000) using the VH-Z20R/Z20T (20× to 200×) zoom lens and the OP-42305 super diffused illumination adapter. Images were stacked for extended depth-of-field and processed using Adobe Photoshop Elements 2021 (Adobe Systems Software Ireland Limited, Republic of Ireland) and then assembled into the figure plates.

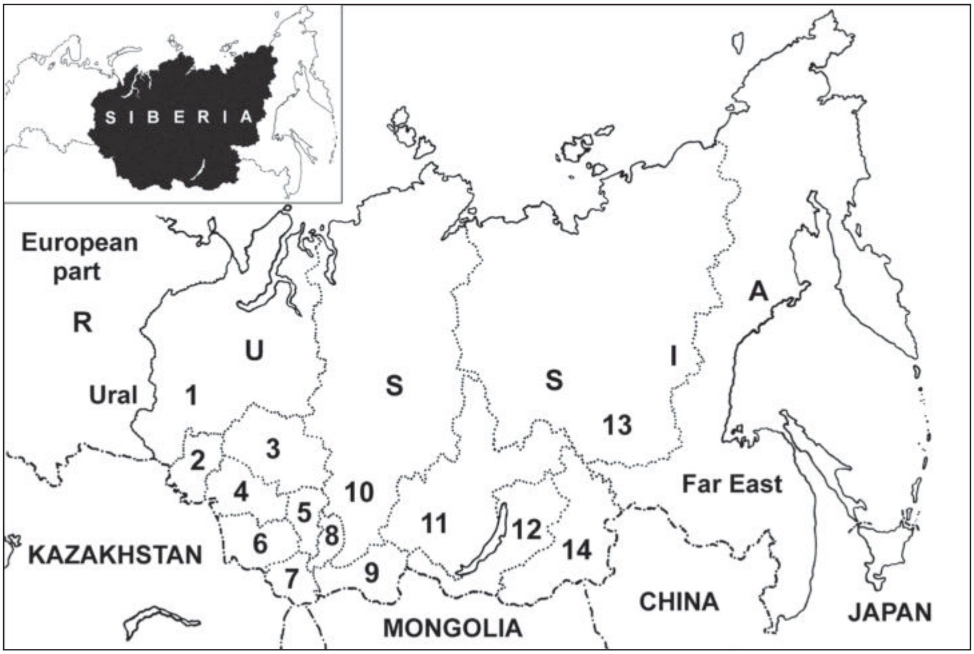

Figure 1. Administrative map of Siberia (**I–II**, **1–14**) (from Proshchalykin and Kuhlmann 2015). **I** Western Siberia. **1** Tyumen Province **2** Omsk Province **3** Tomsk Province **4** Novosibirsk Province **5** Kemerovo Province **6** Altaiskiy Territory **7** Altai Republic. **II** Eastern Siberia. **8** Khakass Republic **9** Tyva Republic **10** Krasnoyarsk Territory **11** Irkutsk Province **12** Buryatia Republic **13** Sakha Republic (Yakutia) **14** Zabaikalskiy Territory.

Images were taken with a digital microscope (Keyence VHX-5000) using the VH-Z20R/Z20T (20× to 200×) zoom lens and the OP-42305 super diffused illumination adapter. Images were stacked for extended depth-of-field and processed using Adobe Photoshop Elements 2021 (Adobe Systems Software Ireland Limited, Republic of Ireland) and then assembled into the figure plates.

Results

List of species for which new geographical data are provided

Colletes caspicus Morawitz, 1873

Colletes caspicus Morawitz, 1873: 174–175, ♀, ♂ (lectotype: ♀, designated by Proshchalykin and Kuhlmann 2019: 160, Derbent, Dagestan Republic, Russia [Oberösterreichisches Landesmuseum, Linz, Austria]).

Material examined. **Russia:** Khakassia Republic, Sosnovoe Lake, 53°15'41"N, 90°54'4"E, 2.VIII.2018, (1 ♂), SL, DS [FSCV]; *Tyva Republic*: 11 km W of Ust'-Elegest, 51°33'9"N, 93°59'22"E, 27.VII.2018, (3 ♀), SL, DS [FSCV/RCMK].

Distribution. Europe, Russia (European part, Urals, Siberia), Georgia, Azerbaijan, Iran, Central Asia, China.

Remarks. *Colletes caspicus* is herein recorded from Khakassia Republic for the first time.

Colletes cinerascens Morawitz, 1893

Colletes cinerascens Morawitz, 1893: 80, ♂ (lectotype: ♂, designated by Kuhlmann 2000: 179, Jagnob: Kol, Tajikistan [ZISP]).

Material examined. **Russia:** Altai Republic, Tydtuyaryk River valley, 50°04'25"N, 88°25'12"E, 12.VI.2022, (4 ♂); idem, 18.VI.2022, (2 ♂), MP [FSCV/ZISP]; 6 km SW of Chagan-Uzun, "Mars", 50°03'50"N, 88°18'45"E, (1 ♂), 22.VI.2022, MP [FSCV]; idem, 25.VI.2022, (1 ♂), AF [RCMK]; 5 km NE of Kokorya, 49°57'00"N, 89°04'19"E, 24.VI.2022, (7 ♂); MP [FSCV/RCMK]; 4 km SW of Tashanta, 49°42'06"N, 89°06'53"E, 27.VI.2022, (1 ♂) MP [FSCV].

Distribution. Russia (Siberia), Kazakhstan, Kyrgyzstan, Tajikistan, Mongolia, China.

Remarks. *Colletes cinerascens* is herein recorded from Altai Republic for the first time.

Colletes ebmeri Kuhlmann, 2002

Colletes ebmeri Kuhlmann in Kuhlmann and Dorn 2002: 95–96, ♀, ♂ (holotype: ♂, Bajanchongor aimak, Changai Gebirge, Ulaan olon, 18 km S vom Pass Egijn davaa, Mongolia [Hungarian Natural History Museum, Budapest, Hungary]).

Material examined. **Russia:** Altai Republic, Tydtuyaryk River valley, 50°04'25"N, 88°25'12"E, 12.VI.2022, (1 ♂), MP [RCMK]; 4 km SW of Tashanta, 49°42'06"N, 89°06'53"E, 27.VI.2022, (1 ♀, 17 ♂), MP [FSCV/ZISP/RCMK]; 14 km SE of Aktash, 50°13'59"N, 87°45'28"E, 28.VI.2022, (1 ♂), MP [FSCV].

Distribution. Russia (Siberia), Kazakhstan, Mongolia.

Remarks. *Colletes ebmeri* is herein recorded from Altai Republic for the first time.

Colletes fulvicornis Noskiewicz, 1936

Colletes fulvicornis Noskiewicz, 1936: 416, ♀, ♂ (lectotype: ♂, designated by Kuhlmann 2000: 180, Cholt, Gobi, Mongolia [Museum of Natural History, University of Wrocław, Poland]).

Material examined. **Russia:** Altai Republic, 4 km SW of Tashanta, 49°42'06"N, 89°06'53"E, 27.VI.2022, (28 ♂) MP [FSCV/ZISP/RCMK].

Distribution. Russia (Siberia), Mongolia, China.

Remarks. This species has been known in Altai Republic only from two females collected in Dzhulukul Lake [50°29'N, 89°42'E] (Proshchalykin and Kuhlmann 2015: 332).

Colletes pseudocinerascens Noskiewicz, 1936

Colletes pseudocinerascens Noskiewicz, 1936: 424, ♀, ♂ (lectotype: ♂, designated by Kuhlmann 2000: 181, Jakutsk, Sakha Republic, Russia [ZISP]).

Material examined. **Russia:** Altai Republic, Tydtuyaryk River valley, 50°04'25"N, 88°25'12"E, 15.VI.2022, (1 ♀, 18 ♂); idem, 18.VI.2022, (12 ♂); idem, 19.VI.2022, (1 ♂) MP [FSCV/ZISP/RCMK]; 15 km SE of Kuray, 50°11'10"N, 88°07'04"E, 17.VI.2022, (1 ♀, 2 ♂), MP; idem, (2 ♂), AF [FSCV/ZISP]; 5 km NE of Kokorya, 49°57'00"N, 89°04'19"E, 24.VI.2022, (1 ♀, 5 ♂); idem, 26.VI.2022 (2 ♂), MP [FSCV/RCMK].

Distribution. Russia (Siberia), Mongolia.

Remarks. *Colletes pseudocinerascens* is herein recorded from Altai Republic for the first time.

Colletes ravuloides Kuhlmann & Proshchalykin, sp. nov.

https://zoobank.org/A9907C6C-0060-46D0-9E85-8A4A69C7E965
Figs 2A, B, 3A, B, 4A, B

Type material. ***Holotype***: 1 ♂, 51.5525°N, 93.9894°E, TYVA, 11 km W of Ust'-Elegest, steppe, 27.VII.18, Luzyanin, Sidorov" (label in Russian) (ZISP).

Paratype: 1 ♂, same data as Holotype (RCMK).

Diagnosis. According to the male S7 the new species is apparently closely related to two other very rarely collected and little-known species: *Colletes tardus* Noskiewicz, 1936, that is only known from southern Ukraine (Proshchalykin and Kuhlmann 2012), and *C. ravulus* Noskiewicz, 1936, that so far has only been recorded by a few specimens from Siberia (Buryatia Republic, Tyva Republic), NE Mongolia and China (Inner Mongolia, Xinjiang, Shanxi) (Kuhlmann and Proshchalykin 2011; Niu et al. 2014; Proshchalykin and Kuhlmann 2015). As far as known no specimen of *C. tardus* has survived in museum collections but according to the detailed description of Noskiewicz (1936: 294) the male of *C. ravuloides* differs from this species by the lack of short appressed hair on the disc of T1 (Fig. 3A), shorter hind basitarsus (Fig. 3B), S7 longer with posteriolateral corner tapered (Fig. 4A) (in *C. tardus* rounded like in *C. ravulus* (Fig. 4C)) and gonostylus slightly narrower. *Colletes ravuloides* and *C. ravulus* apparently occur in the same region and are very similar in appearance (Fig. 2A–D). In *C. ravulus* the punctation of scutum and T1 is finer and denser (Fig. 3C), discs of T3-4 without short erect blackish hair, hind basitarsus longer (Fig. 3D), posteriolateral corner of S7 rounded and apical emargination deeper (Fig. 4C), gonostylus slighthly longer and apically rounded (Fig. 4D). The male of *C. ravuloides* is best identified by the unique shape of S7 (Fig. 4A) in combination with the shortened hind basitarsus (Fig. 3B).

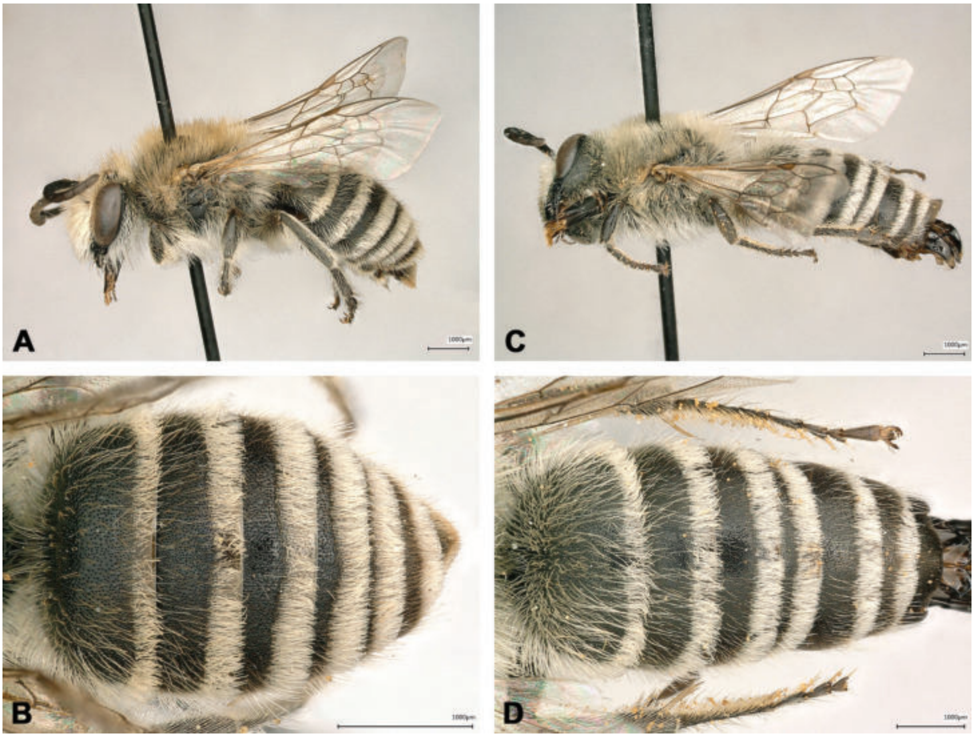

Figure 2. *Colletes ravuloides* Kuhlmann & Proshchalykin, sp. nov., paratype, male **A** habitus, lateral view **B** metasoma, dorsal view. *Colletes ravulus* Noskiewicz, male **C** habitus, lateral view **D** metasoma, dorsal view.

Description. Female: unknown.

Male. ***Body length*:** 9 mm. ***Head*:** Head wider than long. Integument black except mandible partly dark reddish-brown. Face densely covered with long, yellowish-white, erect hairs (Fig. 2A). Malar area medially about 1/3 as long as width of mandible base, finely striate. Antenna black, ventrally dark brown.

***Mesosoma*:** Integument black. Mesoscutal disc sparsely punctate (i = 3–4d), between punctures smooth and shiny. Scutellum an anterior half nearly impunctate, apically densely punctate (i < 1d), surface smooth and shiny. Mesoscutum, scutellum, metanotum, mesepisternum and propodeum covered with long, yellowish-white to light yellowish-brown erect hair (Fig. 2A). Wings slightly yellowish-brown; wing venation and stigma brown. Legs with integument mostly blackish, tarsi partly dark yellowish-brown. Vestiture white (Fig. 2A). Hind basitarsus shortened (Fig. 3B).

***Metasoma*:** Integument black except depressed apical tergal margins posteriorly yellowish-brown translucent (Fig. 3A). T1–2 densely covered with long, erect yellowish-white hairs (Fig. 3A), discs of T3–5 with short, erect blackish-brown hair; apical tergal depression and hair bands of T2 – T5 broad but narrower medially, about as broad as the respective discs and densely covered with long, appressed white hairs (Fig. 2B); apical tergal depression and hair band of T1 only about half the width of the other ones (Fig. 3A). T1 finely and densely punctate (i = 0.5–1d), between punctures

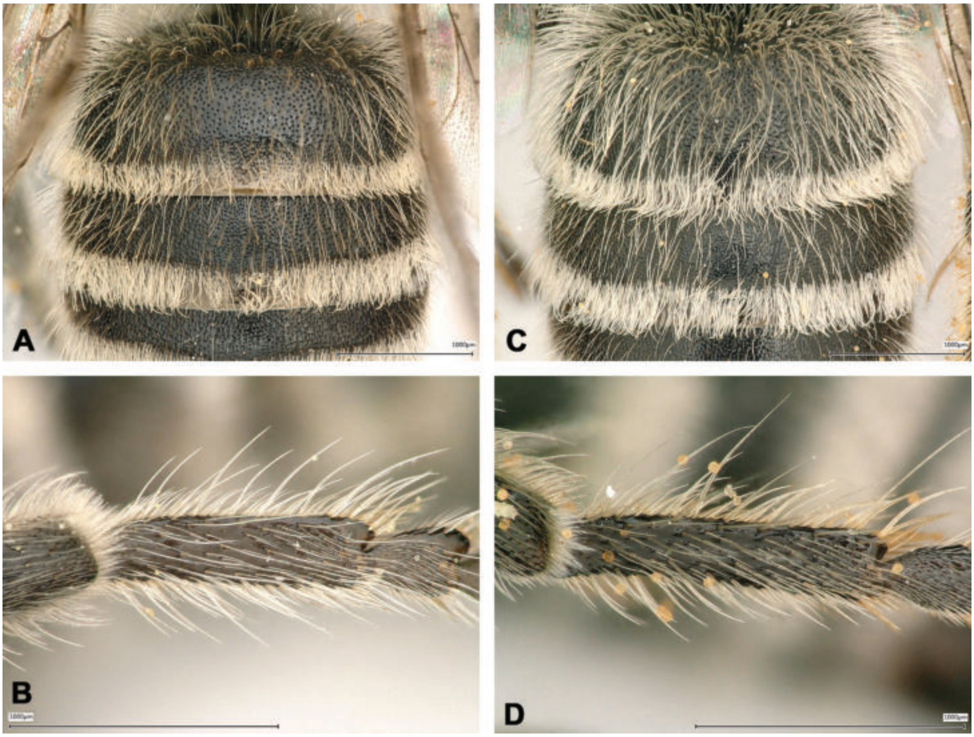

Figure 3. *Colletes ravuloides* Kuhlmann & Proshchalykin, sp. nov., paratype, male **A** metasomal terga 1 and 2, dorsal view **B** hind basitarsus, dorsal view. *Colletes ravulus* Noskiewicz, male **C** metasomal terga 1 and 2, dorsal view **D** hind basitarsus, dorsal view.

smooth and shiny (Fig. 3A), following terga successively with denser punctation. S7 (Fig. 4A) and gonostylus (Fig. 4B) as illustrated.

Etymology. The species name refers to its similarity to the closely related *C. ravulus* that occurs in the same region.

Distribution. The only record is from the type locality in Tyva Republic (Russia).

Phenology. Only recorded in July.

Colletes wacki Kuhlmann, 2002

Colletes wacki Kuhlmann in Kuhlmann and Dorn 2002: 102–103, ♀ (holotype: ♀, Uvs-Aimag, Charchira-ul, 30 km S Ulangom, Mongolia [Zentralmagazin Naturwissenschaftlicher Sammlungen, Martin-Luther-University, Halle, Germany]).

Material examined. Russia: Altai Republic, Tydtuyaryk River valley, 50°04'25"N, 88°25'12"E, 14.VI.2022, (1 ♀); idem, 18.VI.2022, (1 ♀, 2 ♂), MP [FSCV/ZISP].

Distribution. Russia (Siberia), Kazakhstan, Mongolia, China.

Remarks. *Colletes wacki* is herein recorded from Altai Republic for the first time.

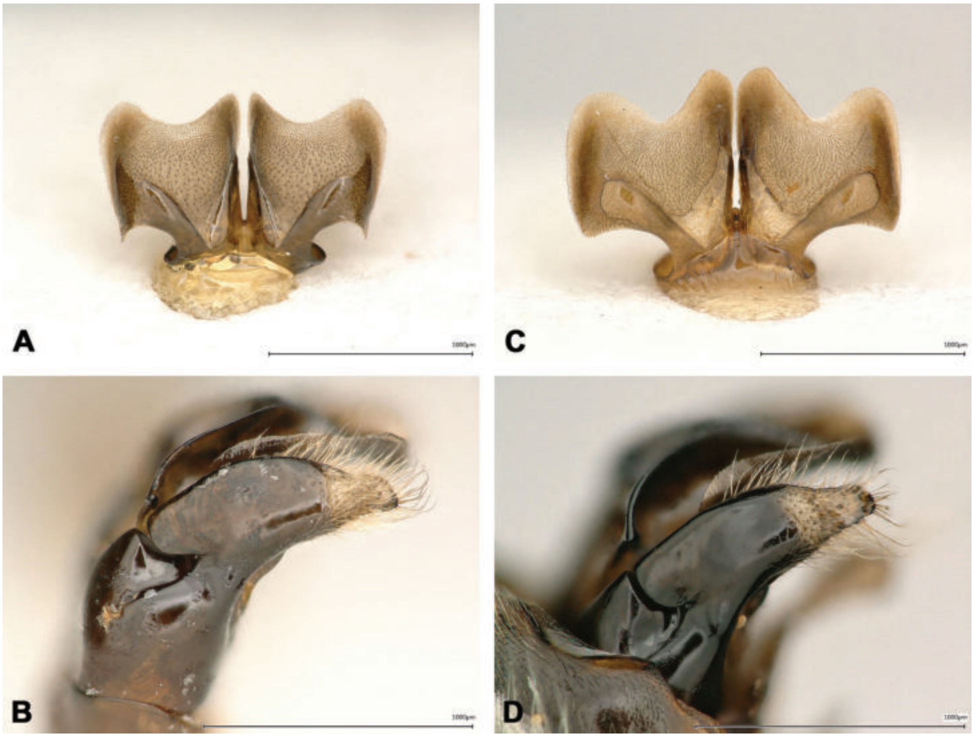

Figure 4. *Colletes ravuloides* Kuhlmann & Proshchalykin, sp. nov., paratype, male **A** metasomal sternum 7, dorsal view **B** gonostylus, lateral view. *Colletes ravulus* Noskiewicz, male **C** metasomal sternum 7, dorsal view **D** gonostylus, lateral view.

Discussion

In the present study, we list new records for six species of the genus *Colletes* from various localities in Siberia and describe a seventh. Together with published records, 27 *Colletes* species are currently known to occur in Siberia (Table 1). For comparison, 54 species have been recorded from Russia so far, with 38 species occurring in the European part, 13 in the Ural and eleven in the Far East (Proshchalykin 2017; Proshchalykin and Kuhlmann 2019, 2020). The Siberian *Colletes* fauna is composed of twelve widespread trans-Palaearctic or Euro-Asian species. Among these, six species are distributed from Europe to the Russian Far East and the eastern provinces of China, such as *Colletes chengtehensis*, *C. collaris*, *C. cunicularius*, *C. daviesanus*, *C. floralis*, and *C. impunctatus*. The other 15 Siberian *Colletes* species have smaller distribution ranges being restricted to the eastern Palaearctic. Among these, *Colletes cinerascens*, *C. ebmeri*, *C. friesei*, *C. kaszabi*, *C. laevifrons*, and *C. ravulus* have their main distribution in Central Asia, Mongolia and China, but also occur in steppes and semi-deserts of the Russian Altai, Buryatia and Tyva Republics. The new species (*Colletes ravuloides* sp. nov.) is steppe Siberian endemic distributed in south part of Tyva Republic.

Table 1. Checklist of the *Colletes* bees of Siberia. White circle – published records (Kuhlmann and Proshchalykin 2011; Proshchalykin and Kuhlmann 2015); black circle – new data.

No.	*Colletes* species	Western Siberia	Eastern Siberia
1	*C. alini* Kuhlmann, 2000		○
2	*C. caspicus* Morawitz, 1873	○	○
3	*C. chengtehensis* Yasumatsu, 1935	○	○
4	*C. cinerascens* Morawitz, 1893	●	○
5	*C. collaris* Dours, 1872	○	○
6	*C. cunicularius* (Linnaeus, 1760)	○	○
7	*C. daviesanus* Smith, 1846	○	○
8	*C. ebmeri* Kuhlmann, 2002	●	○
9	*C. floralis* Eversmann, 1852	○	○
10	*C. fodiens* (Fourcroy, 1785)	○	○
11	*C. friesei* Cockerell, 1918		○
12	*C. fulvicornis* Noskiewicz, 1936	●	○
13	*C. impunctatus* Nylander, 1852	○	○
14	*C. jankowskyi* Radoszkowski, 1891	○	○
15	*C. kaszabi* Kuhlmann, 2002		○
16	*C. kozlovi* Friese, 1913		○
17	*C. laevifrons* Morawitz, 1893	○	
18	*C. marginatus* Smith, 1846	○	○
19	*C. patellatus* Přrez, 1905		○
20	*C. perforator* Smith, 1869		○
21	*C. pseudocinerascens* Noskiewicz, 1936	○	○
22	*C. ravuloides* Kuhlmann & Proshchalykin, sp. nov.		●
23	*C. ravulus* Noskiewicz, 1936		○
24	*C. roborovskyi* Friese, 1913		○
25	*C. sidemii* Radoszkowski, 1891	○	○
26	*C. similis* Schenck, 1853	○	○
27	*C. wacki* Kuhlmann, 2002	●	○
Total:		18	26

The number of Siberian *Colletes* species is supposed to be at least one fourth higher than known so far. We expect that several species that are known from Mongolia, Kazakhstan or northern China also occur in Siberia, such as *Colletes annejohnae* Kuhlmann, 2003, *C. conradti* Noskiewicz, 1936, *C. edentuloides* Kuhlmann, 2011, *C. morawitzi* Noskiewicz, 1936, or *C. pauljohni* Kuhlmann, 2002.

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RESEARCH ARTICLE

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Nest characteristics and associates of *Dolichovespula* (Hymenoptera, Vespidae) in Central Finland

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Abstract

In social vespine wasps, the nest characteristics and associates vary intra- and interspecifically. I studied the nest characteristics and nest associates of three *Dolichovespula* wasp species in boreal Finland. The average number of combs and cells per nest was similar among *D. media*, *D. saxonica* and *D. norwegica*, and similar to *Dolichovespula* in the temperate zone. Most *D. media* and *D. saxonica* colonies produced both gynes and males, whereas *D. norwegica* produced mainly either one. The average colony lifespan of *D. saxonica* was a bit over two months, i.e. shorter than documented for *Dolichovespula* in the temperate zone. The proportion of nests parasitised by the ichneumonid wasp *Sphecophaga vesparum* was 36% in *D. saxonica* and 50% in *D. media*; *S. vesparum* has not been recorded from *D. media* before. The proportion of parasitized cells was 0.6–11% for *D. saxonica* and 0.2–22% for *D. media*. The proportion yellow, overwintering cocoons of *S. vesparum* was highly variable among the nests. The proportion of nests parasitised by the moth *Aphomia sociella* was 36% in *D. saxonica* and 13% in *D. media*. *Sphecophaga* and *Aphomia* were not recorded from *D. norwegica* colonies, which supports studies in the temperate zone. The study adds up to the previous research on the nest structure and nest associates of vespines, and together they indicate that there is geographical variation within Europe and globally in the host use of *Sphecophaga*.

Keywords

Aphomia sociella, colony structure, social wasps, *Sphecophaga vesparum*, Vespinae

Introduction

Social vespine wasps (Vespinae) are divided in four to five genera (Persson 2015; Lopez-Osorio 2017), of which three occur in Finland: *Dolichovespula* (Rohwer, 1916), *Vespa* (Linnaeus, 1758) and *Vespula* (Thompson, 1869). Biology of *Dolichovespula*, especially that of *D. norwegica* (Fabricius, 1781) and *D. media* (Retzius, 1783), is poorly known compared to *Vespula*, partly because of the global invasions of the latter (Beggs et al. 2011). *Dolichovespula* and *Vespula* also differ in their sociality as well as colony and nest characteristics (Foster et al. 2001; Archer 2012) but there are also differences within *Dolichovespula* (Archer 2006). Colony and nest characteristics are biologically interesting as such, and they are needed to interpret possible intra- and interspecific differences in the identity and prevalence of nest associates (parasites, parasitoids, predators and scavengers), which can influence the size, activity and success of vespine colonies (Archer 2012).

In Finland, cuckoo wasps *Dolichovespula adulterina* (Du Buysson, 1905) and *D. omissa* (Bischoff, 1931) parasitize *D. saxonica* (Fabricius, 1793) and *D. sylvestris* (Scopoli, 1763), respectively (Douwes et al. 2012). Cuckoo wasps do not feed on the host larvae but the queen replaces the host queen and use the host workers as slaves to produce reproductive castes. The wasp *Sphecophaga vesparum* (Curtis, 1828) (Hymenoptera: Ichneumonidae) is nearly a cosmopolitan ectoparasitoid of Vespinae (Archer 2012). Two subspecies are known: the European *S. vesparum vesparum* and the North American *S. vesparum burra* (Cresson, 1869). The endoparasitoid beetle *Metoecus paradoxus* (Linnaeus, 1761) (Coleoptera: Ripiphoridae) and related taxa are common parasites of *Vespula* but have rarely been observed from *Dolichovespula* nests (see Carl and Wagner 1982; Makino 1982). Similarly, the syrphid *Volucella pellucens* (Linnaeus, 1758) (Diptera: Syrphidae) parasitizes *Vespula* but not *Dolichovespula*. The moth *Aphomia sociella* (Linnaeus, 1758) (Lepidoptera: Pyralidae) is a common inhabitant of *Dolichovespula* nests (Gambino 1995). It predates eggs, larvae and cocoons, but feeds also on waste found in nests. The species generally attacks declining colonies and thus is likely to have a marginal effect on colony success (Gambino 1995; Archer 2012). The overall prevalence (proportion of occupied nests) of nest associates in vespine nests is usually high but the nest-specific prevalence (proportion of occupied cells or the number of individuals) is usually low (Archer 2012).

The nest characteristics and associates of *Dolichovespula* are poorly studied in comparison with *Vespula*, especially in the boreal region. The extant studies have been conducted in very different geographical locations and suggest geographical variation in the biology of *Dolichovespula* (e.g. US, Greene et al. 1976; Gambino 1995; Japan, Makino 1982; UK, Archer 2000, 2002; Poland, Pawlikowski and Pawlikowski 2010; Nadolski 2012, 2013). I studied the colony and nest characteristics, as well as the nest associates, of *D. saxonica*, *D. media* and *D. norwegica* in boreal Central Finland.

Methods

The study was conducted in the province of Central Finland, which belongs to the middle boreal zone. During 2019–2022 *Dolichovespula* nests were located based on public information and active searching. All nests were within 60 km (mostly within 5 km) from the Jyväskylä city centre. Nests were in a variety of natural and anthropogenic locations, mostly in semiurban broadleaved or mixed forests. Most *D. saxonica* nests were inside wooden bird nest boxes (1.3–2.0 m above ground) that were used for a bird study (Komonen and Torniainen 2022). The nests were removed and their characteristics (number of combs and cells), and the number of nest associates or parasitized cells, were recorded in the laboratory. Small supplementary combs (one *D. saxonica* nest) between the main combs were not counted as separate combs but they were included in the total cell counts. The number of small and large cells in each comb was also counted or estimated but because they are difficult to distinguish in combs having intermediate-sized cells (Greene et al. 1976; Archer 2006), I do not provide quantitative estimates of small-to-large cell ratios. Interspecific differences in the colony size (total number of combs and cells) were analysed with the non-parametric Kruskal-Wallis test. The sample size may vary in different analyses and data summaries because not all characteristics were recorded from every nest for varying reasons. Nest characteristics are available in the Suppl. material 1.

Lifespan was documented for seven *D. saxonica* colonies in bird nest boxes (n = 7), which were monitored about once a week for a bird study from April 2021 onwards. Colony lifespan was determined as the difference between the first date the wasp was observed and the date of colony removal. Because the colonies were initiated earlier than observed at the first time, I estimated the date of colony initiation: the number of days between the date a nest box was observed occupied and the previous date the nest box was empty, divided by two). At the time of removal, four colonies had just ceased and three were still active, although at their final phase with males and gynes.

To make colonies comparable they should be in the same developmental phase. This was not fully possible. Thus, in analyses I focused on the mature colonies, which were determined as having large cells containing sealed brood or large cells from which the adults had emerged (see Archer 1981). All *D. media* (n = 8) and *D. norwegica* (n = 4) nests were mature, whereas two *D. saxonica* (n = 31) nests had only small cells, one had only large cells and two were destroyed by *A. sociella*. To document, if the nests produced both males and gynes, I recorded the adults and opened the closed cells. I also examined each nest for nest associates, of which *S. vesparum* and *A. sociella* were abundant and could be identified to species. All open and closed host cells were examined for *S. vesparum* cocoons. I recorded the number of cocoons (one host cell may host several parasitoid cocoons), the colour of the cocoon (white or yellow), and whether the parasitoid had emerged from the cocoon (i.e. there was an exit hole; Fig. 1). *Sphecophaga vesparum* lays three kinds of eggs: those that produce 1) white cocoons and then brachypterous females; 2) those that produce weak, yellow cocoons and then winged

Figure 1. White *Sphecophaga vesparum* cocoons from which the parasitoid has emerged, and closed yellow cocoons in a nest of *Dolichovespula media*. A host cell may have both white and yellow cocoons. Photo: Atte Komonen.

females and possibly males; and 3) resistant yellow, overwintering cocoons (Donovan 1991). I classified the cocoons as white or yellow because I was not confident in separating the two types of yellow cocoons, except in one nest. *Aphomia sociella* larvae were counted or the past presence of the species was determined by the silk spun by the larvae.

Results

The number of combs and cells was variable among nests but there were no interspecific differences (H = 1.1, p = 0.57 and H = 0.7, p = 0.72, respectively, df = 2, n = 38;

Table 1. Characteristics of the studied nests, the percent parasitized nests, the mean (min–max) percent of parasitized cells in occupied nests, and the mean (min–max) number of individuals per occupied nest.

	Nest	Combs	Cells		*S. vesparum*		*A. sociella*	
	n	Mean (SD)	Med, Mean (SD)	% nests	% cells	Exx./nest	% nests	Exx./nest
D. saxonica	31	3.7 (1.2)*	854, 739 (420)	36[#]	4 (0.6–11)[$]	19 (2–48)[£]	36[£]	33 (2–94)[&]
D. norwegica	4	4.3 (0.5)	712, 1079 (762)	0	0	0	0	0
D. media	8	4.1 (0.8)	626, 674 (275)	50	11 (0.2–22)	104 (1–256)	13	1

[*] n = 26; [#] n = 28; [$] n = 9; [£] n = 10; [&] n = 4

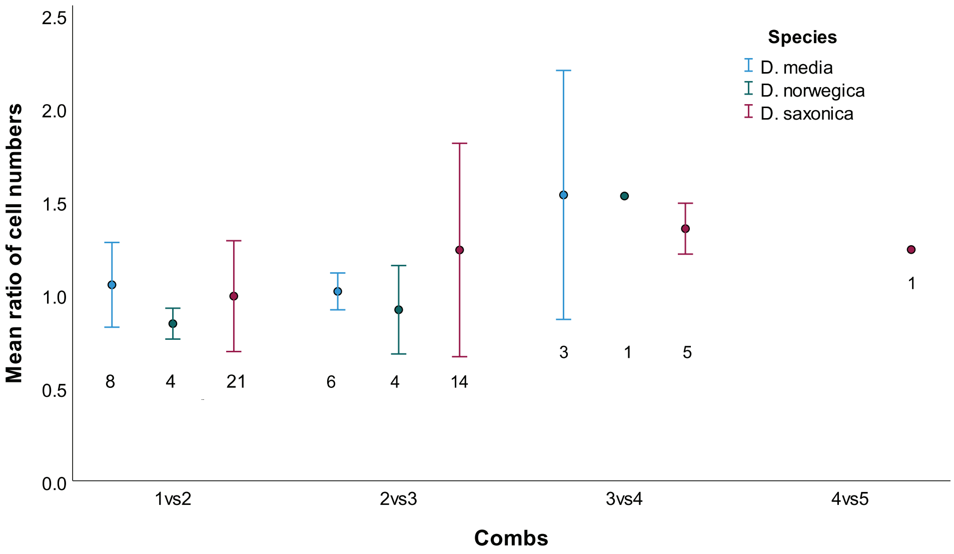

Figure 2. The mean ratio (± 1SD) of the cell numbers in adjacent combs (1 is the basal, oldest comb). Numbers give the number of nests.

Table 1). Of the basal combs (n = 32), 88% had only small cells, and of the newest comb, 47% consisted only of small cells. The middle combs had generally large or medium cells, and if there were small cells (63% of nests), they were peripheral. The mean ratio of cell numbers in adjacent cells was similar among the species and increased from the basal (oldest) towards the outer (newest) combs (Fig. 2). The mean ± SD lifespan of *D. saxonica* colonies was 70 ± 4 days (n = 7).

The most frequent and abundant nest associates were *S. vesparum* and *A. sociella*. These attacked *D. saxonica* and *D. media*, whereas no nest associates were found in *D. norwegica* nests. Both in *D. media* and *D. saxonica*, *S. vesparum* parasitized large and small cells. In *D. media*, there was an average of 1.5 (max. = 8) parasitoid individuals per host cell, and in *D. saxonica* 1.1 (max. = 4). In both species, there was generally more yellow than white *S. vesparum* cocoons (Table 2). In *D. media* colonies, the ratio of white to yellow cocoons was highly variable. The proportion of white or yellow cocoons, from which the parasitoid had emerged, was less variable. Most of the white cocoons were empty, whereas the yellow cocoons were still inhabited. In *D. saxonica*

Table 2. The number and ratio of white and yellow cocoons of *S. vesparum*, and the proportion of open (parasitoid emerged) white and yellow cocoons in *D. media* (Dm) and *D. saxonica* (Ds) nests.

				Empty (%)	
Nest	**White**	**Yellow**	**Ratio**	**White**	**Yellow**
Dm1	15	21	0.71	0.93	0
Dm2	25	231	0.11	0.76	0.02
Dm3	65	55	1.18	0.89	0.11
Dm4	0	1	0	na	0
Ds1	2	31	0.06	0.5	0.06
Ds2	10	21	0.48	0.9	0.05
Ds3	11	37*	0.30	1	0.27
Ds4	4	1	4	0.25	0
Ds5	1	1	1	1	1
Ds6	0	2	0	na	0.5
Ds7	2	22	0.09	0	0
Ds8	0	7	0	na	0.86

* 8 of these were yellowish.

colonies, the ratio of white to yellow cocoons was less variable than in *D. media*. The proportion of white or yellow cocoons, from which the parasitoid had emerged, was more variable than in *D. media*; exceptionally large or small proportions were associated with small number of parasitoids. Similar to *D. media*, white cocoons were more often empty than yellow cocoons. No social vespine parasites were observed.

Discussion

Nest characteristics

The nest locations were variable. All *D. norwegica* nests were aerial in trees or bushes. All *D. media* nests were aerial in natural or anthropogenic objects. Nest locations of *D. saxonica* were the most variable and generally aerial. In addition to natural objects, they were found in many anthropogenic objects. The results underscore flexibility in nesting locations and ability to utilize anthropogenic locations (at least *D. saxonica* and *D. media*; see also Archer 2006; Nadolski 2012). Because nest location can affect colony size, nest characteristics, and the production of sexual castes (for *D. saxonica* see Nadolski 2012), some interspecific differences may result from the ecological context rather than being evolutionary traits. The lifespan of *D. saxonica* colonies was about a month shorter than that of *Dolichovespula* in the temperate zone (cf. Archer 2006). Because the summer of 2021 was record-warm in Central Finland, this might have sped up the colony development and shortened the lifespan.

The studied *Dolichovespula* species had more similarities than differences and the colonies were of typical size for *Dolichovespula* (see Archer 2006). The typical number of combs was three to five in all the studied species (see also Archer 2012; Nadolski 2012). The number of combs in *D. saxonica* nests varied the most, which may result from the diverse nest locations (Nadolski 2012) and larger number of prematurely ceased or collected nests. The average number of cells corroborates those documented for these species in the temperate zone (Makino 1982; Archer 2000, 2006; Nadolski 2012). Although there were no interspecific differences in the average number of cells (see also Makino 1982), *D. media* combs had less cells per unit of comb area than *D. norwegica* and *D. saxonica*, which can be explained by its larger body size. The ratio of cell numbers in adjacent combs was also very constant among the species. Because the newest, outermost combs was left out from this analysis, this result is not biased if some nests were still being enlarged (nest growth at the final stage is mostly enlarging the newest comb).

Most nests, especially the larger ones, had more than one comb that were dominated by small cells (usually the first and the last). Although the middle combs consisted generally of large or medium cells, mixed combs were common. These results support previous studies indicating intra- and interspecific variation in the distribution of cell sizes among combs (Greene et al. 1976; Makino 1982; Archer 2000, 2006; Nadolski 2012). The result that the newest comb was dominated by small cells agrees with that observed for *D. saxonica* (Nadolski 2012). The newest comb is probably used to produce males by the reproductive workers, which can be related to limited queen control in declining colonies or typical kin structure of *Dolichovespula*, resulting in limited worker policing (Foster et al. 2001). In the mixed combs, the small cells were usually peripheral, which differs from previous studies of *Dolichovespula* (Archer 2006). Because it is not always easy to distinguish different cell sizes in mixed combs, especially if there are cells of intermediate size (Archer 2006; Nadolski 2012), I refrain from more quantitative conclusions.

The production of males and gynes varied among species. 75% of the *D. media* nests had both males and gynes; it is likely that also the other two colonies produced or would have produced both sexes, but in one of these nests most individuals had already left and the other was heavily parasitized. 55% of the *D. saxonica* colonies that had sexual castes produced both males and gynes; all the single-sex colonies produced only males. Because larvae were still present it is possible that some would have produced gynes later. It is known, however, that *D. saxonica* colonies usually produce more males than gynes (Nadolski 2012). My results support the observations that colonies of *D. norwegica* often specialize as male-producing or gyne-producing (Archer 2000, 2006), but occasionally both sexes can be produced. Because gynes and males can be produced in phases (Greene et al. 1976; Archer 2002, 2006), prematurely ceased or collected nest may give biased data about the production of sexual castes. Unfortunately, most studies (including this one) cannot conclude anything quantitative about the production of gynes and males, because this would require continuous monitoring of the production of sexual castes.

Nest associates

The most common nest associates were *S. vesparum* and *A. sociella*, whereas no social vespine parasites were observed. *Sphecophaga vesparum* parasitized both *D. media* and *D. saxonica*. To my knowledge, *S. vesparum* has not been recorded from *D. media* before (see also Archer 2012). The lack of parasitism in *D. norwegica* may result from a small sample size, rather than lack of suitability as a host; however, *S. vesparum* has not been recorded from *D. norwegica* in England despite extensive sampling (Archer 2000, 2012), which suggests that there indeed are differences in host suitability. Similarly, *S. vesparum* has not been documented from *D. saxonica* nests in the UK (Archer 2012) but has been observed from those in Poland (Pawlikowski and Pawlikowski 2010; Nadolski 2013). Although *S. vesparum* has also been found from *D. sylvestris* and *Vespula* nests with low prevalence (Archer 2002, 2012), I have not recorded the species from *V. vulgaris* nests in Finland (n = 10). The proportion of nests parasitized by *S. vesparum* was higher in *D. media* (50%) than in *D. saxonica* (36%), which may result from the smaller sample size in *D. media*. These figures are somewhat higher than in other studies on *Dolichovespula* (Greene et al. 1976; Archer 2012; Nadolski 2013). In North American *Vespula*, there seems to be much higher prevalence of *S. v. burra* (up to 80%; MacDonald et al. 1975; Roush and Akre 1978; MacDonald et al. 1980; Akre et al. 1982; Reed and Akre 1983). It is known that the cuticular hydrocarbons of *S. vesparum* differ depending on their *Vespula* host species (Oi et al. 2020), so it is possible that the same phenomenon applies also to *S. vesparum* in different *Dolichovespula* hosts; yet, the acquisition and role of hydrocarbon signatures in host discrimination is not understood. Furthermore, given the geographic variation in morphology and host use of *Sphecophaga*, it is possible that there are more than two subspecies (see Berry et al. 1997).

The nest-specific rate of parasitism was variable but generally low. Again, the average rate of parasitism was higher in *D. media* (11%) than in *D. saxonica* (4%). These figures are like, or slightly higher (*D. media*) than in other studies of *Dolichovespula* (Greene et al. 1976; Pawlikowski and Pawlikowski 2010; Archer 2012). The proportion of parasitized cells was 22% in the smallest *D. media* nest (277 cells), which suggests that parasitism had a significant negative effect on the colony fitness. In North American *Vespula*, there seems to be similar or slightly lower prevalence of *S. v. burra* (Roush and Akre 1978; MacDonald et al. 1980; MacDonald and Matthews 1981; Akre et al. 1982; Reed and Akre 1983). Because I did not record the larvae of *S. vesparum*, the true parasitism rate is higher, but this applies to other studies as well. Furthermore, I estimated parasitism as the proportion of parasitized cells to all cells, not to the cells occupied by the host larvae (see also Akre et al. 1982; Reed and Akre 1983), which also underestimates fitness consequences. Apparently, there are either differences in host suitability and preference, or spatial variation in the distribution of *S. vesparum*, since even closely-related vespines may have different prevalence of *S. vesparum* (MacDonald and Matthews 1976; this study). Although *S. vesparum* can occasionally cause complete mortality of worker larvae in queen-phase nests (Archer 2012), its overall effect in mature colonies seems minor.

In general, there were more yellow than white cocoons. Yellow cocoons are those in which the adult parasitoid overwinters (Donovan 1991), which suggests that most *S. vesparum* overwinter inside the nest in Central Finland. *Sphecophaga vesparum* had emerged from much larger proportion of the white than yellow cocoons, which agrees well with the overwintering scenario. The proportion of white or yellow cocoons from which the parasitoid had emerged was more variable in *D. saxonica* than in *D. media*; exceptionally large or small proportions were associated with small number of parasitoids, so they are likely artefacts of small sample size. It is likely that the yellow cocoons, from which *S. vesparum* had emerged, were weak yellow cocoons, which I generally could not distinguish from the resistant yellow ones. However, the empty yellow cocoons in one *D. saxonica* colony were yellowish cocoons, i.e. probably weak yellow cocoons sensu Donovan (1991). However, many yellow but empty cocoons were not visually different from the closed yellow cocoons.

The prevalence of *A. sociella* was similar to *S. vesparum* in *D. saxonica* nests but lower in *D. media* nests. Low prevalence in *D. media* nests may be explained in that proportionally more nests were active when collected, because *A. sociella* predominantly colonize declining colonies. *Aphomia sociella* was not found from *D. norwegica* nests, and it remains unknown if the species can colonize *D. norwegica* nests. Although *M. paradoxus* has been occasionally observed from the nests of *Dolichovespula* in other parts of the world, no individuals were observed in this study, although the species is common in *V. vulgaris* nests in the study region (Komonen 2022). This indicates that *M. paradoxus* is very rare in *Dolichovespula* nests in Finland and possibly does not parasitize them at all. This supports previous observations from the temperate zone (Carl and Wagner 1982; Makino 1982).

Conclusions

To establish any pattern in biology, studies must be replicated in space and time. This study supports some earlier studies about the biology of *Dolichovespula* but also suggests that some issues need more studies so that their generality can be evaluated. Particularly, the variation in the host use of *S. vesparum* needs more research attention, which requires that different *Dolichovespula* species are studied in the same regions. It is also clear that observed level of parasitism cannot cause significant year-to-year variation in *Dolichovespula* abundance but can occasionally cause moderate damage in individual colonies. Furthermore, more studies are needed on the other *Dolichovespula* than *D. saxonica*, especially since *D. norwegica* has no documented nest associates.

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Supplementary material 1

Nest characteristics

Author: Atte Komonen

Data type: Nest characteristics

Explanation note: Nest locations, combs and cell numbers, and nest associates.

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Perilampus neglectus and other neglected species: new records of Palaearctic Perilampidae (Hymenoptera, Chalcidoidea), with a key to European species of *Perilampus*

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Abstract

New faunistic records of Palaearctic Perilampidae (Hymenoptera: Chalcidoidea) are given, based on newly collected material in South-East Europe, South Korea and specimens from the Natural History Museum in London. *Euperilampus* Walker, 1871 is recorded for the first time in South Korea, with females of *E. sinensis* Bouček, 1978 being discovered and described for the first time. The genera *Perilampus* Latreille, 1809 and *Steffanolampus* Peck, 1974 are recorded for the first time in Greece. *Perilampus noemi* Nikol'skaya, 1952, collected on Crete and Salamina islands (Greece), is recorded for the first time in Europe. The following species are new to Greece: *P. aeneus* (Rossius, 1790), *P. laevifrons* Dalman, 1822, *P. micans* Dalman, 1820, *P. minutalis* Steffan, 1952, *P. neglectus* Bouček, 1956, *P. ruficornis* (Fabricius, 1793), *P. tristis* Mayr, 1905, and *S. salicetum* (Steffan, 1952). The following species are new to Romania: *P. aeneus*, *P. auratus* (Panzer, 1798), *P. aureoviridis* Walker, 1833, *P. chrysonotus* Förster, 1859, and *P. laevifrons*. The following species are new to Turkey: *P. auratus*, *P. cephalotes* Bouček, 1956, *P. ruficornis*, and *P. tristis*. Additionally, *P. cephalotes* and *P. polypori* Bouček, 1971 are new to Austria; *P. masculinus* Bouček, 1956 is new to Sweden; *P. ruficornis* is new to South Korea; and *P. tristis* is new also to Cyprus and Spain. The first host record for *P. cephalotes* and a new host record for *P. laevifrons* are also given. A key to 20 European species of *Perilampus* is included. Each species is diagnosed using macrophotography to facilitate its future recognition. The males of *P. intermedius* Bouček, 1956 and *P. neglectus* are described for the first time.

Keywords
Distribution, *Euperilampus*, host, key, parasitoid, *Perilampus*, *Steffanolampus*

Introduction

The status of the family Perilampidae has been recently revised by Zhang et al. (2021) in the context of a larger group called "the planidial larva clade", which also includes the families Chrysolampidae and Eutrichosomatidae. Thus, the family Perilampidae now consists of six genera: *Burksilampus* Bouček, 1978, *Euperilampus* Walker, 1871, *Krombeinius* Bouček, 1978, *Monacon* Waterson, 1922, *Perilampus* Latreille, 1809, and *Steffanolampus* Peck, 1974. A key to these genera is given by Bouček (1978).

In general, there are no recent data on Palaearctic Perilampidae. While in North-Western Europe the family is somewhat better known, the situation is very different in the South-Eastern part of the continent. For example in Greece the only species known to date is *Philomides paphius* Haliday, 1862 (now placed in Chrysolampidae), while in Romania only five species of *Perilampus* are recorded: *P. cuprinus* Förster, 1859, *P. neglectus* Bouček, 1956, *P. nitens* Walker, 1834, *P. ruschkai* Hellen, 1924 and *P. tristis* Mayr, 1905 (Noyes 2019). No species of Perilampidae are known from South Korea, although the family is mentioned by Paik (1978). An exception to this situation is an investigation of the perilampid fauna of the Arabian Peninsula, where the family has been recently recorded for the first time (Darling and Yoo 2021).

Steffanolampus is monotypic and can be easily identified (e.g., Bouček 1956; the present paper). *Euperilampus* consists of 19 valid species, out of which three are known to occur in East Palaearctic (Noyes 2019): *E. scutellatus* (Girault, 1915), *E. sinensis* Bouček, 1978, and *E. spina* Bouček, 1978. They are keyed by Bouček (1978).

Perilampus is the most speciose genus within Perilampidae, with 158 valid species worldwide and 47 species in the Palaearctic region (Noyes 2019). In addition, five new species with Palaearctic and Afrotropical affinities have been recently described by Darling and Yoo (2021). Although many species of *Perilampus* are among the largest and most colourful chalcid wasps, they are still poorly known even in Europe, as our study demonstrates.

In order to identify the European species of *Perilampus*, users must rely on rather old and often difficult identification keys (Nikol'skaya 1952; Steffan 1952; Bouček 1956, 1983), with no colour illustrations, or no illustrations at all for some of the species. Only recently a handful of species have been illustrated using macrophotography (Darling and Yoo 2021). For a discussion about the taxonomic impediments regarding the study of the Palaearctic fauna of Perilampidae, see Darling and Yoo (2021). Although a taxonomic revision of all Palaearctic species of *Perilampus* would be very useful, it is hoped that until this is accomplished, the present identification key to 20 European species, the first one accompanied by colour macrophotographs and detailed diagnoses, will facilitate the recognition of many European species and encourage future studies.

Methods

Most examined specimens were collected in Greece, Romania and South Korea using a variety of methods, i.e., the sweeping net, yellow pan traps (**YPT**), Malaise traps, or by hand. They were kept in alcohol until air-dried or dried using hexamethyldisilazane (**HMDS**), glued on rectangular or triangular cards and deposited in the first author's collection (**MICO**) and at the Zoological Museum of the University of Athens (**ZMUA**). Another part of the material represents specimens deposited in the Natural History Museum, London, UK (**NHMUK**), which were used mostly for comparison. Observations were made using a Leica S8APO stereomicroscope. Images were taken mostly using a Leica DFC500 digital camera attached to a Leica M205A automated research stereomicroscope. The images were then assembled with Zerene Stacker and their clarity was further enhanced using Adobe Photoshop 7.0; all scale bars are 0.2 mm.

The morphological terminology follows Bouček (1956) and Bouček and Rasplus (1991). The collected specimens were identified using the keys of Steffan (1952), Nikol'skaya (1952), Bouček (1956, 1978, 1983). Comparative material identified mainly by Z. Bouček, but also G.J. Kerrich and Ch. Ferrière, was examined for all recorded and/or keyed species, except *P. aquilus* Nikol'skaya, *P. eximius* Masi and *P. maceki* Bouček, where no material was available for study at this time (see Material examined).

For all treated species a diagnosis for both sexes was given, primarily using the examined material, and supplemented with information from the above mentioned literature when one of the sexes was not available for direct study. The information regarding colour variation and body dimensions was also combined with literature data. When no reference to one sex is mentioned, the diagnosis characters refer to both sexes.

The two sexes can be separated by examining the gastral apex, although this sometimes proves difficult because of the strongly retracted terminal tergites. In males *Perilampus* the scape has pores on at least part of its ventral surface, being slightly to strongly widened distally (e.g., Figs 4B, 5B, 8B, 12B); in the same time, the flagellum is usually thicker and darker than in females. Moreover, in species with frontal keels present, these are more developed and sharper in males (e.g., Fig. 11B) than in females, where they are smaller and rounder (e.g., Fig. 11A). All identified species of *Perilampus* have a more or less indicated ridge between the median ocellus and the lateral ocellus (e.g., Figs 3C, 11C, 14C), but these can be continued with frontal keels that go along the inner eye margin or not. If this feature is not clear in frontal view of the head, observing the head in dorsal view may be useful (e.g., frontal keels present – e.g., Figs 2C, 16C; frontal keels absent – e.g., Figs 3C, 11C, 13C, 14C, 18C). When the face sculpture is evaluated (e.g., smooth or striate), the occasional presence of piliferous punctures is not considered. Body coloration can be rather variable, so it should be used with care.

In *Euperilampus*, a character used by Bouček (1978) in his key is the length of the labio-maxillary complex. This is measured from its apex to the lower clypeal margin and compared with the breadth of the left mandible.

Information on geographic distribution and hosts is taken from Noyes (2019), if not stated otherwise. For generic synonyms, new combinations, and a detailed list of host species, see the previously mentioned source. Information on specimen labels is given *ad litteram*.

Abbreviations used in the figures: **atp** = anterior tentorial pit; **cly** = clypeus; **frk** = frontal keel; **lmc** = labio-maxillary complex; **mdp** = malar depression; **msl** = malar sulcus; **sca** = supraclypeal area; **OOL** = oculo-ocellar line; **scp** = scutellar projection; **vp** = ventral pores.

Results

Euperilampus Walker, 1871

Fig. 1

Euperilampus Walker, 1871: 67. Type species: *Perilampus gloriosus* Walker, 1862; by original designation and monotypy.

Diagnosis. Face without a horn. Scrobes laterally bordered by a complete and distinct carina (Fig. 1C, D). Head with longitudinal striae (Fig. 1C, D). Pronotum without elevations (Fig. 1A, B, E, F). Prepectus narrow, considerably shorter than half of the adjacent pronotal collar (Fig. 1A, B). Scutellum strongly produced over propodeum, its entire free margin with crenulate rim (Fig. 1A, B, E, F, H); marginal vein shorter than postmarginal vein (Fig. 1G). Petiole inconspicuous. Ovipositor sheaths straight, not projecting, hidden under apical tergites (Fig. 1A).

Euperilampus sinensis Bouček, 1978

Fig. 1

Euperilampus sinensis Bouček, 1978: 305.

Diagnosis. Both sexes. Body black, without any metallic reflections (Fig. 1A, B); femora dark (Fig. 1A, B); fore wing slightly infumate (Fig. 1G). Labio-maxillary complex only slightly protruding beyond closed mandibles (Fig. 1C, D). Dorsal side of mesosoma without any rugae (Fig. 1E, F). Inner axillular margins almost parallel (Fig. 1E, F). Sides of scutellum steep in posterior part (Fig. 1E, F, H). Posterior scutellum projection truncate to emarginate (Fig. 1E, F, H). Marginal vein more than 1.5× as long as stigmal vein (Fig. 1G). Female. Flagellum dark orange, claval apex slightly darker (Fig. 1A, C); tibiae blackish brown (Fig. 1A, C). Male. Flagellum dorsally dark brown, ventrally dark reddish-brown (Fig. 1B); tibiae dark brown except distal third getting yellowish-brown or brownish yellow on inner side of fore tibia (Fig. 1B, D). Clypeus with short setae, anterior tentorial pits slightly to distinctly visible (Fig. 1D). Antennal scape normal, not laminate or foliaceous (Fig. 1D).

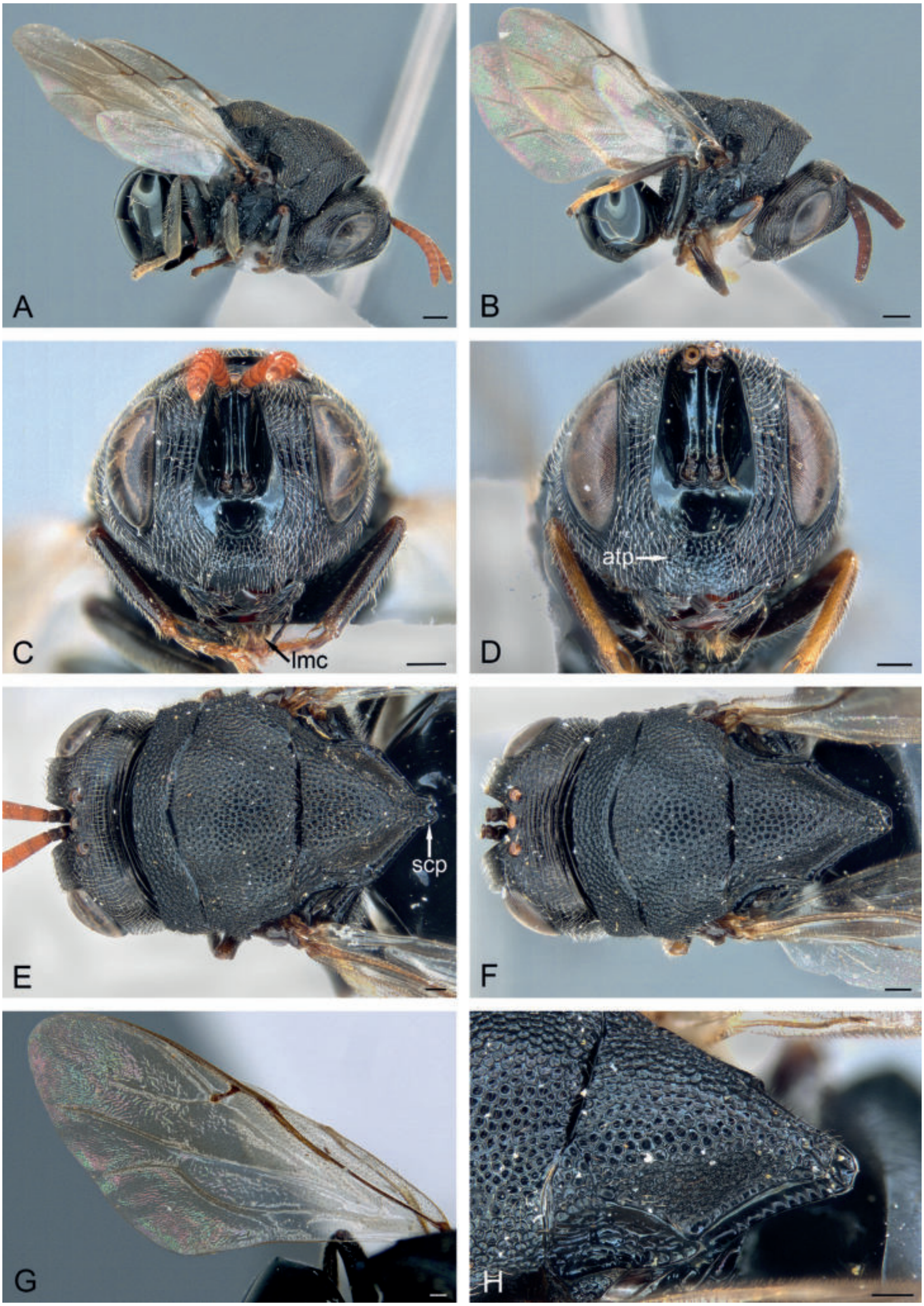

Figure 1. *Euperilampus sinensis* **A** female, habitus in lateral view **B** male, habitus in lateral view **C** female, head in frontal view **D** male, head in frontal view **E** female, mesosoma in dorsal view **F** male, mesosoma in dorsal view **G** female, fore wing **H** male, scutellum in dorso-lateral view.

Material examined. South Korea: 2♀, 2♂, "S. KOREA, GYONGBUK, Ulleungdo, trail in forest, from Nari Basin to Seonginbong Peak / 500–1000 m, 16.VIII.2010, P. Tripotin rec." (MICO).

Description. Female. ***Body length*****:** 4.5–5.0 mm. ***Colour*****.** Body black, without any metallic reflections (Fig. 1A). Body setation brown on dorsal side of mesosoma and whitish on clypeus and face (Fig. 1C, E). Scape and pedicel black; flagellum dark orange, claval apex brownish (Fig. 1A, C). Eyes brown, ocelli dark orange to brown (Fig. 1C). Mandibles dark reddish brown (Fig. 1C). Labio-maxillary complex dark brown. Legs with coxae, trochanters, femora and tibiae blackish brown; knees, extreme tibial apices and most tarsal segments reddish brown; basal tarsal segments and apical segment dark brown (Fig. 1A, C). Tegula dark brown. Fore wing slightly infumate (Fig. 1G).

Head**.** Striae on vertex, parascrobal areas, temples and genae generally strong and dense (Fig. 1C, E). Scrobes with their lateral carinate margins strongly converging both downwards and upwards, very slightly sinuate in the upper part (Fig. 1C). Supraclypeal area poorly defined, subquadrate, slightly convex in middle, its lower corners setose (Fig. 1C). Clypeus nearly flat, with strongly diverging lateral margins, densely setose, anterior tentorial pits indistinct; both upper and lower clypeal margins conspicuously emarginate; setae much longer than distance between dense piliferous punctures; clypeus surface apart from piliferous punctures with fine but conspicuous transverse striae, most visible on sides (Fig. 1C). Piliferous punctures on basal halves of mandibles less dense than those on the clypeus. Labio-maxillary complex protruding beyond clypeal margin to about 1.8× breadth of left mandible (Fig. 1C). Scape very slightly curved and widened distally, without any laminate expansion, its maximum width about 0.7× maximum width of flagellum (Fig. 1C); flagellum subfusiform, funicular segments 1–4 longer than wide (length of first segment 1.25–1.33× width), 5 subquadrate, 6–7 transverse; clava shorter than the three preceding segments (Fig. 1A).

Mesosoma**.** Pronotal collar in middle about 0.3x as long as mesoscutum. Both pronotal collar and mesoscutum regularly punctuate-reticulate, without smooth areas except for a narrow band at posterior margin of pronotal collar (Fig. 1E). Scutellum as coarsely sculptured as mesoscutum except lateral sloping sides with much coarser reticulation; scutellum from very slightly longer than wide to virtually as long as wide; lateral margins almost parallel; postero-lateral sided steep, slightly concave; terminal protruding process slightly (smaller female) to conspicuously emarginate (larger female) (Fig. 1E). Propodeum with carinate spiracular sulci and triangular median depression, the latter with a slightly indicated median carina; median propodeal area irregularly striate; spiracles narrow, reniform. Fore wing with parastigma and marginal vein slightly widened (Fig. 1G). Marginal vein 1.6–1.7× as long as stigmal vein; postmarginal vein about 2.8× as long as marginal vein, but apical end difficult to define.

Metasoma**.** Wider than long, much shorter and wider than mesosoma (Fig. 1A). Posterior margin of first tergite virtually straight; second gastral tergite 2.2–2.6× as wide as long; anterior 1/3–1/4 and anterior 1/2 of second and third tergites respectively with a transverse band of very shallow piliferous punctures.

Male. Differs from the female mainly as follows. Body length: 4 mm. Flagellum dark reddish brown, ventrally slightly lighter, claval apex darker (Fig. 1B). Tibiae dark brown, gradually becoming yellowish brown on apical third on outer surface and brownish yellow on most inner surface of fore tibia; tarsi entirely yellowish brown except dark brown arolia and claws (Fig. 1B, D). Longitudinal striae on upper face (between upper third of eye and scrobes) shallower and more irregular (Fig. 1D). Lateral margins of scrobes less strongly converging upwards (Fig. 1D). Setae on upper half of clypeus shorter (Fig. 1D), their length only slightly greater than distance between piliferous punctures. Anterior tentorial pits slightly to distinctly visible (Fig. 1D). Flagellum thicker (Fig. 1B); length of first funicular segment 1.11–1.15× width. Scutellum longer, length about 1.3× maximum width, terminal protruding process only very slightly emarginate (Fig. 1F). Posterior margin of first tergite broadly emarginate. Piliferous punctures on gastral tergites two and three deeper. For additional information, see the description of the male in Bouček (1978).

Hosts. Unknown.

Distribution. Peoples' Republic of China. New genus and species to South Korea.

Comments. As stated in Darling (1983), *Euperilampus* differs from other perilampid genera mainly in the prepectus size, and in having a distinctly shorter marginal vein, compared to the postmarginal vein. There are currently three species of *Euperilampus* known from East Palaearctic: *E. scutellatus*, *E. sinensis* and *E. spina* (Noyes 2019). So far, the females of *E. sinensis* and *E. spina* have been unknown. Following Bouček's key (1978) we have identified the above listed specimens as being closest to *E. sinensis*. However, the almost indistinct anterior tentorial pits shed some doubt about the identification. Further clarification came after the examination of images of the male holotype of *E. sinensis*, kindly provided by Natalie Dale-Skey (NHMUK). The male specimens we examined differ from the holotype mainly in having (1) tentorial pits barely visible (*versus* conspicuous); (2) longitudinal striae on upper face (between scrobes and upper third of eye) shallow and irregular (*versus* stronger and regular); (3) clypeus aside from piliferous punctures slightly more sculptured (*versus* almost smooth); and (4) body setation very dense (*versus* sparser). The latter difference is probably just a conservation artifact, given the considerably older age of the holotype, in which the bare piliferous punctures indicate that many of the setae have fallen. The other differences are most probable due to intraspecific variability. However, they may indicate a new species, but without any females for comparison and without any evidence about the intraspecific variability of *E. sinensis*, its validity cannot be correctly assessed at present.

Perilampus **Latreille, 1809**

Figs 2–18

Perilampus Latreille, 1809: 30. Type species: *Cynips italica* Fabricius, 1793; by subsequent designation of Westwood (1839: 67).

Diagnosis. Face without a horn. Scrobes laterally not carinate (European species) (e.g., Figs 2A, 3A, 6A, 10A, 12A, 14A). Head mostly without longitudinal striae (or these confined to upper face), sometimes with more or less distinct frontal keels (e.g., Figs 2A–C, 3B, 11B, 16B). Pronotum without elevations (e.g., Figs 2C, 4C, 7C, 10C). Prepectus variable but considerably longer than at least half the adjacent pronotal collar (e.g., Figs 2D, 4D, 8D, 11D, 14D, 18D). Scutellum at most slightly produced over propodeum, its posterior margin sometimes with protruding bilobed process (e.g., Figs 2C, 8C, 14C); marginal vein longer than postmarginal vein; petiole inconspicuous, sometimes with dorsal scale; ovipositor sheaths straight, not projecting, hidden under apical tergites.

Key to European species of *Perilampus*

1 Prepectus poorly defined anteriorly (i.e., appearing virtually fused with pronotum) and very narrow (Figs 7D, 18D); male with scape only slightly widened distally (Figs 7B, 18B).. **2**

– Prepectus well defined anteriorly (i.e., with a conspicuous suture between its anterior margin and pronotum) (e.g., Figs 2D, 4D, 6D, 8D, 11D, 13D, 16D), either narrow or wider; male with scape sometimes strongly widened distally (Figs 4B, 8B).. **3**

2(1) Dorsal side of mesosoma virtually without metallic reflections (Fig. 18C); middle funicular segments strongly transverse (Fig. 18A); male with frontal keels distinct (Fig. 18B); male scape with ventral pores on slightly less than half scape length (Fig. 18B)........................ ***P. tristis*** **Mayr**

– Dorsal side of mesosoma with distinct metallic reflections (Fig. 7C); middle funicular segments at most slightly transverse (Fig. 7A); male with frontal keels absent (Fig. 7B); male scape with ventral pores on slightly more than half scape length (Fig. 7B) .... ***P. intermedius*** **Bouček**

3(1) Mesoscutum with small median tubercle (Fig. 3C); head and pronotum golden green, mesosoma blue (Fig. 3C); prepectus with anterior margin without any row of punctures (Fig. 3D); male scape only slightly widened (Fig. 3B)........................ ***P. auratus*** **(Panzer)**

– Mesoscutum without any median tubercle (e.g., Figs 2C, 4C, 5C, 6C, 11C, 13C, 16C); body colour mostly different; male scape sometimes strongly widened distally (Figs 4B, 8B); prepectus sometimes with anterior margin with complete or incomplete row of punctures (e.g., Figs 5D, 9D, 13D, 15D).... **4**

4(3) Mesosoma narrow (i.e., laterally compressed), length at least 1.5× width, with bright golden green reflections (Fig. 10B); scutellum in dorsal view with double carina at posterior margin (Fig. 10B); face between clypeus and eye strongly and extensively striate (Fig. 10A); propodeum without two large smooth or superficially sculptured areas (Fig. 10D)........................***P. micans*** **Dalman**

– Mesosoma wider, length at most 1.35× width (e.g., Figs 4C, 6C, 8C, 9C, 11C, 13C, 14C), rarely narrower (*P. cephalotes* – Fig. 5C; *P. maceki*; *P. polypori* – Fig. 15C), and then black, or with at most slight metallic reflections; scutellum in dorsal view without double carina (e.g., Figs 5C, 8C, 11C, 15C, 16C); face between clypeus and eye without strong extensive striation (e.g., Figs 5A, 6A, 8A, 9A, 11A, 13A, 15A), rarely with indication of striation along gena near mouth corner (Figs 4B, 9B); propodeum with two large smooth or superficially sculptured areas (Fig. 17D).. **5**

5(4) Head in frontal view only slightly wider than high, supraclypeal area higher than wide (Fig. 6A, B); mesoscutum and scutellum with sparse punctures, interspaces larger than punctures (Fig. 6C); prepectus narrow, anterior margin without a row of punctures (Fig. 6D).......................... ***P. chrysonotus* Förster**

– Head in frontal view distinctly wider than high, supraclypeal area at least slightly wider than high (e.g., Figs 8A, 9A, 11A, 13A, 16A); mesoscutum and scutellum with denser punctures, interspaces smaller than punctures (e.g., Figs 8C, 9C, 11C, 13C, 14C, 16C); prepectus sometimes wider and/or its anterior margin with a row of punctures (e.g., Figs 9D, 13D, 15D, 17C).................... **6**

6(5) Ocelli large, OOL only 1.4–1.5× diameter of lateral ocellus in female (Fig. 11C) and 1.0–1.1× in male (Fig. 11B); clypeal margin strongly convex (Fig. 11A, B); mesosoma black (Fig. 11C) .... ***P. minutalis* Steffan**

– Ocelli smaller, OOL usually longer in both sexes (e.g., Figs 5D, 6C, 9C, 13C, 16C); if approaching the above (female of *P. noemi*), mesosoma with distinct metallic reflections (Fig. 14C)... **7**

7(6) Female with funicular segments longer than wide; male with funicular segments quadrate; face between scrobes and eye smooth; head and mesosoma dark blue, metasoma black... ***P. aquilus* Nikol'skaya**

– Female with most funicular segments quadrate to transverse (e.g., Figs 4A, 5A, 11A, 13A, 15A, 18A); male with funicular segments mostly transverse (e.g. Figs 2B, 11B, 16B, 18B); if proximal funicular segments longer than wide (female of *P. laevifrons*), than face between scrobes and eye at least slightly striate (Fig. 8A); body colour variable... **8**

8(7) Head with frontal keels, these usually stronger in males (Figs 2A–C, 16A–C) **9**

– Head without frontal keels (e.g. Figs 13A–C, 14A–C), although sometimes more or less striate between scrobes and eye (Figs 4A, B, 8A, B) **11**

9(8) Anterior margin of prepectus with complete row of punctures (Fig. 2D); female antenna black (Fig. 2A); ocelli large (Fig. 2C); dorsal side of mesosoma bright golden green (Fig. 2C)... ***P. aeneus* (Rossius)**

– Anterior margin of prepectus without any row of punctures (Fig. 16D); female antenna entirely bright reddish except dark claval apex (Fig. 16A); ocelli smaller (Fig. 16C); dorsal side of mesosoma with pink, green or bluish green reflections (Fig. 16C) **10**

10(9) Head and mesosoma with pink and greenish reflections; clypeus more strongly transverse .... ***P. eximius* Masi**

– Head and mesosoma bluish green (Fig. 16A–C); clypeus less strongly transverse (Fig. 16A).. ***P. ruficornis* (Fabricius)**

11(8) Body black, at most with very slight metallic reflections (Figs 5, 12, 15)..... **12**

– Body with more distinct, sometimes bright, metallic reflections (Figs 4, 8, 9, 13, 14, 17).. **15**

12(11) Male only; mesosoma narrow (i.e., laterally compressed – cf. Fig. 10B), length 1.9–2.0× width; mesoscutum and scutellum with interspaces between punctures as wide as or wider than punctures ....***P. maceki* Bouček**

– Both sexes; mesosoma wider, length 1.2–1.5× width (e.g., Figs 4C, 5C, 12C, 14C, 15C); mesoscutum and scutellum with interspaces between punctures less than 1/3 the diameter of punctures (e.g., Figs 4C, 5C, 12C, 14C, 15C)........**13**

13(12) Head width about 1.8× length in dorsal view; temples large and separated from eye by wide sulcus, also visible in frontal view of head (Fig. 5A, B); supraclypeal area distinctly transverse (Fig. 5A, B); mesoscutum and scutellum with interspaces between punctures relatively wide (Fig. 5C); mesosoma with dark metallic reflections (Fig. 5C) ....***P. cephalotes* Bouček**

– Head width hardly less than twice as broad as long; temples smaller, at most with very narrow sulcus near posterior eye margin, not visible in frontal view of head (Figs 12A, B, 15A, B); supraclypeal area only slightly transverse (Figs 12A, B, 15B); mesoscutum and scutellum with interspaces between punctures very narrow (Figs 12C, 15C); mesosoma virtually without metallic reflections (Figs 12C, 15C) **14**

14(13) Mesosoma wide, length about 1.2× width (Fig. 12C); prepectus narrow, anterior margin with at most a row of tiny punctures (Fig. 12D)......................... ....***P. neglectus* Bouček**

– Mesosoma narrower, length 1.4–1.5× width (Fig. 15C); prepectus wider, with an incomplete row of small punctures along anterior margin (Fig. 15D)........ ....***P. polypori* Bouček**

15(11) Frons between eye and scrobes without any striation, although sometimes strongly punctuate (Figs 13A, 14A, B, 17A)...**16**

– Frons between eye and scrobes with at least some traces of striation among punctures, which are usually stronger in males (Figs 4A, B, 8A, B, 9A, B) .**18**

16(12) Mesosoma dorsally dark, with bronze-violet reflections (Fig. 14C); prepectus narrow, almost entirely punctuate, leaving only a small smooth central area (Fig. 14D).. ***P. noemi* Nikol'skaya**

– Mesosoma dorsally bright green or blue (Figs 13C, 17D); prepectus wider, always with a larger smooth central area (Figs 13D, 17C) **17**

17(16) Frons between eye and scrobes not strongly punctuate (Fig. 17A); supraclypeal area rather well defined (Fig. 17A); male eyes large (Fig. 17A); body green, except darker metasoma (Fig. 17).................................... ***P. ruschkai* Hellen**

– Frons between eye and scrobes strongly punctuate (Fig. 13A, B); supraclypeal area poorly defined (Fig. 13A, B); male eyes smaller (Fig. 13B); body entirely blue (Fig. 13) ....***P. nitens* Walker**

18(15) Clypeal margin slightly (Fig. 4A) to strongly emarginate (Fig. 4B); metasoma with distinct metallic reflections; male face with large oval impressions at each side of supraclypeal area (Fig. 4B) ....***P. aureoviridis* Walker**

– Clypeal margin truncate (Figs 8A, B, 9A, B); metasoma black; male face without any impressions (Figs 8B, 9B)..**19**

19(18) Supraclypeal area less transverse, less than 1.5× as wide as high, and less wide than clypeal area (Fig. 8A, B); male scape strongly widened distally (Fig. 8B); face blue-green (Fig. 8A, B).......................... ***P. laevifrons* Dalman**

– Supraclypeal area transverse, at least 1.5× as wide as high, and almost as wide as clypeal area (Fig. 9A, B); male scape only slightly widened distally (Fig. 9B); face mostly dark green, with bronze reflections (Fig. 9A, B) .... ***P. masculinus* Bouček**

Perilampus aeneus (Rossius, 1790)

Fig. 2

Chalcis aenea Rossius, 1790 in Rossi (1790: 59).
Cynips italica Fabricius, 1793: 103. Synonymy by Steffan (1952: 73).

Diagnosis. Head and mesosoma except propodeum dorsally bright bronze green, head sometimes bluish; propodeum and metasoma blue green; female flagellum black. Body size: 2.50–5.00 mm. Head shape in frontal view (Fig. 2A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 2A, B) truncate. Supraclypeal area (Fig. 2A, B) slightly transverse (less than 1.5× as wide as high), sides not defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter in female, about equal in male. Frontal keels (Fig. 2A, B) well developed. Face between scrobes and eye (Fig. 2A, B) almost smooth. Face between clypeus and eye (Fig. 2A, B) smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female (Fig. 2A): most segments quadrate to transverse. Male scape (Fig. 2B) slightly widened distally; ventral pores on about half scape length. Mesosoma (Fig. 2C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 2C) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 2C) without a double carina, with large bilobed protruding projection. Prepectus (Fig. 2D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); all sides with punctures, leaving a large smooth central area.

Material examined. GREECE: 1♀, "Kerkini Lake N. Park, Promohonas, Procom site, Malaise, 23.V to 29.V.2007, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel" (MICO); 1♀, "Kerkini Lake N. Park, Promohonas, Procom site, Malaise, 22–28.VIII.2007, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel" (MICO); 1♀, "Kerkini lake; Malaise trap; Krousia Mts. Site, 12.IX to 18.IX.2007, 41°11'32.4"N, 23°03'59.5"E, Leg. Gordon Ramel" (MICO); 3♀♀, "Kerkini Lake N. Park, Kerkini, Krousia Mts site, Malaise tr., 13.VI-19.VI.2007, 41°11'32.4"N, 23°03'59.5"E, 190 m, Leg. Gordon Ramel" (MICO); 1♂, "Rizari, nr. Edessa, 40.792366°N, 22.107232°E", "OP cherry, M2 – P1-2, 3.05.2019, leg. F. Karamaouna" (MICO).

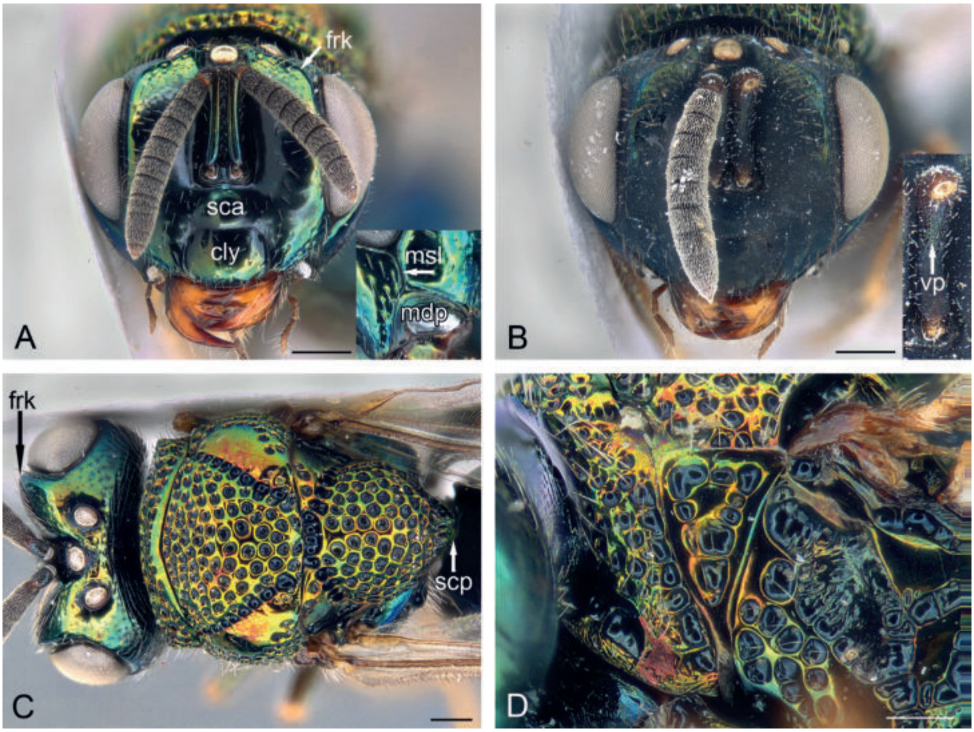

Figure 2. *Perilampus aeneus* **A** female, head in frontal view (insert: detail of the genal area) **B** male, head in frontal view (insert: detail of scape) **C** female, head and mesosoma, dorsal view **D** female, prepectus.

Romania: 1♀, "IS, Ciric-Izvor, 10.VIII.2006, leg. M.-D. Mitroiu" (MICO); 1♀, "Iași county, Valea lui David Natural Reserve, 02.viii.1998, sweep, M.-D. Mitroiu leg." (MICO); 1♀, "Brăila county, Smârdan, 30.viii.2005, herbaceous vegetation along canal, Popovici O. & Moglan I." (MICO); 1♀, 1♂, "Tulcea county, near Babadag, 15–17.v.2009, L. Fusu leg." (MICO); 1♂, "Constanța county, Gura Dobrogei Natural Reserve, 12.v.2007, L. Fusu leg." (MICO). Turkey: 1♀, "Turkey: Kastamonu, Kastamonu area, 18.vii.1962, 1000 m", "Guichard & Harvey, B.M. 1962-299", "♀ Perilampus aeneus (Rossius), Z. Bouček det. 1972" (NHMUK); 1♂, "Turkey: Amasya, Alt. I. 400 Ft", "6.6.1959, K.M. Guichard", "♂ Perilampus aeneus (Rossius), Z. Bouček det. 1972" (NHMUK).

Hosts. Associated with Curculionidae (Coleoptera), Tenthredinidae (Hymenoptera), and Tortricidae (Lepidoptera); presumably a hyperparasitoid.

Distribution. Bosnia Herzegovina, Croatia, Czechia, Germany, Hungary, Italy, Moldova, Netherlands, Russia, Serbia, Slovakia, Spain, Sweden, Turkey, United Kingdom. New species to Greece and Romania.

Comments. *Perilampus aeneus* is somewhat similar to *P. eximius* and *P. ruficornis* due to its bright colour and presence of frontal keels. From both species it can be separated by the sculpture of the prepectus, which has a complete (although sometimes shallow) row of punctures near its anterior margin (Fig. 2D), and the bigger ocelli (Fig. 2C). Furthermore, the female of *P. aeneus* can be separated from the females of the previously mentioned species by the colour of the flagellum, which is black and not reddish (Fig. 2A).

Perilampus auratus (Panzer, 1798)

Fig. 3

Cynips auratus Panzer, 1798: table 1.

Diagnosis. Head and pronotum bronze gold, with slight green reflections; mesosoma blue green; metasoma green, with blue and bronze reflections; female flagellum orange, clava slightly darker. Body size: 1.75–5.00 mm. Head shape in frontal view (Fig. 3A, B), much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temples. Clypeal margin (Fig. 3A, B) slightly emarginate to truncate. Supraclypeal area (Fig. 3A, B) slightly transverse (less than 1.5× as wide as high), sides not defined; in male without oval lateral impressions. Malar sulcus versus length of anterior margin of malar depression longer in female, about equal in male. Frontal keels (Fig. 3A, B) poorly developed. Face between scrobes and eye (Fig. 3A, B) almost smooth. Face between clypeus and eye (Fig. 3A, B) smooth. Lateral ocellus small (OOL at least twice the largest lateral ocellus diameter). Funicular segments in female (Fig. 3A): most segments transverse. Male scape (Fig. 3B) slightly widened distally; ventral pores on less than half scape length. Mesosoma (Fig. 3C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 3C) with smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 3C) without a double carina, with small more or less bilobed protruding projection. Prepectus (Fig. 3D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e., suture with pronotum very distinct); anterior margin without punctures.

Material examined. Romania: 2♀♀, 1♂, “Iași county, Iași city, inside apartment, 25.i.2008, M.-D. Mitroiu leg.” (MICO). Turkey: 1♀, 1♂, “Turkey: Ankara, Kavaklidere, 6.viii.1960. 2,700'”, “Guichard & Harvey, B.M. 1960-364”, “♀/♂ Perilampus auratus (Panz.), Z. Bouček det. 1972” (NHMUK).

Hosts. Associated with Crabronidae (Hymenoptera) and Tenthredinidae (Hymenoptera); presumably a hyperparasitoid.

Distribution. Croatia, Czechia, Germany, Hungary, Kazakhstan, Moldova, Netherlands, Russia, Slovakia, Sweden, Ukraine. New species to Romania and Turkey.

Comments. This is one of the easiest species to identify, being the only one with a median tubercle on the mesoscutum (Fig. 3C). Moreover, the colour pattern of this species seems unique at least among the European species.

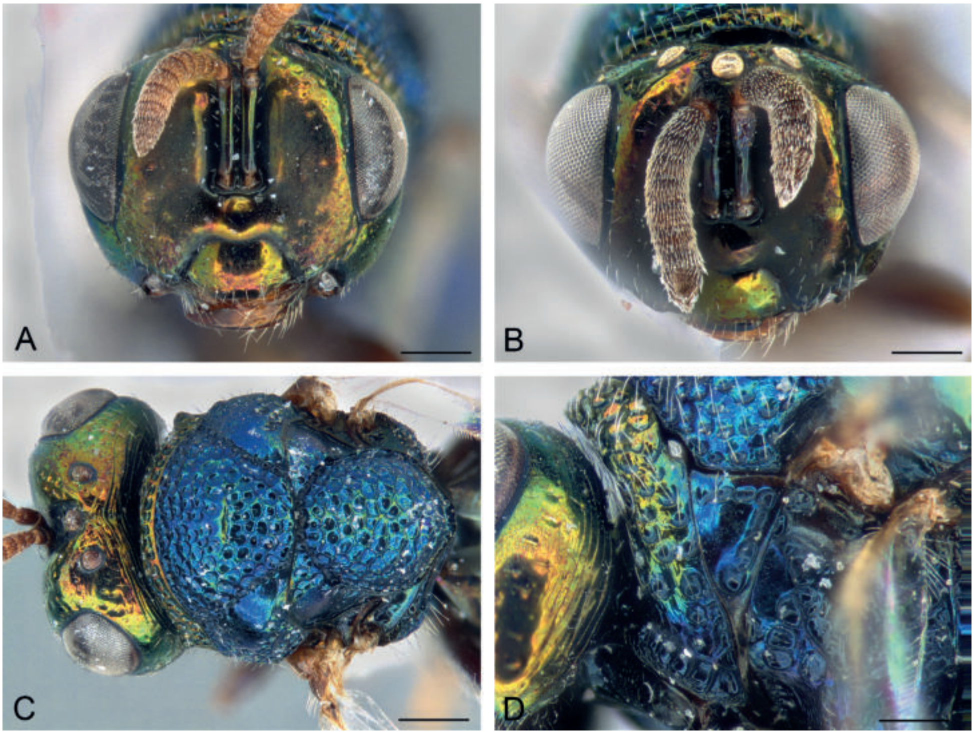

Figure 3. *Perilampus auratus* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

Perilampus aureoviridis Walker, 1833

Fig. 4

Perilampus aureoviridis Walker, 1833: 142.
Perilampus emarginatus Thomson, 1876: 23. Synonymy by Bouček and Graham (1978: 72).
Perilampus lacunosus Nikol'skaya, 1952: 195. Synonymy by Bouček (1983: 116).

Diagnosis. Head and mesosoma green, with bronze gold reflections; metasoma blue green; female flagellum dark brown, ventrally reddish-brown. Body size: 2–3 mm. Head shape in frontal view (Fig. 4B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 4B) slightly emarginate. Supraclypeal area (Fig. 4B) slightly transverse (less than 1.5× as wide as high), sides slightly defined; in male with oval lateral impressions (Fig. 4B). Malar sulcus versus anterior margin of malar depression shorter in female. Frontal keels (Fig. 4B) absent. Face between scrobes and eye (Fig. 4B) striate. Face between clypeus and eye (Fig. 4A, B) almost smooth. Lateral ocellus large (OOL less than twice the largest ocellar diameter). Funicular segments in female (Fig. 4A): most segments quadrate to transverse. Male scape (Fig. 4B) strongly widened distally,

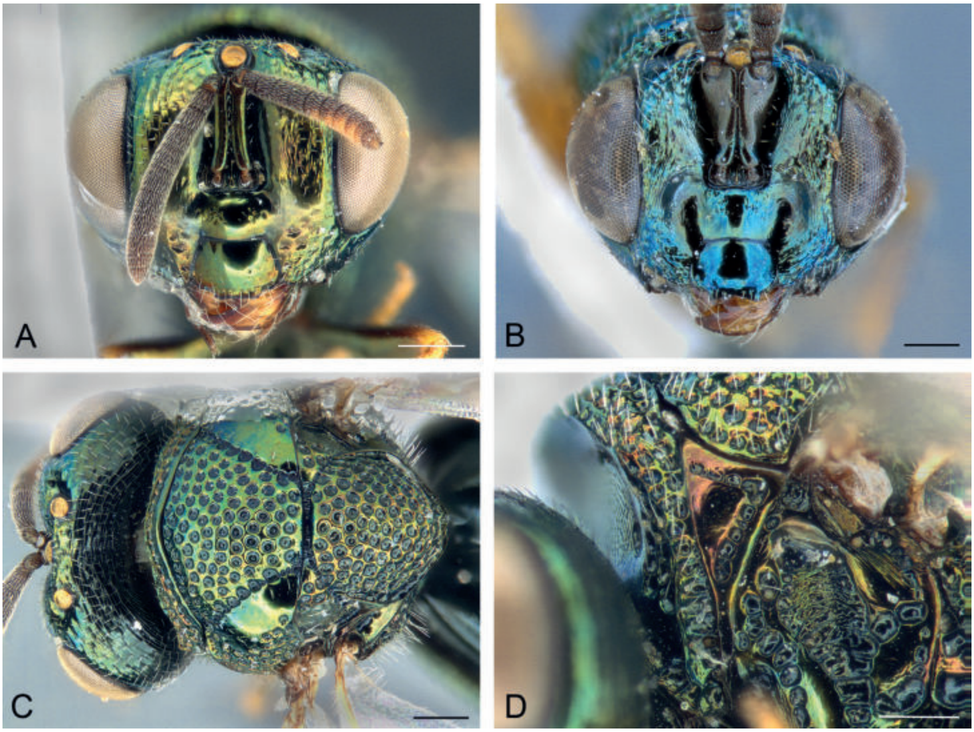

Figure 4. *Perilampus aureoviridis* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

ventral pores on nearly all scape length. Mesosoma (Fig. 4C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 4C) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 4C) without a double carina, with small more or less bilobed protruding projection. Prepectus (Fig. 4D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); anterior margin without punctures.

Material examined. Mongolia: 1♀, “Mongolia: Central aimak, 12 km S von Somon Bajanbaraat, 1380 m, Exp. Dr. Z. Kaszab, 1967”, “Nr. 918, 13.VII.1967”, “Perilampus lacunosus Nik. ♀, Bouček det. 1982” (NHMUK). Romania: 1♀, “Iaşi county, Gorban, 29.viii.2005, Popovici O. & Moglan I.” (MICO).

Hosts. Unknown.

Distribution. Czechia, Germany, Mongolia, Netherlands, Russia, Slovakia, Sweden, Ukraine, United Kingdom. New species to Romania.

Comments. The female of *P. aureoviridis* can be confused to those of *P. laevifrons* and *P. masculinus*; it can be distinguished from those mainly by the larger interspaces on mesoscutum and scutellum (Fig. 4C) and the entirely green body, with slight golden or bronze reflections (Fig. 4A). The males of *P. aureoviridis* should be easily recognizable being the only ones with oval lateral impressions adjacent to the supraclypeal area and ventral pores on nearly all scape length (Fig. 4B).

Perilampus cephalotes Bouček, 1956
Fig. 5

Perilampus cephalotes Bouček, 1956: 89–90.

Diagnosis. Head and metasoma black, mesosoma dark green; female flagellum dark brown. Body size: 3.0–3.5 mm. Head shape in frontal view (Fig. 5A, B) much wider than high. Head in lateral view unusually long, with distinct sulcus separating posterior eye margin from temple (Fig. 5D). Clypeal margin (Fig. 5A, B) truncate. Supraclypeal area (Fig. 5A, B) transverse (more than 1.5× as wide as high), sides not defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 5A, B) absent in female, poorly developed in male. Face between scrobes and eye (Fig. 5A, B) smooth. Face between clypeus and eye (Fig. 5A, B) smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female (Fig. 5A): most segments transverse. Male scape (Fig. 5B) slightly widened distally; ventral pores on less than half scape length. Mesosoma (Fig. 5C) narrow (more than 1.4× as long as wide). Mesoscutum sculpture (Fig. 5C) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 5C) without a double carina, without bilobed

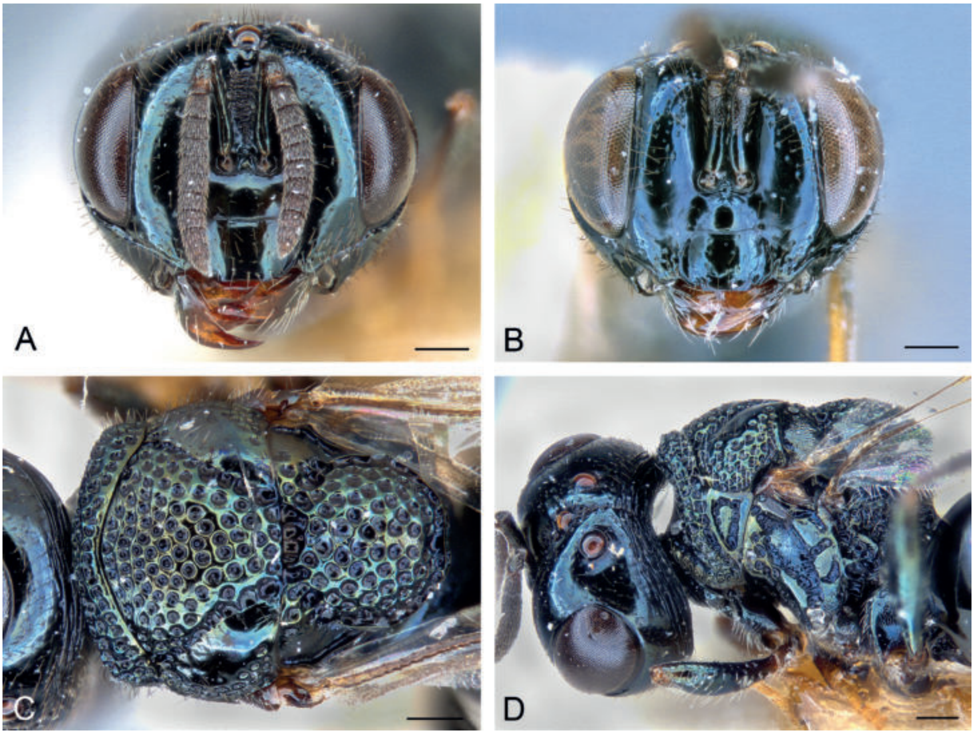

Figure 5. *Perilampus cephalotes* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

protruding projection. Prepectus (Fig. 5D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); all sides with punctures, central area smooth.

Material examined. Austria: 1♂, "Austria inferior, Dürnstein, 1973. H. Aspock, ex Raphidia", "ex Nemeritis sp. in Raphidia ratzeburgi Brauer", "Perilampus cephalotes Bčk. ♂, Z. Bouček det. 1973" (NHMUK). Turkey: 1♀, "Prov. Bolu 75/03, Bolu-Abantsee, 950 m, 40°41'N, 31°25'E, 17.V.", "Iran-Anatolien Expedition 1975, H. & U. Aspock, H. & R. Rausch, P. Ressl", "Perilampus cephalotes Bčk. ♀, Z. Bouček det. 1975" (NHMUK).

Hosts. *Nemeritis* sp. (Hymenoptera: Ichneumonidae) in *Puncha* (= *Raphidia*) *ratzeburgi* (Brauer) (Raphidioptera: Raphidiidae) – new biological association. The female specimen listed above was glued near the remains of a raphidiopteran larva, but without additional information.

Distribution. Slovakia. New to Austria and Turkey.

Comments. Easy to distinguish from all other species due to its unusually large head (Fig. 5D), with a conspicuous sulcus posterior to eye (Fig. 5A–C).

Perilampus chrysonotus Förster, 1859

Fig. 6

Perilampus chrysonotus Förster, 1859: 120–121.
Perilampus nigellus Nikol'skaya, 1952: 194. Synonymy by Trjapitzin (1978: 54).

Diagnosis. Head and mesosoma except propodeum dorsally dark green to bronze, with slight golden reflections; or black, with bluish reflections mostly on dorsal side of mesosoma; propodeum and metasoma black; female flagellum dark brown, ventrally reddish-brown. Body size: 1.5–3.0 mm. Head shape in frontal view (Fig. 6A, B) only slightly wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 6A, B) truncate to slightly emarginate. Supraclypeal area (Fig. 6A, B) higher than wide, sides well defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression about equal. Frontal keels (Fig. 6A, B) absent. Face between scrobes and eye (Fig. 6A, B) smooth. Face between clypeus and eye (Fig. 6A, B) smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female: most segments quadrate to transverse. Male scape (Fig. 6B) slightly widened distally; ventral pores on less than half scape length. Mesosoma (Fig. 6C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 6C) without smooth median tubercle; interspaces as large as or larger than punctures, smooth. Scutellum hind margin (Fig. 6C) without a double carina, without any protruding projection. Prepectus (Fig. 6D) narrow, dorsal margin about as long as pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); all sides with punctures, leaving just a very small smooth central area.

Material examined. Czechia: 1♀, 1♂, "Moravia mer., Mohelno, Bouček lgt. / 6.7.57", "Perilampus chrysonotus Först. ♀/♂, Det. Z. Bouček 1957" (NHMUK). Romania: 1♀,

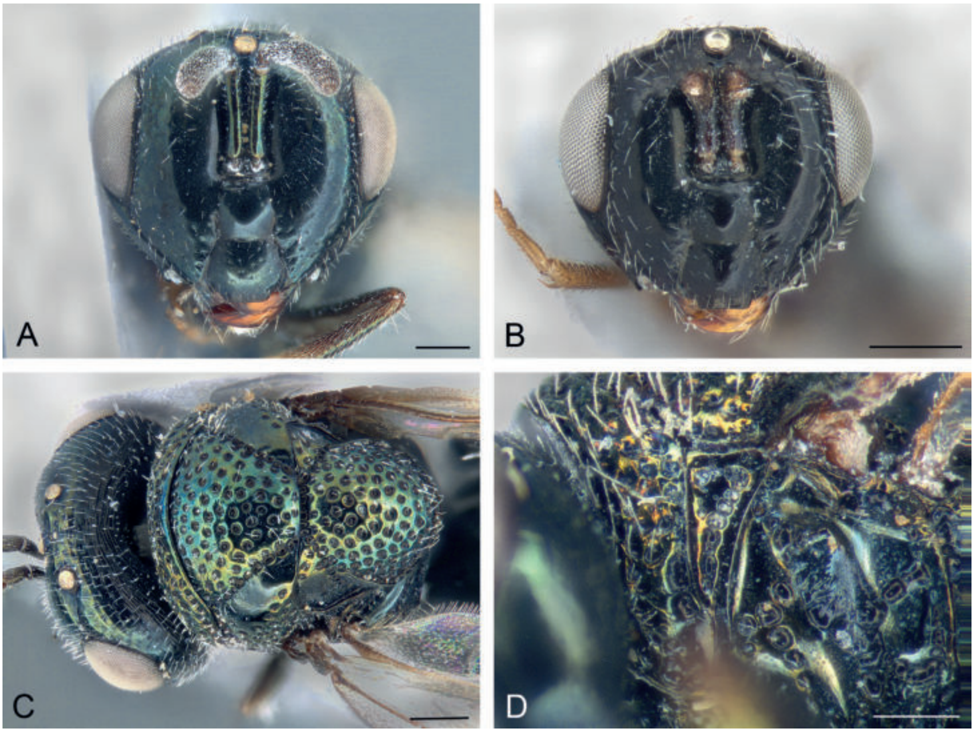

Figure 6. *Perilampus chrysonotus* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

"Iași county, Breazu village, near Mârzești forest, steppic vegetation, 05.vii.2011, L. Fusu leg." (MICO); 1♂, "Constanța county, Gura Dobrogei Natural Reserve, 12.v.2007, L. Fusu leg." (MICO). Sweden: 1♀, "Sk. Åhus, 8/8 1967, K.-J. Hedqvist", "Standing over: Perilampus maceki in Hedqvist coll., NHMUK(E) 2011-27" (NHMUK).

Hosts. Associated with Lymantriidae (Lepidoptera); hyperparasitoid of Ichneumonidae (Hymenoptera).

Distribution. Czechia, France, Germany, Hungary, Mongolia, Netherlands, Russia, Serbia, Slovakia, Sweden, Ukraine. New species to Romania.

Comments. This is one of the two European species having a high head in both sexes (Fig. 6A, B). The other species with a similar head is *P. intermedius* (Fig. 7), which greatly differs from *P. chrysonotus* mainly in having the prepectus poorly defined anteriorly (i.e., appearing virtually fused with pronotum) and very narrow (Fig. 7D).

***Perilampus intermedius* Bouček, 1956**
Fig. 7

Perilampus intermedius Bouček, 1956: 90–91.

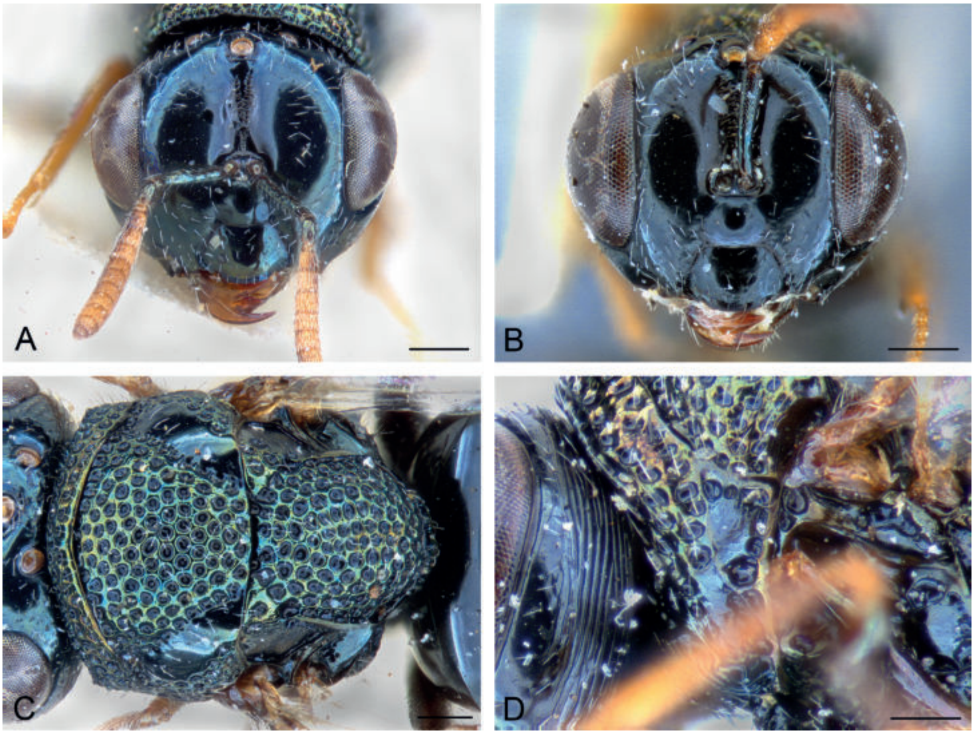

Figure 7. *Perilampus intermedius* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** male, prepectus.

Diagnosis. Head, lateral sides of mesosoma and metasoma black, dorsal side of mesosoma mainly dark olive green, with slight bronze reflections; female flagellum reddish brown. Body size: 2.2–2.7 mm. Head shape in frontal view (Fig. 7A, B) slightly wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 7A, B) convex. Supraclypeal area (Fig. 7A, B) transverse (about 1.5× as wide as high), sides not defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 7A, B) absent in both sexes. Face between scrobes and eye (Fig. 7A, B) smooth. Face between clypeus and eye (Fig. 7A, B) smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female (Fig. 7A): most segments quadrate to transverse. Male scape (Fig. 7B) slightly widened distally; ventral pores on half scape length. Mesosoma (Fig. 7C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 7C) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 7C) without a double carina, without bilobed protruding projection. Prepectus (Fig. 7D) narrow, dorsal margin shorter than pronotal collar; poorly defined anteriorly (i.e. suture with pronotum indistinct); anterior margin without punctures.

Material examined. Mongolia: 1♀, "Suchebaator aimak, 44 km SSW von Barum urt, 1050 m, Exp. Dr. Z. Kaszab, 1965", "Nr. 349, 2–3.VIII.1965", "Perilampus intermedius Bčk., Bouček det. 1982" (NHMUK); 1♂, "Bajanchongor aimak, Oase Echin gol, 90 km NO von Grenzposten Caganbulag, 950 m, Exp. Dr. Z. Kaszab, 1967", "Nr. 855, 27–28.VI.1967", Perilampus intermedius Bčk., Bouček det. 1982" (NHMUK).

Hosts. Unknown.

Distribution. Croatia, Finland, Germany, Mongolia, Slovakia.

Comments. This species is closest to *P. tristis* (Fig. 18), based on the narrow prepectus, which is completely fused with the pronotum. The main features to distinguish both sexes of the two species are given in the key.

Perilampus laevifrons Dalman, 1822

Fig. 8

Perilampus laevifrons Dalman, 1822: 400–401.
Perilampus inaequalis Förster, 1859: 122. Synonymy by Mayr (1905: 569).
Perilampus nigriventris Förster, 1859: 119. Synonymy by Mayr (1905: 569).

Diagnosis. Head black, dorsally with blue green reflections; mesosoma dorsally green with golden or bronze reflections; female flagellum brown. Body size: 1.75–3.00 mm. Head shape in frontal view (Fig. 8B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 8B) truncate. Supraclypeal area (Fig. 8B) slightly transverse (less than 1.5× as wide as high), sides well defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 8B) absent. Face between scrobes and eye (Fig. 8B) striate (more strongly so in male). Face between clypeus and eye (Fig. 8A, B) almost smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female (Fig. 8A): most segments quadrate to transverse. Male scape (Fig. 8B) strongly widened distally; ventral pores on more than half scape length. Mesosoma (Fig. 8C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 8C) without smooth median tubercle; interspaces smaller than punctures, rugose. Scutellum hind margin (Fig. 8C) without a double carina, with large bilobed protruding projection. Prepectus (Fig. 8D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); anterior margin without punctures.

Material examined. Greece: 1♂, "Attiki, Salamina, Patris hill, 37.970°N, 23.489°E, xi.2020, By hand Leg. Koutsoukos, V." (MICO). Italy: 1♂, "Italia (Ferrara): Comacchio, Lido d. Naz., 19.8./11.xi.83. Pantaleoni", "ex planidium fixed to Chrysopa viridana and transferred on Anisochrysa flavifrons", "Perilampus laevifrons Dalm., Bouček det. 1983" (NHMUK). Mongolia: 1♀, "Mongolia: Central aimak, Tosgoni ovoo, 5–10 km N von Ulaan-Baator, 1500–1700 m, Exp. Dr. Z. Kaszab, 1967", "Nr. 926, 19–20.–23–24.VII.1967", Perilampus laevifrons Dalm., Bouček det. 1982"

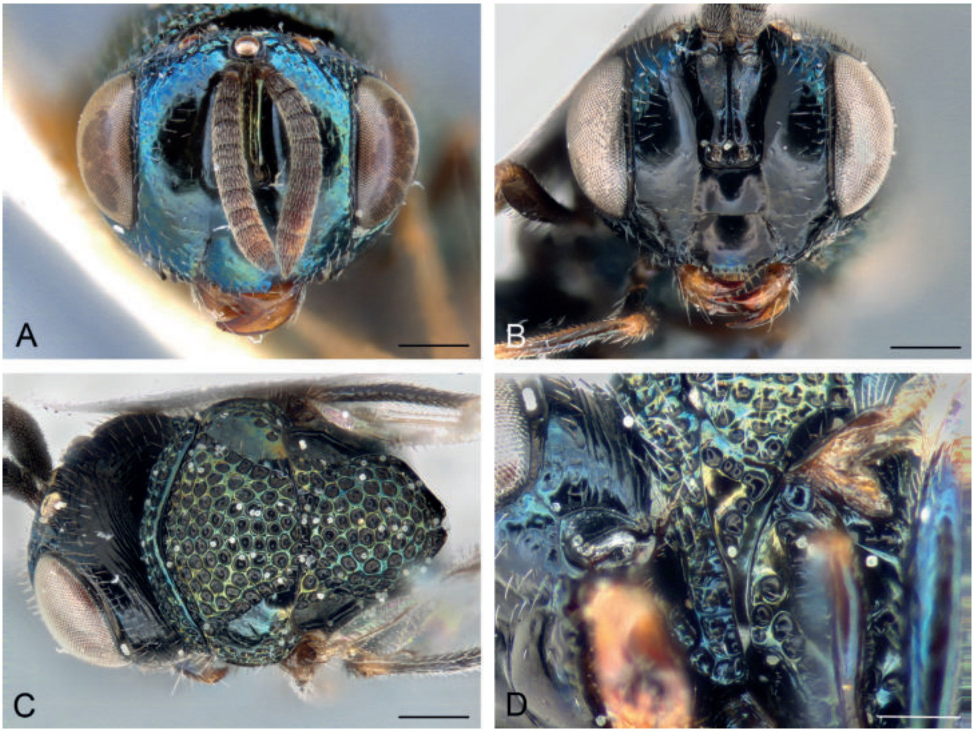

Figure 8. *Perilampus laevifrons* **A** female, head in frontal view **B** male, head in frontal view **C** male, head and mesosoma, dorsal view **D** male, prepectus.

(NHMUK). Romania: 1♀, "Cornereva, Caraș-Severin, 44.98325°N, 22.49011°E, 617 m, 16.07.2015, Popovici & Trufin" (MICO); 1♀, "Tulcea county, Măcin National Parc, meadow, Malaise trap, 23–25.vii.2004, M.-D. Mitroiu leg." (MICO).

Hosts. Associated with Tortricidae (Lepidoptera); hyperparasitoid of Braconidae and Ichneumonidae (Hymenoptera). According to Steffan (1952) a primary parasitoid of Chrysopidae (Neuroptera). This seems to be confirmed by the information above, the species being reared from *Pseudomallada* (=*Anisochrysa*) *flavifrons* (Brauer) (Neuroptera: Chrysopidae) – new biological association.

Distribution. Belarus, Bulgaria, Czechia, France, Germany, Hungary, Italy, Moldova, Mongolia, Netherlands, North Africa, Russia, Serbia, Slovakia, Sweden, Ukraine, United Kingdom. New species to Greece and Romania.

Comments. The female of *P. laevifrons* can be confused to those of *P. aquilus*, *P. masculinus* (Fig. 9) and *P. aureoviridis* (Fig. 4). It differs from females of *P. aquilus* in having at least the distal funicular segments quadrate to transverse (Fig. 8A) and the face at least slightly striate between scobes and eye (face smooth in *P. aquilus* according to Nikol'skaya (1952)) (Fig. 8A, B); from females of *P. masculinus* mainly in having the supraclypeal area less than 1.5× as wide as high and narrower than the clypeal area (Fig. 8A, B); for differences between *P. laevifrons* and *P. aureoviridis*, see the comments on the latter species.

Perilampus masculinus Bouček, 1956
Fig. 9

Perilampus masculinus Bouček, 1956: 91–92.

Diagnosis. Head black, upper face and vertex with blue green or bronze green reflections; mesosoma dorsally bronze green, occasionally dark bronze or with slight violet reflections; female flagellum brown. Body size: 2.50–3.25 mm. Head shape in frontal view (Fig. 9A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 9A, B) truncate. Supraclypeal area (Fig. 9A, B) strongly transverse (at least 1.5× as wide as high), sides well defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 9A, B) absent. Face between scrobes and eye (Fig. 9A, B) slightly striate. Face between clypeus and eye (Fig. 9A, B) slightly striate near anterior margin of malar depression. Lateral ocellus large (OOL less than twice the largest ocellar diameter). Funicular segments in female (Fig. 9A): most segments quadrate to transverse. Male scape

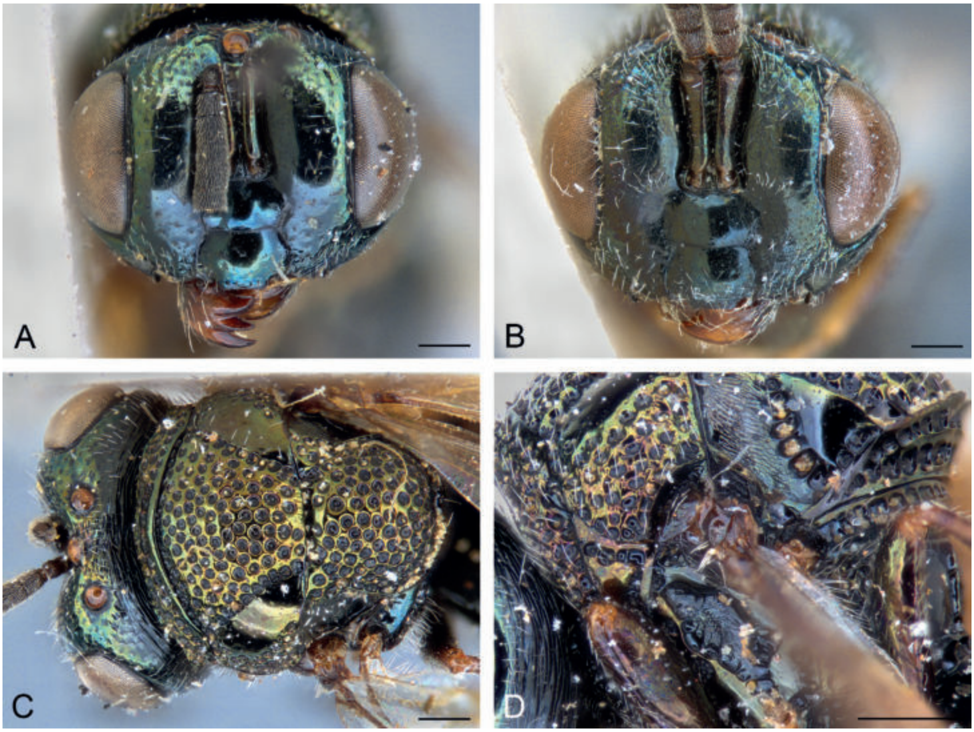

Figure 9. *Perilampus masculinus* **A** female paratype, head in frontal view **B** male paratype, head in frontal view **C** female paratype, head and mesosoma, dorsal view **D** female paratype, prepectus.

(Fig. 9B) slightly widened distally, ventral pores on more than half scape length. Mesosoma (Fig. 9C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 9C) without smooth median tubercle; interspaces smaller than punctures, rugose. Scutellum hind margin (Fig. 9C) without a double carina, with large bilobed protruding projection. Prepectus (Fig. 9D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); anterior margin without punctures.

Material examined. SLOVAKIA: 1♀ paratype, "Somotor. Slov. or. 28. VI. 48. Bouček", "Paratype", "Perilampus masculinus Bčk. ♀, Det. Bouček, 1955", "Pres by Com Inst Ent, B.M. 1957-682" (NHMUK); 1♂ paratype, "V. Kevežd, Slov. or. 28. VI. 48. Bouček", "Paratype", "Perilampus masculinus Bčk. ♂, Det. Bouček, 1955", "Pres by Com Inst Ent, B.M. 1957-682" (NHMUK). SWEDEN: 1♀, "Upl. Vallentuna 13/7 1961, K-J Hedvist", "Standing over: Perilampus aquilus in Hedqvist coll., NHMUK(E) 2011-27" (NHMUK).

Hosts. Unknown.

Distribution. Czechia, Kazakhstan, Moldova, Russia, Slovakia, Ukraine. New species to Sweden.

Comments. The females can be confused to those of *P. laevifrons* (Fig. 8) and *P. aureoviridis* (Fig. 4); see comments on those species.

Perilampus micans Dalman, 1820

Fig. 10

Perilampus micans Dalman, 1820: 173.
Perilampus auriceps Walker, 1833: 142. Synonymy by Kerrich (1958: 77).
Perilampus femoralis Walker, 1833: 142. Synonymy by Darling (1996: 119).
Chrysolampus lycti Crawford, 1914: 75. Synonymy by Darling (1986: 918).

Diagnosis. Head green or blue-green; mesosoma dorsally blackish with slight blue-green reflections; metasoma black; female flagellum dark brown. Body size: 2.0–3.5 mm. Head shape in frontal view (Fig. 10A) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 10A) truncate. Supraclypeal area (Fig. 10A) quadrate, sides well defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression slightly shorter. Frontal keels (Fig. 10A) not developed. Face between scrobes and eye (Fig. 10A) almost smooth. Face between clypeus and eye (Fig. 10A) strongly striate. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female: most segments quadrate to transverse. Mesosoma (Fig. 10B) narrow (more than 1.4× as long as wide). Mesoscutum sculpture (Fig. 10B) without smooth median tubercle; interspaces smaller than punctures, carinate. Scutellum hind margin (Fig. 10B) with a double carina, without bilobed

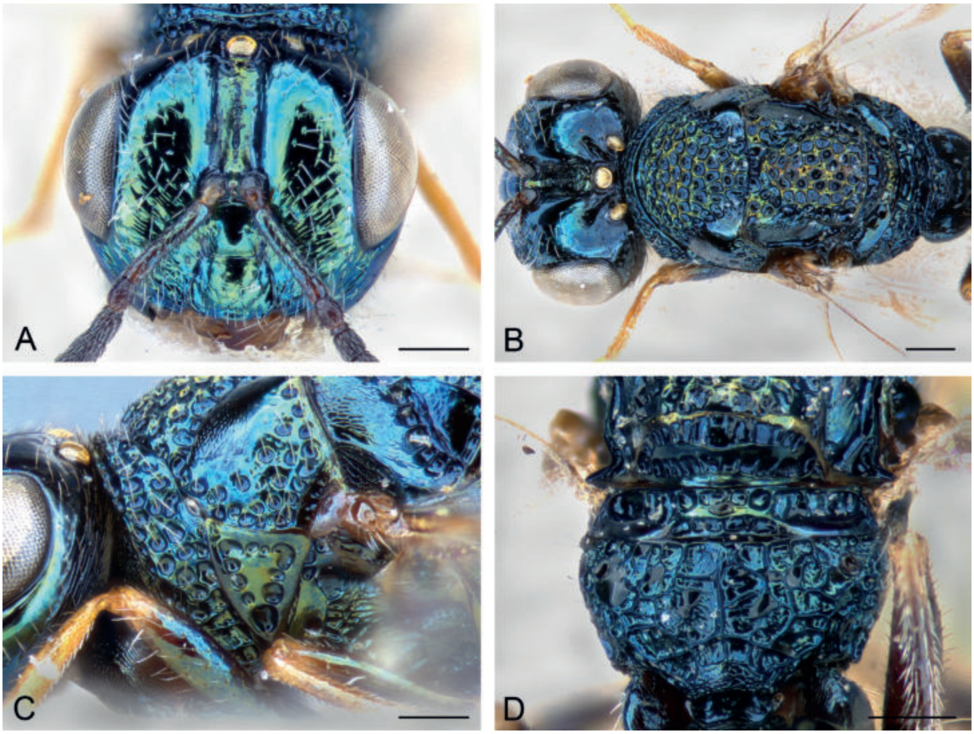

Figure 10. *Perilampus micans* **A** female, head in frontal view **B** female, head and mesosoma, dorsal view **C** female, prepectus **D** female, propodeum.

protruding projection. Prepectus (Fig. 10C) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); all sides with punctures, leaving a smooth central area.

Material examined. Germany: 1♀, "Germany, Munich, VI.1922, Prof. Esehenie l", "Ex Lyctus linearis", "Pres. by Imp. Inst. Ent. Brit. Mus. 1933-190", "Perilampus micans Dlm., Ch. Ferrière det." (NHMUK). Sweden: 1♀, "Sm., Hornsö, Långemåla, 9/7 1941, O. Lundblad", "Standing over Perilampus micans in Hedqvist coll., NHMUK(E) 2011-27" (NHMUK).

Hosts. Associated with Lyctidae (Coleoptera), Oecophoridae, Pyralidae (Lepidoptera); hyperparasitoid of Braconidae (Hymenoptera). According to Bouček, the "micans-group [contains] primary parasites of xylophagous beetles" (Bouček 1956: 89).

Distribution. Armenia, Croatia, France, Germany, Hungary, India, Indonesia, Malaysia, Slovakia, Sweden, United Kingdom, United States of America.

Comments. This is one of the most distinct species of *Perilampus* due to the strongly striate lower face (Fig. 10A), the narrow mesosoma (Fig. 10B), the double carina at the posterior margin of scutellum (Fig. 10D), and the completely reticulate propodeum (Fig. 10D).

Perilampus minutalis Steffan, 1952
Fig. 11

Perilampus minutalis Steffan, 1952: 74.

Diagnosis. Head, mesosoma and metasoma black; female flagellum dark brown, ventrally lighter. Body size: 1.8–2.7 mm. Head shape in frontal view (Fig. 11A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 11A, B) convex. Supraclypeal area (Fig. 11A, B) slightly transverse (less than 1.5× as wide as high), sides well defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 11A, B) poorly developed (stronger in male). Face between scrobes and eye (Fig. 11A, B) smooth. Face between clypeus and eye (Fig. 11A, B) smooth. Lateral ocellus large (OOL less than twice the largest ocellar diameter). Funicular segments in female (Fig. 11A): most segments quadrate to transverse. Male scape (Fig. 11B) slightly widened distally; ventral pores on less than half scape length. Mesosoma (Fig. 11C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 11C) without smooth median tubercle; interspaces smaller than punctures, almost smooth. Scutellum hind margin (Fig. 11C) without a double carina, with small hardly bilobed protruding projection. Prepectus (Fig. 11D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); anterior margin without punctures.

Material examined. France: 1♀, 1♂, “France, Var: St. Tropez, 16.VI.80 Bouček”, “♀/♂ Perilampus minutalis Steff., det. Z. Bouček, 1981” (NHMUK). Greece: 7♀♀, “Kerkini Lake N. Park, Kerkini, Krousia Mts site, Malaise tr. 13.VI-19.VI.2007, 41°11'32.4"N, 23°03'59.5"E, 190 m, Leg. Gordon Ramel” (MICO); 3♀♀, “Kerkini Lake N. Park, Kerkini, Krousia Mts site, Malaise tr. 27.VI-03.VII.2007, 41°11'32.4"N, 23°03'59.5"E, 190 m, Leg. Gordon Ramel” (MICO); 7♀♀, “Kerkini Lake N. Park, Kerkini, Krousia Mts site, Malaise tr. 20.VI-26.VI.2007, 41°11'32.4"N, 23°03'59.5"E, 190 m, Leg. Gordon Ramel” (MICO); 2♀♀, “Kerkini lake, Malaise trap, Krousia Mts. Site, 04.VII to 10.VII.2007, 41°11'32.4"N, 23°03'59.5"E, Leg. Gordon Ramel” (MICO); 1♀, “Kerkini lake, Malaise trap, Ecotourism Site, Lithotopos, 29.VIII-04.IX.2006, 41°18'15.6"N, 23°13'01.2"E, Leg. Gordon Ramel” (MICO); 1♀, “Kerkini Lake N. Park, Kerkini, Krousia Mts site, Malaise tr. 06.VI-12.VI.2007, 41°11'32.4"N, 23°03'59.5"E, 190 m, Leg. Gordon Ramel” (MICO); 1♀, “Kerkini lake; Malaise trap; Krousia Mts. Site, 12.IX to 18.IX.2007, 41°11'32.4"N, 23°03'59.5"E, Leg. Gordon Ramel” (MICO); 1♀, 1♂, “Kerkini Lake N. Park, Promohonas, Procom site, Malaise, 22–28.VIII.2007, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel” (MICO); 1♀, “Kerkini Lake N. Park, Promohonas, Procom site, Malaise, 20.VI to 26.VI.2007, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel” (MICO); 6♂♂, “Attiki, Salamina, Ano Vasilika, 37.98822°N, 23.49196°E, ix.2020, By hand Leg. Koutsoukos, V.” (MICO); 3♂♂, “Attiki, Salamina, Ano Vasilika, 37.98822°N, 23.49196°E,

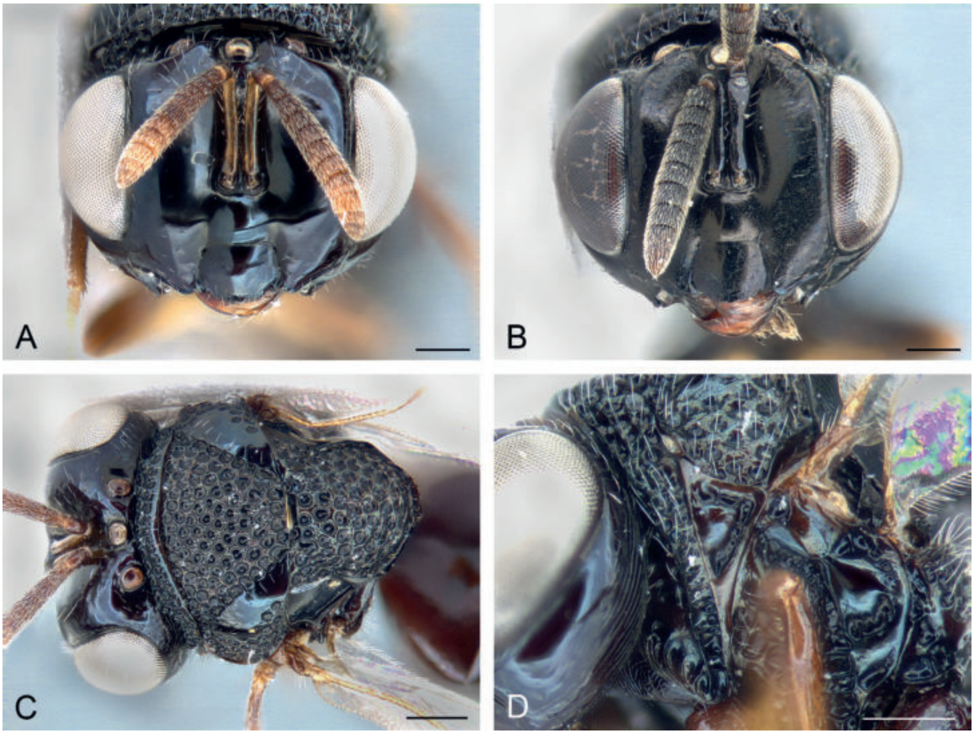

Figure 11. *Perilampus minutalis* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

14.ix.2020, By hand Leg. Koutsoukos, V." (MICO) ; 1♂, "Attiki, Salamina, Ano Vasilika, 37.98822°N, 23.49196°E, 14.ix.2020, By hand Leg. Koutsoukos, V." (ZMUA).

Hosts. Unknown.

Distribution. Croatia, France, Germany, Italy, Moldova, Spain. New species to Greece.

Comments. This species is similar to *P. neglectus* (Fig. 12) and *P. noemi* (Fig. 14). From the first species it can be separated by the larger ocelli in both sexes, while from the latter mainly by the body colour (without metallic reflections) and larger ocelli, at least in male.

Perilampus neglectus Bouček, 1956
Fig. 12

Perilampus neglectus Bouček, 1956: 92–93.

Diagnosis. Head, mesosoma and metasoma black; female flagellum dark brown. Body size: 2.0–2.6 mm. Head shape in frontal view (Fig. 12A, B) much wider than high.

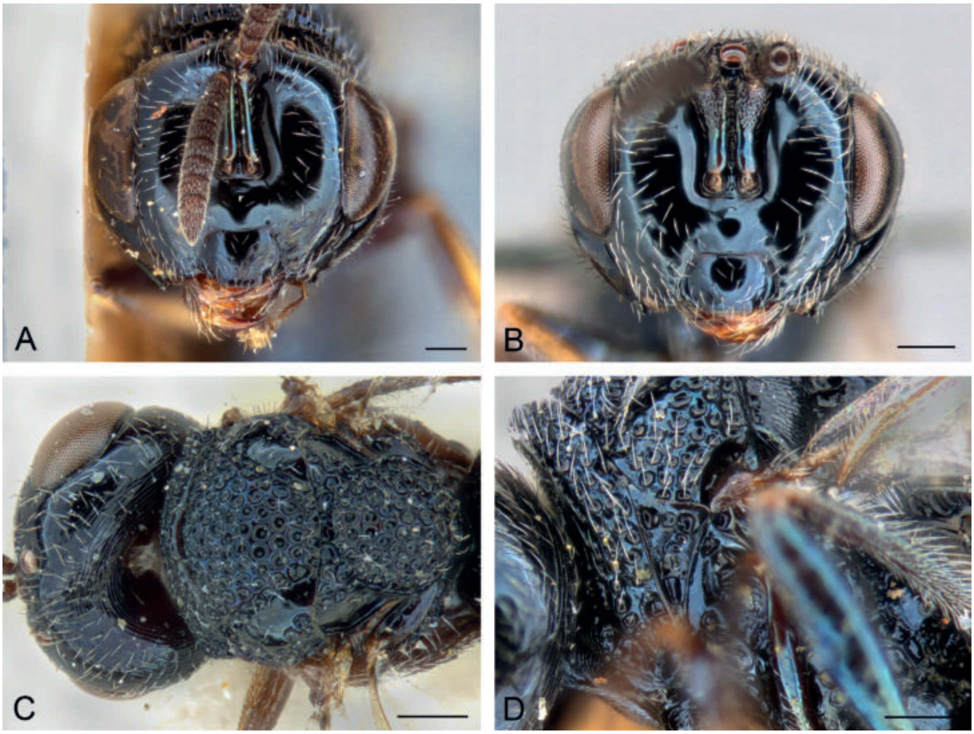

Figure 12. *Perilampus neglectus* **A** female, head in frontal view **B** male, head in frontal view **C** female paratype, head and mesosoma, dorsal view **D** female, prepectus.

Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 12A, B) truncate to very slightly convex. Supraclypeal area (Fig. 12A, B) slightly transverse (less than 1.5× as wide as high), sides slightly defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 12A, B) absent. Face between scrobes and eye (Fig. 12A, B) smooth. Face between clypeus and eye (Fig. 12A, B) smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female (Fig. 12A): most segments quadrate to transverse. Male scape (Fig. 12B) slightly widened distally; ventral pores on half scape length. Mesosoma (Fig. 12C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 12C) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 12C) without a double carina, with small hardly bilobed protruding projection. Prepectus (Fig. 12D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); anterior margin at most with extremely small punctures.

Material examined. Greece: 1♀, "Kerkini Lake N. Park, Promohonas, Procom site, Malaise, 13.VI to 19.VI.2007, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel" (MICO). Moldova: 1♀, "Onițcani MCCP, 7.VII.69, Talitzki [in Russian]", Yp.

malinellus 44 (18.VI.69 – N. armillata", "Presented to NHMUK 1974, Z. Bouček", "Perilampus neglectus Bčk. ♀, Z. Bouček det. 1973". Slovakia: 1♀ Paratype, "Slovakia or. Turňa nad Bodv., Bouček", "Paratype", "Perilampus neglectus ♀, n, Bčk., Det. Z. Bouček 1955" (NHMUK).

Hosts. Associated with Gelechiidae, Lymantriidae, Pyralidae, Tortricidae (Lepidoptera); hyperparasitoid of Braconidae (Hymenoptera).

Distribution. Austria, Croatia, Czechia, Germany, Italy, Moldova, Romania, Slovakia. New species to Greece.

Comments. For differences from similar species see *P. minutalis* (Fig. 11). The male was not described by Bouček (1956), or by subsequent authors. It is very similar to the female in most characters (see the diagnosis above), but differs mainly in having darker and thicker antennae, including the scape, with ventral pores visible on half the scape length (Fig. 12B).

***Perilampus nitens* Walker, 1834**

Fig. 13

Perilampus nitens Walker, 1834: 163.
Perilampus antennatus Walker, 1834: 163. Synonymy by Mayr (1905: 566).
Perilampus selectus Walker, 1874: 313. Synonymy by Kerrich (1958: 77).

Diagnosis. Head and mesosoma blue, with slight green or bronze reflections; metasoma bluish-black; female flagellum brownish-black, partly lighter ventrally. Body size: 3–5 mm. Head shape in frontal view (Fig. 13A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 13A, B) emarginate. Supraclypeal area (Fig. 13A, B) slightly transverse (less than 1.5× as wide as high), sides not defined; in males without oval lateral impressions. Malar sulcus versus anterior margin of malar depression about equal in female. Frontal keels (Fig. 13A, B) absent. Face between scrobes and eye (Fig. 13A, B) smooth. Face between clypeus and eye (Fig. 13A, B) smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female (Fig. 13A): most segments quadrate to transverse. Male scape (Fig. 13B) slightly widened distally, ventral pores on more than half scape length. Mesosoma (Fig. 13C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 13C) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 13C) without a double carina, with small hardly bilobed protruding projection. Prepectus (Fig. 13D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); all sides with punctures (anterior side sometimes with much smaller punctures or partly interrupted), leaving a large smooth central area.

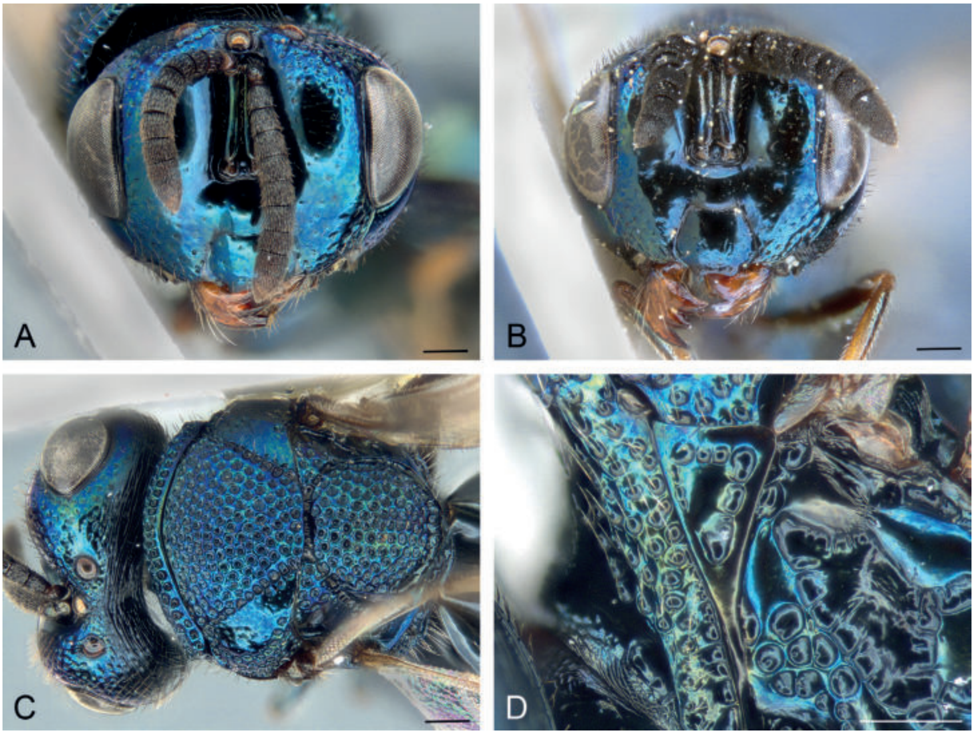

Figure 13. *Perilampus nitens* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

Material examined. France: 2♀, "Ventoux: Col de Perrache (4) 8. 8. 1988", "fts descr. of chlorinus Fö.", "Perilampus nitens Wlk. ♀, Bouček det. 1989" (NHMUK); 1♂, "Mont Ventoux, Col de Perrache (2) 22. 7. 1978", "Perilampus nitens Wlk. ♂, Bouček det. 2001" (NHMUK). Romania: 1♀, 1♂, "Iași county, Bârnova forest, Poiana Ciobanului, 21.vi.2007, L. Fusu & O. Popovici leg." (MICO); 1♀, "Iași county, Bârnova forest, Poiana cu Schit Nat. Res., 28.vi.2017, ent. net, Leg. M.-D. Mitroiu" (MICO).

Hosts. Associated with Lasiocampidae (Lepidoptera); hyperparasitoid of Braconidae (Hymenoptera).

Distribution. Bulgaria, Croatia, Czechia, France, Germany, Hungary, North Macedonia, Netherlands, Romania, Russia, Slovakia, Slovenia.

Comments. *Perilampus nitens* is part of the group of species without any frontal keels. It most closely resembles *P. ruschkai* (Fig. 17) and can be separated from it mainly by the more strongly punctuate gena and frons between eye and scrobes (Fig. 13A, B), the supraclypeal area poorly defined (Fig. 13A, B), and the body entirely blue (Fig. 13). According to Bouček (see Material examined), *P. chlorinus* Förster, 1859 could be the same as *P. nitens*; however, these have not been formally synonymized, as the type of *P. chlorinus* is probably lost.

Perilampus noemi Nikol'skaya, 1952
Fig. 14

Perilampus noemi Nikol'skaya, 1952: 194.

Diagnosis. Head and metasoma black; mesosoma dorsally black, with distinct violet, bronze or/and golden green reflections; female flagellum brownish-black, clava somewhat lighter. Body size: 1.75–3.00 mm. Head shape in frontal view (Fig. 14A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 14A, B) slightly convex. Supraclypeal area (Fig. 14A, B) slightly transverse (less than 1.5× as wide as high), sides slightly or not defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 14A, B) absent. Face between scrobes and eye (Fig. 14A, B) smooth. Face between clypeus and eye (Fig. 14A, B) smooth. Lateral ocellus large (OOL less than twice the largest ocellar diameter). Funicular segments in female (Fig. 14A): most segments quadrate to transverse. Male scape (Fig. 14B) slightly widened distally, ventral pores on about half scape length. Mesosoma (Fig. 14C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 14C) without smooth median tubercle; interspaces smaller than punctures, rugose. Scutellum hind margin (Fig. 14C) without a double carina, with large bilobed protruding projection. Prepectus (Fig. 14D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); all sides with punctures (anterior side with much smaller punctures or partly interrupted), leaving just a very small smooth central area.

Material examined. Greece: 1♀, "Attiki, Salamina, Agios Lavrendios, 37.962996°N, 23.514664°E, v.2020, By Hand, Leg. Koutsoukos, V." (MICO); 1♀, "Attiki, Salamina, Agios Lavrendios, 37.962996°N, 23.514664°E, vii.2020, By Hand, Leg. Koutsoukos, V." (MICO); 1♀, 3♂♂, "Attiki, Salamina, Ano Vasilika, 37.98822°N, 23.49196°E, ix.2020, By hand, Leg. Koutsoukos, V." (MICO); 1♀, 1♂, "Attiki, Salamina, Patris hill, 37.970°N, 23.489°E, x.2020, By hand Leg. Koutsoukos, V." (MICO); 1♂ "Greece/Crete; 35.094319°N, 24.706687°E; 18.10.2022 on Urginea maritima", "E. Klimsa leg.". Mongolia: 1♀ "Mongolia, Gobi Altaj aimak, Zachuj Gobi, 10 km N von Chatan chajrchan Gebirge, 1150 m, Exp. Dr. Z. Kaszab, 1966", "Nr. 591, 27.VI.1966", "Perilampus noemi Nik. ♀ Bouček det. 1982" (NHMUK); 1♂ "Mongolia: Bajanchongor aimak, Cagan Bogd ul, zw. Talyn bilgech bulag und Caganbulag, 25 km WSW v. Quelle, 1450 m, Exp. Dr. Z. Kaszab, 1966", "Nr. 842, 24.VI.1967", "Perilampus noemi Nik. ♂ Bouček det. 1982", "NHMUK014583387" (NHMUK).

Hosts. Unknown.

Distribution. Mongolia and Tadzhikistan, the latter cited by Bouček (1983). New species to Europe.

Comments. In Bouček's key (1956) specimens of *P. noemi* go to couplet 17 (*P. laevifrons* and *P. neglectus*). However, *P. noemi* differs from both these species mainly in the shape and sculpture of the prepectus (Fig. 14D) and body colour (Fig. 14). Additionally, from *P. laevifrons* (Fig. 8) it differs mainly in having the

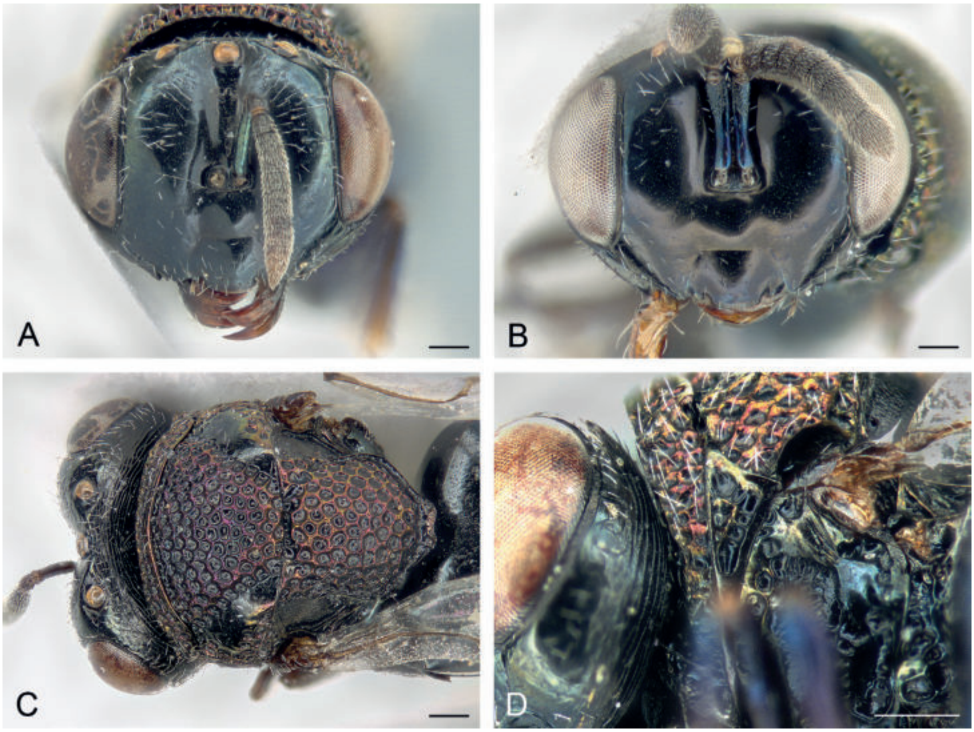

Figure 14. *Perilampus noemi* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

upper face smooth and the clypeal margin slightly convex (Fig. 14A, B), while from *P. neglectus* (Fig. 12) in having the posterior margin of scutellum with a larger bilobed protruding projection (Fig. 14C). According to Darling and Yoo (2021), females of *P. noemi* are undistinguishable from females of *P. khor* Yoo & Darling, 2021 (described from the United Arab Emirates), while the males of the two species can be separated based on several features, the structure of the scape being the most striking (Darling and Yoo 2021: 114). However, the scape of the NHMUK014583387 male (identified as *P. noemi* by Bouček, see Material examined) is much more similar to the scape of the *P. khor* male (Darling and Yoo 2021: fig. 4J, K) than the scape of the ROME188145 male (Darling and Yoo 2021: fig. 5D, also identified as *P. noemi*), although in NHMUK014583387 the ventral pores occupy a rather larger portion of the scape as compared to those in *P. khor*. Concerning scape morphology, all males from Greece (Fig. 14B) are similar to NHMUK014583387 and different from ROME188145. One possibility is that ROME188145 is in fact not *P. noemi*, as also indicated by differences from the *P. noemi* female: the arrangement of the ocelli, the shape of the clypeal margin, and the relative dimensions of the clypeal and supraclypeal areas. However, Nikols'kaya's original material of *P. noemi* as well as additional specimens should be examined before assessing the variability of the involved species and taking any taxonomic decisions.

Perilampus polypori **Bouček, 1971**
Fig. 15

Perilampus polypori Bouček, 1971: 52–54.

Diagnosis. Head, mesosoma and metasoma black; female flagellum dark brown. Body size: 2.8–3.4 mm. Head shape in frontal view (Fig. 15A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 15A, B) truncate to very slightly convex. Supraclypeal area (Fig. 15B) slightly transverse (less than 1.5× as wide as high), sides well defined; in male without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 15A, B) absent. Face between scrobes and eye (Fig. 15A, B) smooth. Face between clypeus and eye (Fig. 15A, B) smooth. Lateral ocellus large (OOL less than twice the largest ocellar diameter). Funicular segments in female (Fig. 15A): most segments quadrate to transverse. Male scape (Fig. 15B) slightly widened distally; ventral pores on less than half scape length. Mesosoma (Fig. 15C) narrow (more than 1.4× as long as wide). Mesoscutum sculpture (Fig. 15C) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 15C) without a double carina, without bilobed

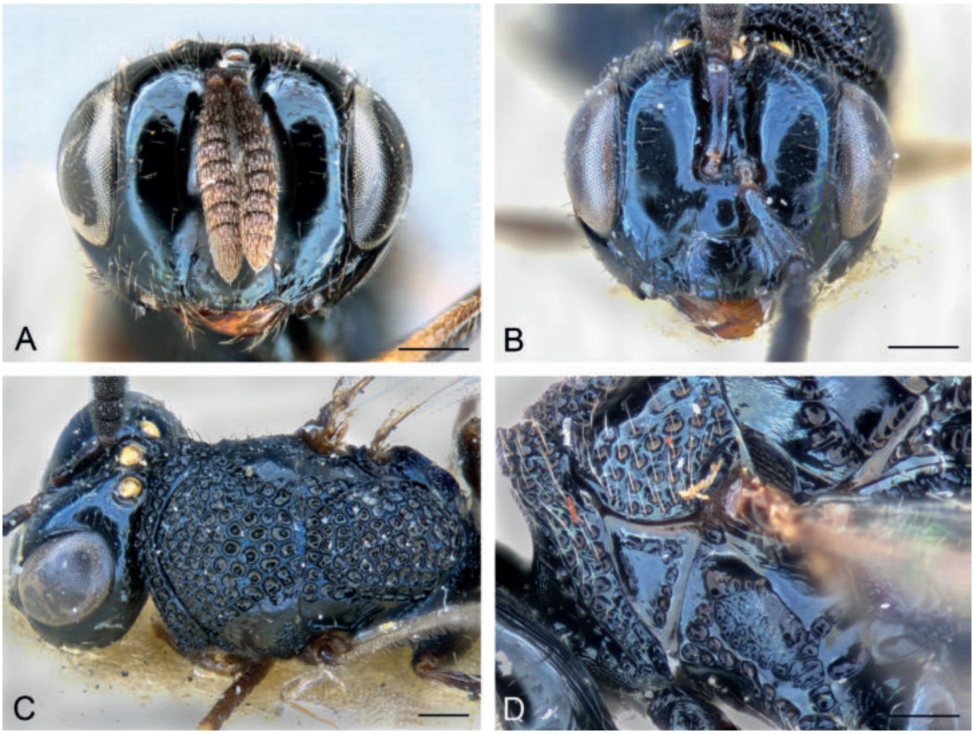

Figure 15. *Perilampus polypori* **A** female, head in frontal view **B** male, head in frontal view **C** male, head and mesosoma, dorsal view **D** female, prepectus.

protruding projection. Prepectus (Fig. 15D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); anterior margin with incomplete row of small punctures.

Material examined. Austria: 1♀, "Austria Inferior, Bezirk Scheibbs, ex Raphidia, 1973. H. Aspock", "1075", "Perilampus polypori Bčk. ♀, Z. Bouček det. 1973" (NHMUK). Sweden: 1♂, "Ör. dist. – A.J., 14/8 82", "Sweden: Örebro distr., leg. A. Jansson", "Perilampus polypori Bčk. ♂, Z. Bouček det. 1972" (NHMUK).

Hosts. *Raphidia* sp. (Raphidioptera: Raphidiidae).

Distribution. Croatia, Czechia, Slovakia, Sweden, United Kingdom. New species to Austria.

Comments. Superficially similar to other small black species, e.g., *P. cephalotes* (Fig. 5), *P. maceki*, *P. minutalis* (Fig. 11), *P. neglectus* (Fig. 12) or *P. tristis* (Fig. 18), from which it can be separated using the characters given in the key.

Perilampus ruficornis (Fabricius, 1793)

Fig. 16

Cynips ruficornis Fabricius, 1793: 103.
Diplolepis violacea Fabricius, 1804: 149. Synonymy by Dalla Torre (1898: 356).
Perilampus nigricornis Walker, 1833: 141. Synonymy by Dalla Torre (1898: 356).
Perilampus scaber Nikol'skaya, 1952: 194. Synonymy by Bouček (1983: 112).

Diagnosis. Head blue, with slight green reflections; mesosoma except propodeum dorsally dark green, with slight golden bronze reflections; propodeum and metasoma blue with violet reflections; female flagellum orange, claval apex dark. Body size: 3.0–3.8 mm. Head shape in frontal view (Fig. 16A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 16A, B) truncate. Supraclypeal area (Fig. 16A, B) slightly transverse (less than 1.5× as wide as high), sides slightly defined; in males without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 16A, B) well developed. Face between scrobes and eye (Fig. 16A, B) smooth. Face between clypeus and eye (Fig. 16A, B) smooth. Lateral ocellus small (OOL at least twice the largest ocellar diameter). Funicular segments in female (Fig. 16A): most segments quadrate to transverse. Male scape (Fig. 16B) slightly widened distally; ventral pores on about half scape length. Mesosoma (Fig. 16C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 16C) without smooth median tubercle; interspaces smaller than punctures, rugose. Scutellum hind margin (Fig. 16C) without a double carina, without any protruding projection. Prepectus (Fig. 16D) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); anterior margin without punctures.

Material examined. France: 1♂, "France, Vaucluse, Mt. Ventoux, III. 1981. P. du Merle", "ex Lypha dubia in T. viridana", "♂ Peril. ruficornis (F.), Z. Bouček det. 1984" (NHMUK). Greece: 1♀, "Kerkini Lake nr. Promahonah, Procom site, Malaise

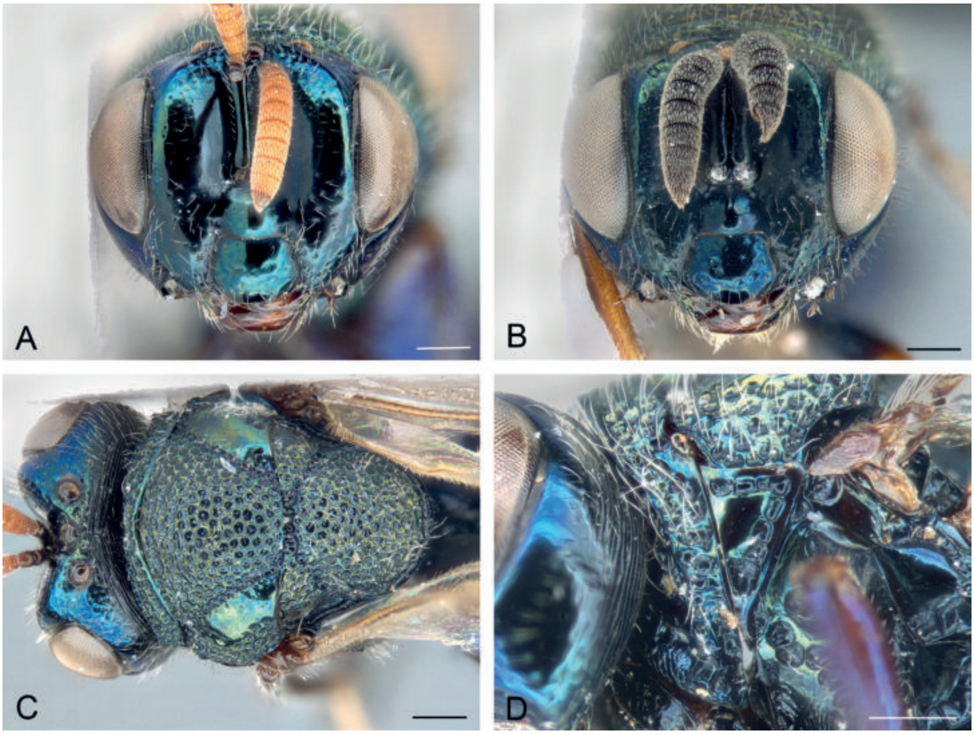

Figure 16. *Perilampus ruficornis* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

tr. 21–27.IV.2008, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel" (MICO); 2♂♂, "Kerkini Lake N Park, Kerkini Mts, nr. Ramna st., YPT, temp. forest nr. stream, 640 m, 41°17'44"N, 23°11'37"E, 08.IV.2010, Leg. Gordon Ramel" (MICO). South Korea: 1♀, "S. Korea Gyeongido Gapyeong-gun Seo-myeon Magok-I / 3 Mal. tr. in forest. area, 37°42.97'N, 127°35.45'E, 4.V–6.VI.2006 Tripotin rec." (MICO). Turkey: 1♀, "Turkey, Artvin. Above Artvin. 900 m., 6.vi.1962, Guichard & Harvey. B.M. 1962-299", "♀ Perilampus ruficornis (F.), Z. Bouček det. 1971" (NHMUK).

Hosts. Associated with Glossinidae (Diptera), Crabronidae, Cynipidae (Hymenoptera), Geometridae, Lasiocampidae, Lymantriidae, Noctuidae, Pyralidae, Tortricidae (Lepidoptera); hyperparasitoid of Tachinidae (Diptera), Braconidae, Ichneumonidae (Hymenoptera).

Distribution. Austria, Bulgaria, Canada, Croatia, Czechia, France, Germany, Hungary, Italy, Japan, Lithuania, Netherlands, Nigeria, Peoples' Republic of China, Russia, Serbia, Slovakia, Sweden, Ukraine, United Kingdom, United States of America. New species to Greece, South Korea and Turkey.

Comments. Very similar to *P. eximius*. Except for body colour, the separation characters given by Nikol'skaya (1952), Steffan (1952) and Bouček (1956) are difficult to interpret without comparative material. In the examined specimens the pronotal collar is considerably shorter medially than laterally (as stated for *P. eximius*), but the scutellum is hardly convex in the female (as in *P. ruficornis*), but clearly convex in the male (as in *P. eximius*). Because the body colour (Fig. 16) better matches *P. ruficornis* than *P. eximius* and the posterior margin of the scutellum has a very slight emargination (as stated by Nikol'skaya for *P. ruficornis*) we decided in the favour of the latter species; however, more material should be examined before deciding if these are meaningful differences to separate the two species. The comparative material from NHMUK identified by Z. Bouček is very similar to our specimens, but unfortunately we could not find any specimens of *P. eximius* in NHMUK.

***Perilampus ruschkai* Hellén, 1924**

Fig. 17

Perilampus ruschkai Hellén, 1924: 13.

Diagnosis. Head and mesosoma mostly green, with golden or bronze reflections; metasoma black, dark green or bronze green in distal half; female flagellum dark brown, lighter ventrally. Body size: 3–4 mm. Head shape in frontal view (Fig. 17A) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 17A) truncate. Supraclypeal area (Fig. 17A) slightly transverse (less than 1.5× as wide as high), sides well defined; in males without oval lateral impressions. Malar sulcus versus anterior margin of malar depression shorter. Frontal keels (Fig. 17A) absent in female, slightly defined in male. Face between scrobes and eye (Fig. 17A) smooth. Face between clypeus and eye (Fig. 17A) smooth. Lateral ocellus large (OOL less than twice the largest ocellar diameter). Funicular segments in female: most segments quadrate to transverse. Male scape slightly widened distally, ventral pores on more than half scape length. Mesosoma (Fig. 17B) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 17B) without smooth median tubercle; interspaces smaller than punctures, smooth. Scutellum hind margin (Fig. 17B) without a double carina, without bilobed protruding projection. Prepectus (Fig. 17C) wide, dorsal margin longer than pronotal collar; well defined anteriorly (i.e. suture with pronotum very distinct); all sides with punctures, leaving a large smooth central area.

Material examined. FINLAND: 1♂, “17093”, “Lojo”, “Forsius”, “coll. Hellen”, “Perilampus ruschkai Hellén ♂, G.J. Kerrich det. 1957”, “Pres by Com Inst Ent BM 1958-391” (NHMUK). SWEDEN: 1♀, “Gotska Sandön, 17/7 1952, K.-J. Hedqvist”, “Perilampus ruschkai Hellén ♀, G.J. Kerrich det. 1960” (NHMUK).

Hosts. Associated with Geometridae (Lepidoptera); presumably a hyperparasitoid.

Distribution. Finland, Germany, Hungary, Netherlands, Romania, Russia, Sweden.

Comments. Very similar to *P. nitens* (Fig. 13), from which it differs in having the frons between eye and scrobes not punctate (Fig. 17A), the supraclypeal area rather well defined (Fig. 17A), the male eyes larger (Fig. 17A), and the head and mesosoma mostly green (Fig. 17).

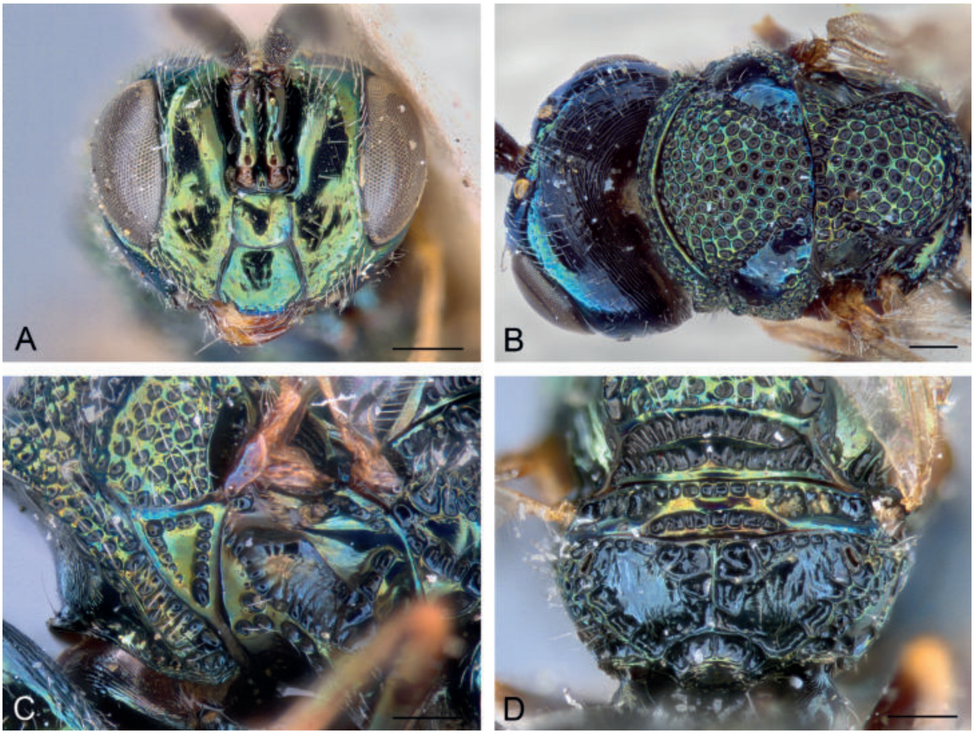

Figure 17. *Perilampus ruschkai* **A** male, head in frontal view **B** female, head and mesosoma, dorsal view **C** female, prepectus **D** female, propodeum.

Perilampus tristis Mayr, 1905
Fig. 18

Perilampus tristis Mayr, 1905: 566.
Perilampus batavus Smits van Burgst, 1919: 146. Synonymy by Ruschka (1924: 93).
Perilampus capitatus Smulyan, 1936: 397. Synonymy by Steffan (1952: 72).
Perilampus orcula Nikol'skaya, 1952. Synonymy by Bouček (1983: 119).

Diagnosis. Head, mesosoma and metasoma black; mesosoma rarely with faint bluish or bronze reflections; female flagellum brown, ventrally reddish-brown. Body size: 1.50–2.75 mm. Head shape in frontal view (Fig. 18A, B) much wider than high. Head in lateral view not unusually long, without distinct sulcus separating posterior eye margin from temple. Clypeal margin (Fig. 18A, B) truncate to slightly convex. Supraclypeal area (Fig. 18A, B) slightly transverse (less than 1.5× as wide as high), sides slightly defined; in males without oval lateral impressions. Malar sulcus versus anterior margin of malar depression about equal in female, shorter in male. Frontal keels (Fig. 18A, B) poorly developed. Face between scrobes and eye (Fig. 18A, B) smooth. Face between clypeus and eye (Fig. 18A, B) smooth. Lateral ocellus small (OOL at least twice the

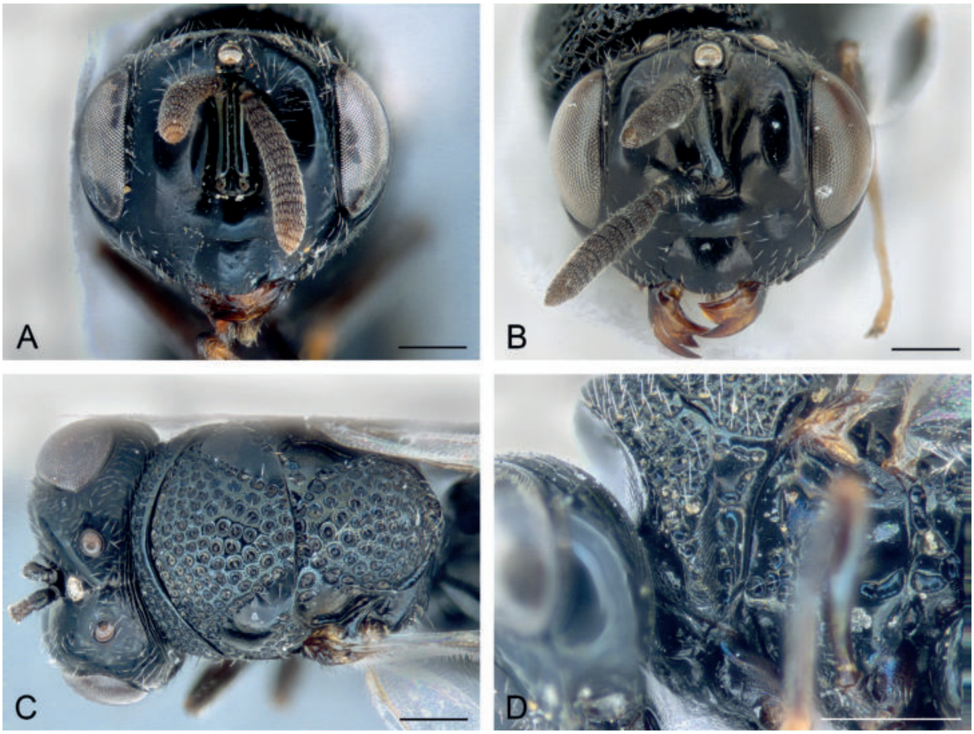

Figure 18. *Perilampus tristis* **A** female, head in frontal view **B** male, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, prepectus.

largest ocellar diameter). Funicular segments in female (Fig. 18A): most segments quadrate to transverse. Male scape (Fig. 18B) strongly widened distally; ventral pores on about half scape length. Mesosoma (Fig. 18C) not narrow (less than 1.4× as long as wide). Mesoscutum sculpture (Fig. 18C) without smooth median tubercle; interspaces smaller than punctures, smooth to finely striate. Scutellum hind margin (Fig. 18C) without a double carina, without any protruding projection. Prepectus (Fig. 18D) narrow, dorsal margin shorter than pronotal collar; poorly defined anteriorly (i.e. suture with pronotum almost indistinct); anterior margin without punctures.

Material examined. Cyprus: 2♀ “Cyprus: Pera Pedi., 13.vi.1937.”, “G.A. Mavromoustakis, B.M. 1937-808”, “♀ Perilampus tristis Mayr, Z. Bouček det. 1972” (NHMUK); 1♂ “Cyprus: Limassol, 21.viii.1934, G.A. Mavromoustakis, B.M. 1935-55”, “Perilampus tristis Mayr ♂, Z. Bouček det. 1981” (NHMUK). Greece: 3♀♀, “Attiki, Zografou, Panepistimioupolis, 37.9719°N, 23.7584°E, v.2020, By Hand, Koutsoukos, V.” (MICO); 1♀, “Attiki, Zografou, Panep/lis, 37.97191°N, 23.7584°E, 2.v.18, 130 m, Coll: Demetriou, J.” (MICO); 1♀, “Attiki, Salamina, Kokkinovraxos, 37.9422°N, 23.5020°E, iv.2020, By hand Leg. Koutsoukos, V.” (MICO); 1♀, 1♂, “Attiki, Salamina, Kokkinovraxos, 37.9422°N, 23.5020°E, 30.iv.2020, By hand Leg. Koutsoukos, V.” (MICO); 1♀, “Attiki, Athens, Geoponiko, 37.9832°N, 23.7048°E, 11.ix.2020, By hand Leg. Koutsoukos, V." (MICO); 1♂, "Attiki, Salamina, Kokkinovraxos, 37.9422°N, 23.5020°E, v.2020, By hand Leg. Koutsoukos, V." (MICO); 1♂, "Attiki, Salamina, Patris hill, 37.970°N, 23.489°E, x.2020, By hand Leg. Koutsoukos, V." (MICO); 4♂♂, "Attiki, Salamina, Pilos, 37.92358°N, 23.49558°E, 3.v.2020, By hand Leg. Koutsoukos, V." (MICO); 1♂, "Attiki, Salamina, Lamprano, 37.8921°N, 23.4266°E, 1.v.2020, By hand Leg. Koutsoukos, V." (MICO); 1♀, "Attiki, Salamina, Kokkinovraxos, 37.9422°N, 23.5020°E, 17.iv.2021, By hand Leg. Koutsoukos, V." (ZMUA). Romania: 1♀, "MH, P. Fier, Dubova, Ciucaru Mare, 14–16.VII.09, 44°36'01.8"N, 22°15'34.8"E, OP & LF, sweep, 200 m" (MICO); 1♀, "Iași county, Valea lui David Natural Reserve, 11.vi.1999, sweep, Fusu leg." (MICO); 12♀♀, 10♂♂, "Iași county, Breazu village, near Mârzești forest, steppic vegetation, 05.vii.2011, L. Fusu leg." (MICO); 2♂♂, "Tulcea county, Măcin National Parc, meadow, Malaise trap, 23–25.vii.2004, M.-D. Mitroiu leg." (MICO). Spain: 3♀, "Calella d. Costa (Barcelona) Spain, Bouček VI.1971" (NHMUK); 1♀, "Spain (Granada): La Herradura, 2.vii.74. Z. Bouček", "BM1974-321", "Perilampus tristis Mayr ♀, Bouček det. 1974" (NHMUK); 2♀, "Spain (Madrid): Escorial, 7.vii.1974. Z. Bouček", "BM1974-321", "♀ P. tristis Mayr, det. Z. Bouček 1981" (NHMUK); 1♀, "Spain (Malaga): Estepona, 29–30.vi.74. Z. Bouček", "BM1974-321", "Perilampus tristis Mayr ♀, Bouček det. 1974" (NHMUK). Turkey: 1♀, "Turkey, Ankara, 7.viii.1951, S. Erkilic", "ex larva of Carpocapsa pomonella", "Com. Inst. Ent., coll. no. 12540", "Perilampus tristis Mayr ♀, G.J. Kerrich det. 1962", "Pres by Com Inst Ent BM 1953-623" (NHMUK); 4♀, 1♂, "Turkey: Kutahya, Murat Dagi. 1200 m, 31.vii.1962", "Guichard & Harvey, B.M. 1962-299", "Perilampus tristis Mayr ♀, Bouček det. 1981" (NHMUK).

Hosts. Associated with Cossidae, Gelechiidae, Oecophoridae, Pyralidae, Tortricidae (Lepidoptera), Raphidiidae (Neuroptera); hyperparasitoid of Tachinidae (Diptera), Braconidae, Ichneumonidae (Hymenoptera). During our field work, this species was abundantly found on *Phlomis fruticosa*.

Distribution. Argentina, Austria, Belgium, Canada, Czechia, France, Germany, Hungary, Iraq, Israel, Italy, Kazakhstan, Lebanon, Moldova, Mongolia, Netherlands, Peoples' Republic of China, Romania, Russia, Serbia, Slovakia, Sweden, Switzerland, Syria, Ukraine, United Kingdom, United States of America. New species to Cyprus, Greece, Spain and Turkey.

Comments. *Perilampus tristis* is one of the most easily recognizable species due to the black body colour (Fig. 18) and prepectus structure, which is virtually fused with the pronotum, with virtually no suture line separating it from the pronotum, and very narrow (Fig. 18D).

Steffanolampus Peck, 1974

Fig. 19

Steffanolampus Peck, 1974: 555. Type species: *Perilampus salicetum* Steffan, 1952; by original designation and monotypy.

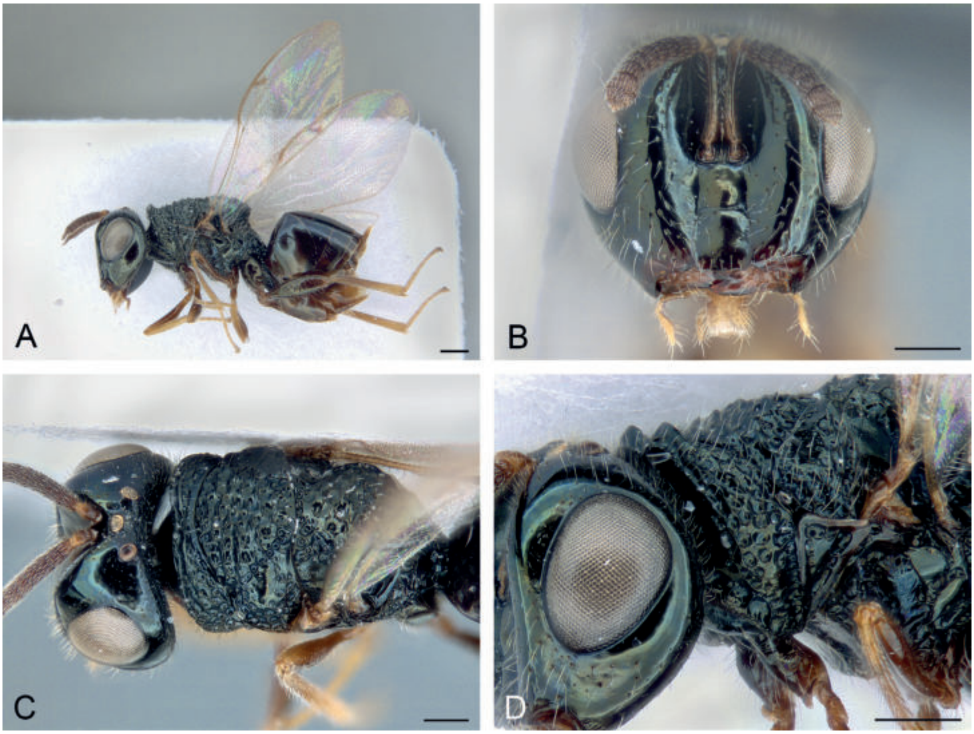

Figure 19. *Steffanolampus salicetum* **A** female, habitus in lateral view **B** female, head in frontal view **C** female, head and mesosoma, dorsal view **D** female, detail of head and mesosoma in lateral view.

Diagnosis. Face without a horn (Fig. 19B). Scrobes laterally not carinate (Fig. 19B). Pronotum with two transverse projections (Fig. 19C, D). Prepectus about equal to length of adjacent pronotal collar (Fig. 19D). Scutellum only slightly produced over propodeum (Fig. 19A). Marginal vein longer than postmarginal vein (Fig. 19A). Petiole inconspicuous, ovipositor sheaths curved upwards and projecting (Fig. 19A).

Steffanolampus salicetum (Steffan, 1952)
Fig. 19

Perilampus salicetum Steffan, 1952: 72.

Diagnosis. See generic diagnosis.

Material examined. Greece: 1♀, "Kerkini Lake N. Park, Promohonas, Procom site Malaise, 04.VII -10.VII.2007, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel" (MICO); 1♀, "Kerkini Lake N. Park, Promohonas, Procom site, Malaise, 20.VI to 26.VI.2007, 41°22'38.1"N, 23°21'58.8"E, Leg. Gordon Ramel" (MICO); 1♀, "Kerkini Lake N. Park, Kerkini, Krousia Mts site, Malaise tr. 13.VI-19.VI.2007, 41°11'32.4"N, 23°03'59.5"E, 190 m, Leg. Gordon Ramel" (MICO).

Table 1. The European species of *Perilampus*, indicating new faunistic records.

Species / new to	Europe	Austria	Cyprus	Greece	Romania	South Korea	Spain	Sweden	Turkey
P. aeneus				+	+				
P. aquilus									
P. auratus					+				+
P. aureoviridis					+				
P. cephalotes		+							+
P. chrysonotus					+				
P. eximius									
P. intermedius									
P. laevifrons				+	+				
P. maceki									
P. masculinus								+	
P. micans									
P. minutalis				+					
P. neglectus				+					
P. nitens									
P. noemi	+			+					
P. polypori		+							
P. ruficornis				+		+			
P. ruschkai									+
P. tristis			+	+			+		+

Hosts. Associated with Anobiidae (Coleoptera).

Distribution. Austria, Canada, Hungary; recently recorded from Poland (Wiśniowski and Olbrycht 2021); introduced to Europe from the Nearctic realm (United States of America) (Peck 1974). New species to Greece.

Comments. Apart from the characters mentioned in the diagnosis, *Steffanolampus* is otherwise very similar to *Perilampus*.

Discussion

We here report taxonomic and faunistic data for three genera of Perilampidae. *Euperilampus* is recorded for the first time in South Korea, with the first description of the *E. sinensis* female. *Perilampus* and *Steffanolampus* are recorded for the first time in Greece. The new records of *Perilampus* species are summarized in Table 1.

One of the most surprising discoveries was the presence of *P. noemi* in Salamina and Crete islands, Greece. Previously, the species has been recorded only from Mongolia and Tajikistan (Nikol'skaya 1952; Bouček 1983). Its presence in the Mediterranean area may be explained either by its introduction from central Asia or by its natural distribution in both geographical areas; we tend to favor the second hypothesis, but only future faunistic studies in Middle East, or perhaps molecular investigations, could confirm or reject it.

The most common species identified in this study, as reflected by the number of collected specimens, was *P. tristis*. This species is widely distributed in the Holarctic (Noyes

2019) and appears to be associated with many species of Lepidoptera, being a hyperparasitoid of Braconidae and Ichneumonidae (Hymenoptera), as well as Tachinidae (Diptera).

Given the scarcity of studies regarding the Palaearctic fauna of Perilampidae, there is a high probability that most of the European species (and even some Central Asian ones) will prove to have much wider distributions than currently known. Thus, we expect the number of species especially in South–Eastern Europe to be considerably higher, and hope that this study will stimulate further investigations.

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RESEARCH ARTICLE

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A new gregarious parasitoid species, *Microplitis idreesae* (Hymenoptera, Braconidae, Microgastrinae) reared from *Mythimna* sp. (Lepidoptera, Noctuidae), with a key to the species of *Microplitis* in the Kingdom of Saudi Arabia

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Abstract

A new species of parasitoid wasp (Braconidae, Microgastrinae) from the kingdom of Saudi Arabia (KSA) is described, *Microplitis idreesae* **sp. nov.** The genus is reported for the first time in the Eastern province of the KSA. This is the first host-parasitoid association for *Microplitis* documented in the country. The new species attacks *Mythimna* Ochsenheimer (Lepidoptera, Noctuidae). Natural history information is provided such as the association of males with females, geographical location, possible food plants, and details of wasp cocoons. In addition, a fragment of the mitochondrial cytochrome b gene is presented. A taxonomic key to the species of *Microplitis* reported from the KSA is provided. Characters of this new species and its affinities with the three previous species described from the KSA and four of the closely related to Palaeartic species are also discussed.

Keywords
Armyworm, biological control, host-parasitoid association, Middle East, taxonomy

Introduction

Microplitis Foerster, 1863 is a diverse and cosmopolitan genus within the braconid subfamily Microgastrinae. The name *Microplitis* word derives from the Greek prefix “micro” (meaning “small”) and “oplitēs” (meaning “armed”) and means small sword/weapon, referring to the generally short ovipositor present in the females (Foerster 1863; Fernandez-Triana et al. 2020). Currently, 192 species have been described (Fernandez-Triana et al. 2020). The Palaearctic (102 spp.), Oriental (40 spp.), and Nearctic (39 spp.) regions hold the great majority of the species followed by Australasian (25 spp.) region and to a lesser extent the Neotropical (11 spp.) and Afrotropical (1 spp.) regions (Fernandez-Triana et al. 2020). The Afrotropical and Neotropical regions are extremely understudied and there is potential to add new species. More than five hundred *Microplitis* species are estimated worldwide (Fernández-Triana et al. 2020).

Microplitis species are larval koinobiont endoparasitoids, meaning that their hosts continue to develop after being attacked. They are largely specialized in attacking two of the most recently derived superfamilies of Lepidoptera: Noctuoidea and Bombycoidea (Fernandez-Triana et al. 2015; Yu et al. 2016). As for the Middle East host records, 18 lepidopteran families have been reported (detailed host information from the species hosts can be found in Yu et al. 2016; Whitfield et al. 2022).

The Arabian Peninsula is the world’s largest peninsula and extraordinarily little is known regarding the Microgastrinae fauna (Fernandez-Triana and van Achterberg 2017). It is traditionally included in the Middle East region (Whitfield et al. 2022), and a total of 21 species in 12 genera have been reported in four countries of the Arabian Peninsula. Most of the species were described from Yemen (17 species in 11 genera) followed by the Kingdom of Saudi Arabia – KSA (five species in three genera), the United Arab Emirates – UAE (three species in three genera), and Oman (one species in one genus) (Fernandez-Triana and van Achterberg 2017; Whitfield et al. 2022).

Of the seven countries that comprise the Arabian Peninsula, including the southern portions of Iraq and Jordan, the KSA is the largest in terms of area. In 2017, even though one morphospecies (*Microplitis* sp. 6) was reported from the KSA, no formal species description is available (Fernandez-Triana and van Achterberg 2017). Later in 2020, three *Microplitis* species were described, all authored by Ghramh and Ahmad 2020: *M. faifaicus* (Faifa town, Asir mountain range, Jazan Province), *M. khamisicus* (Khamis Mushyat city, Asir Province), and *M. tihamicus* (Abha city, Almanaf, Asir Province). All the specimens included in the previous study were collected with Malaise traps set up in the southwestern corner of the country. Only females were collected, and information about herbivore hosts and food plants was not available at that time (Ghramh et al. 2020). To date, the KSA is the only country in the Arabian Peninsula where described species of *Microplitis* have been reported.

The aim of this paper is to describe and illustrate one new species of *Microplitis* from the KSA. The specimens were reared from an armyworm caterpillar at the campus of King Faisal University (KFU), in Al-Ahsa region of the KSA. An identification key for all the valid *Microplitis* species reported in the KSA is provided. Additional information such as geographical location, association of males with females, potential food plants, details of wasp cocoons, and DNA sequence for a fragment of the mitochondrial cytochrome b (Cyt-b) gene are also provided.

Materials and methods

Collecting site and rearing

Hofuf is the major urban city in the Al-Ahsa Oasis, in the Easter Province of the KSA. Al-Ahsa is the largest oasis in the world and is one of the two most important oases in the Arabian Peninsula; the other is Al Ain in the UAE, on the border with Oman. The climate of Hofuf is a hot desert (*BWh*) (Köppen 2022), the summers are extremely hot and long, while the winters are mild and short (National Meteorology and Environment Center 2015). It is known for being one of the largest date palm (*Phoenix dactylifera*, Arecales: Arecaceae) producers in the world. The crops thrive on salty soils that are fed from an underground aquifer and irrigated by the flow of many artesian springs, which allows agriculture all year round in a region that is otherwise a sandy desert (Mohammed et al. 2022).

On the 18th of December 2020, a caterpillar (3cm in length, Fig. 1A) was found crawling on a botanic wall, two meters away from the grass on the student residential housing, inside the campus of KFU, Hofuf city. The caterpillar was carefully removed and placed inside a plastic container and transported to one of the residential rooms. It was later observed that 15 silk cocoons were spun beside the caterpillar (Fig. 1B). To avoid the effects of decomposition of the caterpillar and use it for further identification, the pupae with cocoons already hardened were gently detached from the back of the caterpillar, placed in a clean dry container, and divided into two groups to study the effect of different incubation conditions on the duration of pupation. The first group of cocoons (n=8) was incubated at room temperature (22 °C), 20–30% relative humidity (RH), and 10.5 light (L):13.5 dark (D) photoperiod in a polypropylene tube with a loose cap for aeration (Fig. 1C). The second group of coccons (n=7) was incubated at 29 °C and 60% RH in an environmental chamber (Shell Lab, USA) in complete darkness until the emergence of the adult parasitoids. After adult emergence, all were kept at -20 °C and later point mounted or kept in the freezer for molecular analysis. The time it took for the pupae to become adult wasps was recorded for both groups. The still-living caterpillar was kept in a plastic vial in the environmental chamber and observed daily until its death. The dead caterpillar was photographed immediately (Fig. 2), and only then preserved at 70% ethanol.

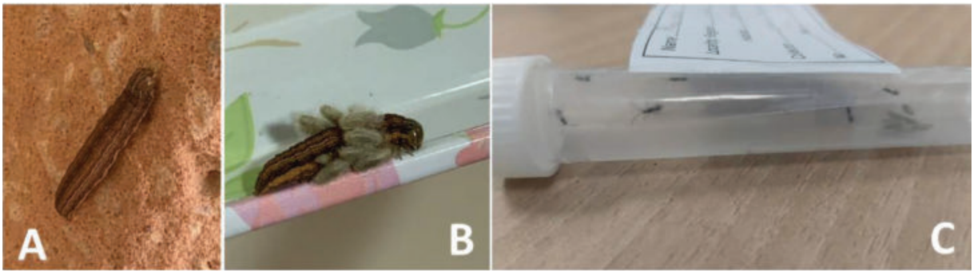

Figure 1. Lepidoptera host (*Mythimna* sp., Noctuidae: Hadeninae, Leucaniini) and parasitoid wasps (cocoons and adults of *Microplitis idreesae* sp. nov.) **A** living caterpillar of *Mythimna* sp. in its last instar larval **B** wasp cocoons attached to the back and sides of the living caterpillar **C** Adult wasps emerged after their incubation at room temperature.

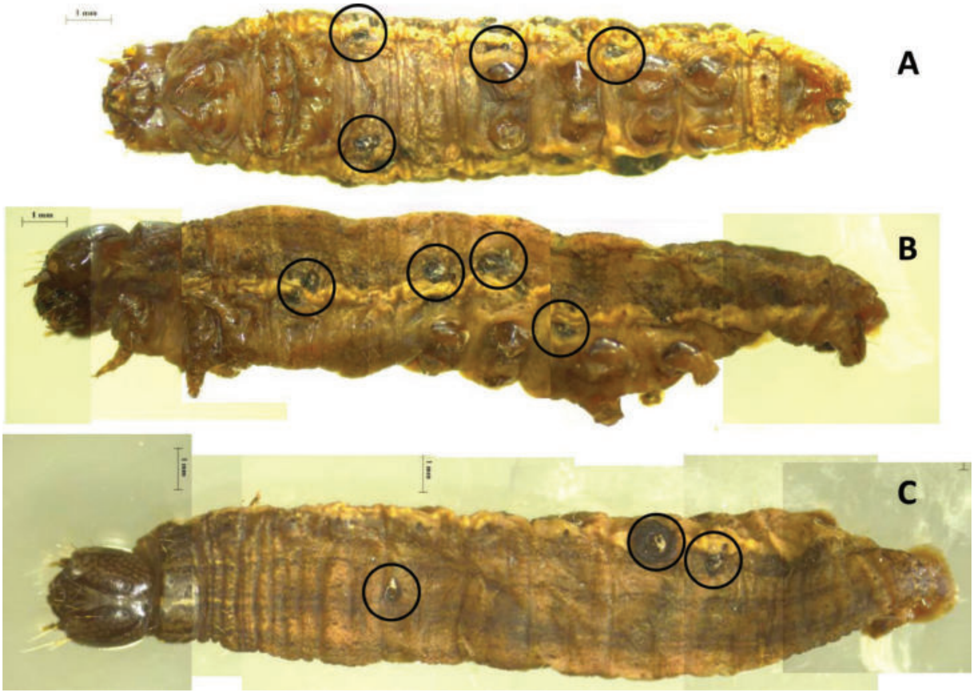

Figure 2. Dead caterpillar of Lepidoptera host (*Mythimna* sp., Noctuidae: Hadeninae, Leucaniini) showing exit holes (black circles) from which larvae of *Microplitis idreesae* sp. nov. have emerged **A** ventral side **B** lateral side **C** dorsal side.

Taxonomic identifications

The caterpillar identification was performed by Dr. Steven Passoa from the United States Department of Agriculture, Animal and Plant Health Inspection Service, and Plant Protection and Quarantine Department in the United States. The caterpillar was not picked up on a specific plant and for this reason, the plants surrounding the place where the caterpillar was collected were identified following Chaudhary and Akram (1987) as indications of possible food source.

As for the parasitoid wasp, initial identification at the genus level follows Whitfield (1997). Original *Microplitis* species descriptions from the KSA (Ghramh et al. 2020) and Palaeartic *Microplitis* keys and papers (Nixon 1970; Papp 1984; Shaw 2012) were also consulted. The geographic distribution of the genus *Microplitis* was obtained from published data (Fernandez-Triana and van Achterberg 2017; Fernandez-Triana et al. 2020; Whitfield et al. 2022), and the elevation data from the previously collected *Microplitis* species in the KSA was retrieved by using: https://www.advancedconverter.com. Terminology for surface sculpturing follows Harris (1979), wing venation follows van Achterberg (1993), and morphology follows Mason (1981), Austin and Dangerfield (1992), Sharkey and Wharton (1997), and Whitfield (1997). Additionally, morphological terms used recently to refer to structures mainly in the scutellum and the metanotum follows Arias-Penna et al. (2019 –figs 2 and 3 in pp. 27 and 31, respectively). All measurements are expressed in mm. Morphological terms and their abbreviations used within the text are: OOL = ocular ocellar line (the shortest distance between lateral ocellus and adjacent compound eye margin), POL = posterior ocellar line (the shortest distance between the lateral ocelli); **S** = metasomal sternum: S1 = sternum 1, S2 = sternum 2 and so on; T = metasomal tergum: T1 = tergum 1, T2 = tergum 2 and so on.

Digital imaging

Digital photos were obtained using a Canon EOS 5DS R digital camera (Canon, Inc. Japan) with an affixed Canon MP-E 65mm f/2.8 1-5x Macro lens. The light was emitted from two fixed monolight sources (Interfit S1a 500Ws HSS TTL AC Powered Monolight). Specimen pictures were taken using an 18% gray background. The camera was mounted on an automated WeMacro^{TM} rail to create a series of partially focused images, that were exported to Helicon Focus^{TM} version 8.0.2. (http://www.heliconsoft.com) to produce a focused image. Further processing of the final images was done using Microsoft Photos^{TM}.

Images were also obtained by a Scanning Electron Microscope (SEM). Wings were not removed, and no pre-cleaning procedure was done before SEM. The wasps were sputter-coated in gold (Spi-Module Sputter Coater, UK), and photographed using a JSM 5200 electron probe microanalyzer (JEOL, Japan) at the Department of Microbiology, College of Veterinary Medicine at KFU (KFU-Vet).

The total number of adults as well as the number of females and males of the emerged parasitoids were reported. All the material, including the type specimens, are deposited in the Insect Collection of the Entomology Laboratory at KFU-Vet, KSA, under Item N^{o}: PW (Parasitoid Wasp): 12-2020, *Microplitis idreesae* reference items 3: females & 3: males.

DNA extraction

DNA from one adult female wasp was extracted as adapted from the method of Dellaporta et al. (1983). Briefly, the wasp was manually ground in a 1.5 ml microcentrifuge tube containing 50µL extraction buffer (100 mM Tris-HCl, 500 mM NaCl, 10 mM β-mercaptoethanol, 50 mM EDTA). The mixture was then incubated in a heating block set at 65 °C for 10 min. 10µL of 5M potassium acetate together with 50µL of phenol/chloroform/isoamyl alcohol (25:24:1) were then added. The new mixture was cooled by keeping the tube on ice for 10 min, followed by centrifugation at 10k rpm for 20 min. The supernatant was then transferred to a new tube and isopropanol of equal volume was added. This mixture was then incubated at -20 °C for 10 min, and the pellet was obtained by centrifugation at 10k rpm for 10 min. The supernatant was discarded, and the lid of the tube was left for air drying. The pellet containing DNA was then washed with 70% ethanol and eluted in sterile deionized distilled water (ddH_2O).

DNA amplification condition and sequencing

A fragment (381 bp) of the mitochondrial cytochrome b (Cyt-b) gene was amplified using previously reported primers: Cyt-b forward primer: TATGTACTACCATGAGGACAAATATC, reverse primer: ATTACACCTCCTAATTTATTAGGAAT (Simon et al. 1994). DNA amplification was performed using a high-fidelity polymerase enzyme and the accompanying PCR master mix according to the manufacturer's conditions (Accu Taq™ LA DNA polymerase, Sigma-Aldrich, USA). The PCR reaction was conducted in the thermocycler (Applied Biosystems™ Veriti™, USA), with initial denaturation at 95 °C for 5 min, followed by 40 cycles of 95 °C for 1 min, 48 °C for 1 min, and 72 °C for 1 min, and the final extension was 72 °C for 7 min. The PCR product was visualized in a 1.5% agarose gel stained with EZView Stain (Biomatik, Wilmington, USA). Amplicons were purified using a commercial kit according to the manufacturer's protocol (QIAquick, QIAGEN, Valencia, CA, USA). Sequences were generated via Sanger cycle-sequencing on both directions using the same primers (Macrogen, South Korea). The obtained sequences were assembled and edited using MEGA11 (Tamura et al. 2021). The partial nucleotide sequence of the Cyt-b gene was uploaded to GenBank (http://www.ncbi.nlm.nih.gov/genbank/).

Results

Taxonomy

Key to the species of *Microplitis* Foerster reported from the Kingdom of Saudi Arabia

1 Notauli weakly impressed, indicated only by narrow depressions posterolaterally (figs 1A, 2A, Ghramh et al. 2020, pp. 3, 4)....................................**2**
– Notauli strongly impressed and coarsely sculptured (Fig. 3B, D) **3**

2(1) Fore wing with triangular areolet (fig. 1C, Ghramh et al. 2020, p. 3); vein 1SR+M almost straight (fig. 1C, Ghramh et al. 2020, p. 3) ....***M. tihamicus* Ghramh & Ahmad**

– Fore wing with quadrangular areolet (fig. 2C, Ghramh et al. 2020, p. 4); vein 1SR+M slightly curved downwards (fig. 2C, Ghramh et al. 2020, p. 4)........ ....***M. faifaicus* Ghramh & Ahmad**

3(1) T1 with a median knob posteriorly (fig. 3B, Ghramh et al. 2020, p. 6); notauli strongly impressed throughout and meeting posteriorly but not reaching scutoscutellar sulcus (fig. 3A, Ghramh et al. 2020, p. 6); fore wing with vein 2-SR+M longer than vein 2-M (fig. 3C, Ghramh et al. 2020, p. 6); medial furrow of mesoscutum complete (fig. 3A, Ghramh et al. 2020, p. 6)............ ....***M. khamisicus* Ghramh & Ahmad**

– T1 slightly elevated and rounded posteriorly (Fig. 3B, E); notauli strongly impressed anteriorly but indistinct posteriorly (Fig. 3B, D); fore wing with vein 2-SR+M as long as vein 2-M (Fig. 3J); medial furrow of mesoscutum incomplete, distinct only anteriorly (Fig. 3B, D)...........***M. idreesae* sp. nov.**

Species description

Genus *Microplitis* Foerster, 1863

Microplitis Foerster, 1863: 245. Type species: *Microgaster sordipes* Nees, 1834, by original designation.

Diagnosis. Fore wing usually with a large areolet; mesopleuron with epicnemial carina absence; propodeum with reticulated sculpture and often with a strong median longitudinal carina; T1 with a median longitudinal sulcus for most of its length, T2 and T3 unsculptured and separated by a weak suture; ovipositor short; hind coxa small, not surpassing T2, usually not surpassing T1; hind tibial spurs usually shorter than half length of first hind tarsomere; mesoscutum with notauli variable, ranging from weakly impressed (virtually absent indicated by indentations at anterior margin of mesoscutum or by pair of depressions postero-medially) to strongly impressed and coarsely sculptured (Nixon 1965; Mason 1981; Austin and Dangerfield 1992, 1993; Ranjith et al. 2015; Fernandez-Triana and van Achterberg 2017; Fernandez-Triana and Boudreault 2018).

Comments. After its establishment, the genus *Microplitis* has been beset by two problems: taxonomic and nomenclatural instability and an appreciable deficiency of distribution data (Fernandez-Triana et al. 2020). *Microgaster* Latreille, was the first genus of Microgastrinae to be described and is the basis for the subfamily name (Latreille 1804, Mason 1981, Fernandez-Triana et al. 2020). Some species that were described as *Microgaster* turned out to belong to the group we now call *Microplitis*. As for the associated geographic data, those reports have either been questioned or are scarce for the vast majority of the species (Fernandez-Triana et al. 2020).

Microplitis is part of a well-defined but informal group of eight genera that is probably monophyletic (Fernandez-Triana and Boudreault 2018; Fernandez-Triana et al. 2020). The other seven genera are: *Alloplitis* Nixon, *Gilbertnixonius* Fernandez-Triana, *Jenopappius* Fernandez-Triana, *Philoplitis* Nixon, *Silvaspinosus* Fernandez-Triana, *Snellenius* Westwood, and *Tobleronius* Fernandez-Triana (Fernandez-Triana and Boudreault 2018; Fernandez-Triana et al. 2020). Within this group of genera, *Microplitis* most resembles *Snellenius*, and the two genera have been considered closely related.

Microplitis idreesae Arias-Penna & Al-Sabi, sp. nov.

https://zoobank.org/34DEAC3F-4B21-4A3C-94AC-7376DB57A635
Figs 3A–J, 4A–K

Type material. ***Holotype.*** The Kingdom Of Saudi Arabia. 1 Female; the Eastern Province, Al-Ahsa Oasis, Hofuf, King Faisal University student housing; 25°20'34.1412"N, 49°36'6.2316"E; 154m; 18.xii.2020; Nabila Idrees leg.; reared on undetermined species of *Mythimna* (Lepidoptera: Noctuidae); caterpillar collected from the wall of the housing compound at KFU; cocoons formed on 19.xii.2020; adults emerged on 27.xii.2020, 29.xii.2020, and 30.xii.2020; PW: 12-2020; (KFU-Vet).

Paratypes. 5 (2 females, 3 males); same data as for holotype; (KFU-Vet).

Diagnosis. T1 slightly elevated and rounded posteriorly; fore wing with quadrangular areolet and vein r straight; notauli strongly impressed anteriorly but disappearing gradually as they approach the scutoscutellar sulcus.

Description. Female. Body length (head to apex of metasoma): 2.6, fore wing length: 2.45, antenna length: 3.36. Body length in females varies between 2.6 to 2.9.

Colour (Fig. 3 A, B, E). General body coloration black except for scape, pedicel, first ten proximal antennal flagellomeres, labrum, mandibles, maxillary and labial palps, and tegula dark yellow-brown. All legs dark yellow-brown except: all claws dark brown and hind coxae with basal third dark brown, second third black, and distal third yellow-brown. T1 dark brown-black, posteriorly with a dark yellow-brown area, lateral ends of T1 dark brown; T2 completely dark yellow-brown; T3 with anterior half dark yellow-brown and posterior half black; T4 and following completely black. In lateral view, T1–T2 completely dark yellow-brown; T3 with anterior half dark yellow-brown and posterior half black, T4 and following completely black. S1–S2 dark yellow-brown, S3 with anterior half dark yellow-brown and posterior half black, and hypopygium brown.

Head (Figs 3A, C, G). In frontal view, rounded with pubescence long and moderately dense. Proximal thirteen antennal flagellomeres longer than wide (0.18:0.06), last antennal flagellomere pointed and longer than penultimate (0.16:0.05, 0.12:0.05), all antennal flagellomeres setose, antenna longer than body (3.36, 2.6); scrobes shallow. Face rounded with dense fine punctations, interspaces wavy, and longitudinal median carina incomplete, visible only at the anterior third. Fronto-clypeal suture absent. Temple wide, punctate, and interspaces wavy. Inner eye margins diverge slightly at scrobes. POL shorter than OOL (0.10, 0.12). Malar suture present but long and

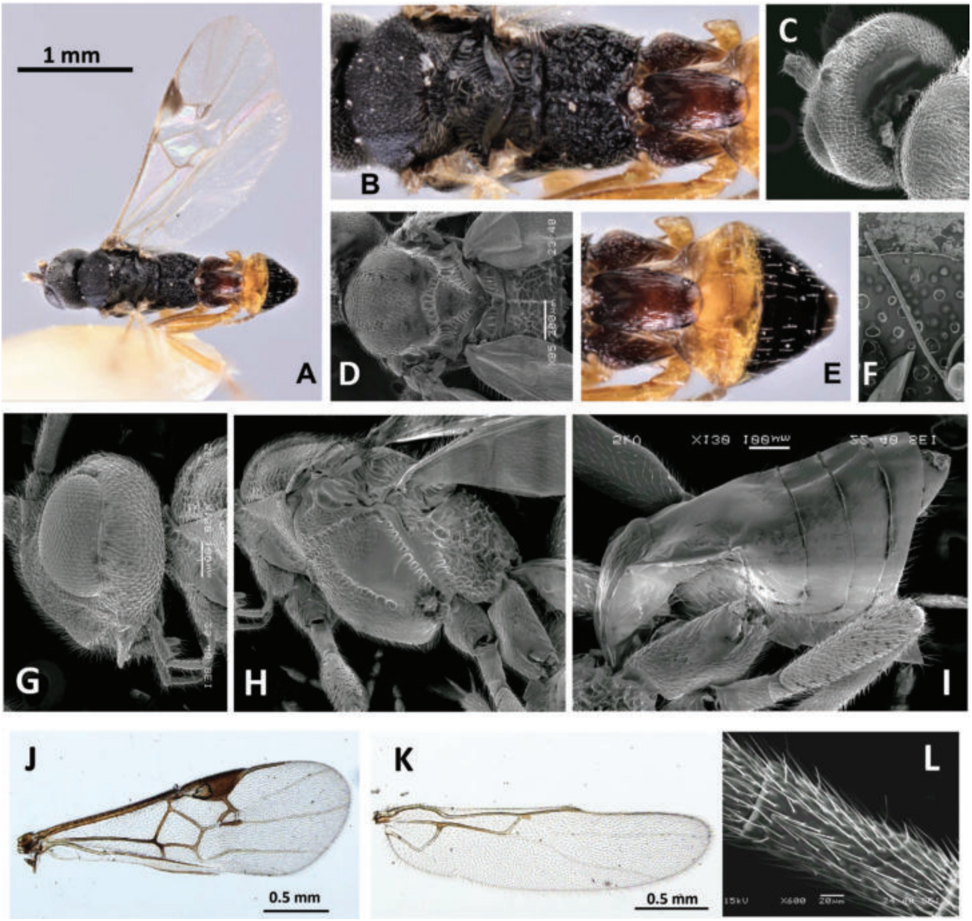

Figure 3. *Microplitis idressae* sp. nov. female **A** habitus **B** mesosoma and T1, dorsal view **C, G** head **C** dorsolateral view **G** lateral view **D, H** mesosoma **D** dorsal view **H** lateral view **E, I** metasoma **E** dorsal view **I** lateral view **F, L** antenna **F** antenna **L** flagellomere **J, K** wings **J** fore **K** hind.

moderately dense pubescence makes its observation difficult. Median area between lateral ocelli with a depression. Vertex, rounded in lateral view, narrow in dorsal view.

Mesosoma (Figs 3A, B, D, H). Mesosoma dorsoventrally convex, length: 1.4. Mesoscutum anteriorly convex and posteriorly flat with punctation distinct anteriorly, satiny posteriorly, and interspaces wavy/lacunose; medial furrow of mesoscutum incomplete, distinct only anteriorly. Notauli distinct anteriorly but disappearing gradually as they approach the scutoscutellar sulcus. Scutellum long and slender, posteriorly sloped and fused with medioposterior band of scutellum, scutellar punctation fine scattered throughout, in profile scutellum flat and on the same plane as mesoscutum, phragma of the scutellum slightly visible; medioposterior band of scutellum sculptured and overlapping slightly the medioanterior pit of metanotum; axillary trough of scutellum demilune and dorsal axillary trough of scutellum groove with complete undulate/reticulate carinae. Scutoscutellar sulcus markedly bowed with seven irregular and deep foveae, the two middle ones larger than the others, area just behind scutoscutellar sulcus smooth, shiny, and nearly at the same level as mesoscutum (flat). Anterior furrow of metanotum with setiferous lobes and not as well delineated as posterior furrow which is thick and smooth; medioanterior pit of metanotum elongated with a complete transverse carina in its third posterior, overlapping completely the medioposterior band of metanotum which is difficult to differentiate; axillary trough metanotum with few incomplete parallel carinae. Propodeum with a distinct median longitudinal carina and areolate rugose sculpturing covering its entire surface; propodeal spiracles surrounded by carina; nucha ringed by radiating carinae. In lateral view, upper pronotum with imbricate sculpture throughout, centrally with a distinct furrow of deep irregular foveae, and lower pronotum with two types of sculpture, anterior half imbricate and posterior half smooth. Propleuron finely sculptured. Metasternum convex. Mesopleuron convex, lower mesopleuron finely imbricate, centrally smooth, dorsal margin with a distinct row of foveae forming an L-shape inverted, precoxal sulcus crenulate. Epicnemial ridge truncate-pyramid shape, anteriorly convex, posteriorly truncate.

Legs (Fig. 3A, B). Ventral margin of fore telotarsus entire, with a tiny straight seta, fore telotarsus basally narrow and apically wide, and longer than the fourth tarsomere (0.14, 0.08). Hind coxa finely punctate throughout, without outer depression; inner spur of hind tibia slightly longer than outer spur (0.13, 0.12); entire surface of hind tibia with dense strong spines uniform by color and length; hind telotarsus longer than the fourth tarsomere (0.17, 0.09); hind femur length:wide (0.70:0.17), hind tibia length (0.42), hind basitarsus length (0.13).

Wings (Fig. 3J, K). Fore wing: length 2.45; stigma dark brown but paler at base; quadrangular areolet, vein r-m spectral; vein 3-SR shorter than vein r-m, both veins forming an angle at their junction; vein 2-SR curved and longer than 3-SR; vein 2-M straight and swollen; r vein straight; 1-R1 length 0.58; vein 1-M straight; vein 1-SR+M slightly curved; vein 2-SR+M spectral; vein 3CU1 tubular; vein CU1a mostly spectral but a small anterior portion absent; vein CU1b absent; vein 2-1A tubular; vein cu-a slightly curved, reaching the edge of 1-1A vein, anterior half tubular, and posterior half spectral. Hind wing (length 2.0) with vannal lobe narrow, convex, with long setae.

Metasoma (Fig. 3A, E, I). T1 virtually parallel-sided (barrel-shaped) over most of its length but narrowing over the posterior 1/3 (length 0.41; maximum width 0.2; minimum width 0.13), distally rounded, slightly elevated medially, almost nitid with scarce sculpturing laterally and scattered pubescence in the posterior third. Median area on T2 polished, truncate-trapezoidal, slightly wider than longer (length 0.16, maximum width 0.17; minimum width 0.12); lateral grooves delimiting the median area clearly defined and not reaching the posterior edge (length median area 0.17, length T2 0.2); T3 smooth, as long as T2 (0.2, 0.2). Pubescence on the hypopygium scattered.

Cocoons (Fig. 4H). Cocoons are oval with light olive drab coloration, lacking any kind of remarkable ornament, and the silk fibers looking disordered and fluffy. Cocoons are located both on the anterior part of the back and lateral sides of the alive host caterpillar.

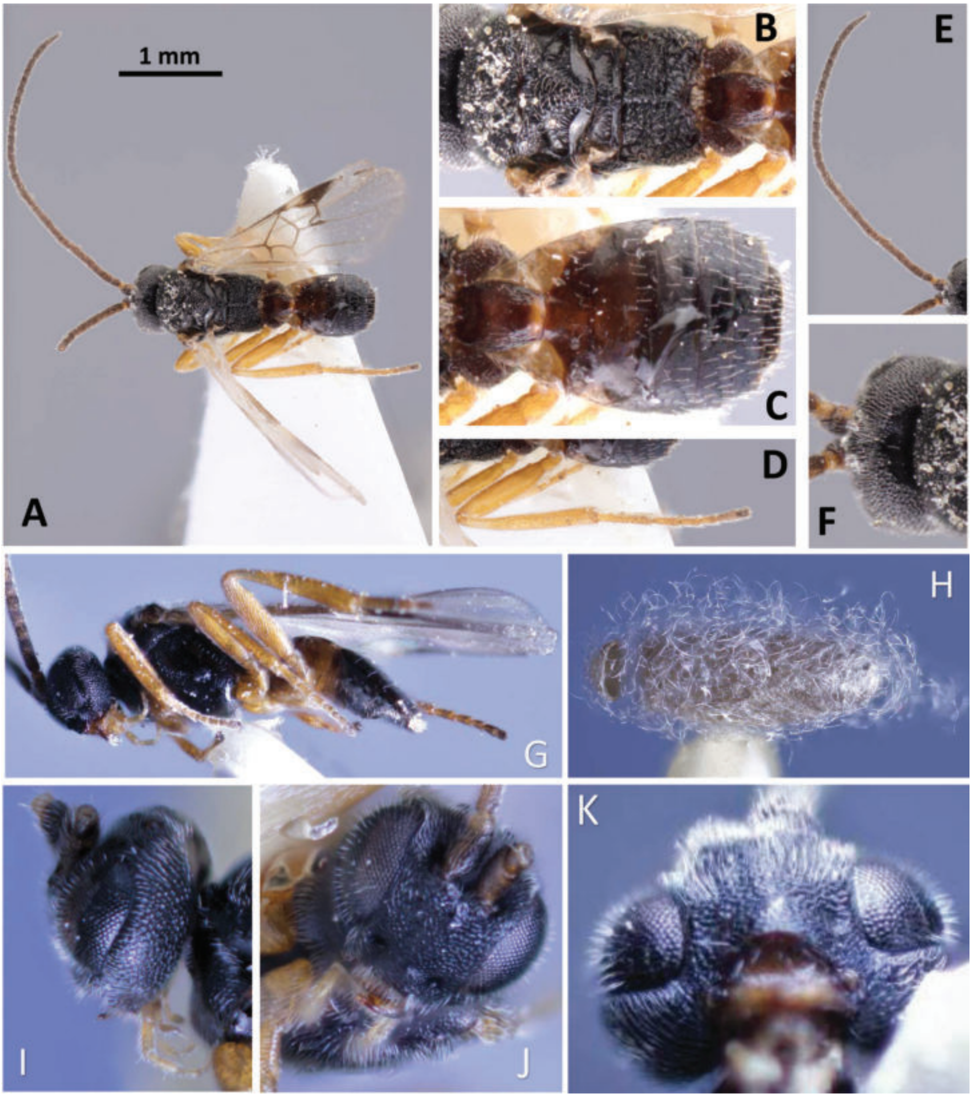

Figure 4. *Microplitis idressae* sp. nov. male **A, G** habitus **A** dorsal view **G** lateral view **B** mesosoma and T1, dorsal view **C** metasoma, dorsal view **D** legs **E** antenna **F, I–K** head **F** dorsal view **I** lateral view **J** frontal view **K** ventral view **H** cocoon.

Male (Fig. 4A–K). Similar to female except T2 with lateral areas dark yellow-brown and T3 completely dark brown. Body length varies between 2.5 to 2.8.

Etymology. This species is named in honor of Nabila Rayed Nashaat Idrees who found the infested caterpillar. She is a bachelor student from the College of Veterinary Medicine at the King Faisal University, Al-Ahsa, KSA.

Distribution. The Kingdom of Saudi Arabia, Eastern Province, Hofuf.

Biology. Gregarious larval endoparasitoid wasp. Essentially all but one of the larvae successfully spun their cocoons (15 out of 16), out of which emerged 8 females and 7 male adults. The adults obtained from pupae incubated at room temperature (n=8) eclosed on the eighth day after pupation, whereas those incubated in the environmental chamber (n=7) took one to two days longer to emerge. It is worth mentioning that in nature, eclosion is tied to both internal physiological processes and externally received cues (e.g., evaporative cooling, heat retention by moist litter, –Janzen et al. 2003). This may suggest the adaptation of the wasps to different environmental conditions and suggest the existence of different habits related to the ambient conditions.

Hosts (Figs 1, 2). Undetermined species of the oriental armyworm *Mythimna* Ochsenheimer (Noctuidae: Hadeninae, Leucaniini). The living caterpillar was collected in the fifth instar. It took four days for *Mythimna* to die after the cocoons were detached from its body. In the living *Mythimna* caterpillar, the cocoons of *M. idreesae* were more clustered in the central part of the caterpillar body forming a dorsal band and a few were in the latero-posterior side (Fig. 1B). In the dead caterpillar, the holes were observed in the dorsal, ventral, and lateral sides of the body (Fig. 2).

Three potential food plant species were identified in the vicinity of the collected caterpillar, *Ipomoea pes-caprae* (Convolvulaceae, bay-hops), *Euphorbia serpens* (Euphorbiaceae, matted sandmat), and *Cynodon dactylon* (Poaceae, bermudagrass).

Molecular data. The partial nucleotide sequence of Cyt-b gene (381 bp) is available in the GenBank database, accession number: OP485682.

Remarks. Morphological and distributional data that allow the separation of all the *Microplitis* species reported in the KSA is listed in Table 1.

Microplitis idreesae is closely related to Palaeartic species that exhibit the T1 barrel-shaped with scarce sculpturing; the legs with a light coloration (at least moderately, as it can be variable) except the hind coxa; and the fore wing with pterostigma bicoloured (dark with a pale basal spot). Considering this, four *Microplitis* species look similar to *M. idreesae*. In alphabetic order, these are *M. albipennis* Abdinbekova, *M. hispalensis* Marshall, *M. mandibularis* Thomson, and *M. spectabilis* Haliday. Similarities and differences between *M. idreesae* from these species are listed below.

***Microplitis idreesae* and *M. albipennis*.** In both species the wings are hyaline, the fore wing with the 1-R1 vein short, half as long as the pterostigma, the position of the r vein is oblique concerning the pterostigma, and the r vein is only somewhat shorter than the 2-SR vein.

Microplitis idreesae can be separated from *M. albipennis* by the following characters: 1) length of the T1: in *M. albipennis* is 1.6–1.7 times as long as broad, whereas in *M. idreesae* is 2.0 times as long as broad; 2) the colour on the tegula: in *M. albipennis* is black, whereas in *M. idreesae* is dark yellow-brown; 3) in the hind wings, the length of the 1-SR and 2M veins: in *M. albippenis* the 2-M vein hardly is 1.5 times longer than 1-SR, whereas in *M. idreesae* the 2-M vein is 1.7 times longer than 1-SR.

Microplitis albipennis has been reported in Azerbaijan, Hungary, Mongolia, Poland, Russia, and Turkey (Fernandez-Triana et al. 2020); and its lifestyle is unknown.

Table 1. All *Microplitis* species from the Kingdom of Saudi Arabia displaying their morphological differences and distributional data.

	M. faifaicus **Ghramh & Ahmad, 2020**	***M. idreesae*** **Arias-Penna & Al-Sabi, sp. nov.**	***M. khamisicus*** **Ghramh & Ahmad, 2020**	***M. tihamicus*** **Ghramh & Ahmad, 2020**
Body size	2.5 mm	2.59 mm	3.0–3.1 mm	2.1–2.2 mm
Colour on body	Body generally black, T1 brown, palps and hind tibial spurs yellow, legs yellow except hind coxae	Body generally black, all legs dark yellow-brown except all claws dark brown and hind coxae with basal third dark brown, second third black, and distal third yellow-brown, T2 and anterior half of T3 yellow-brown	Body entirely dark brown to black excluding all legs and laterotergites dorsolaterally yellowish	Body entirely dark brown to black excluding yellowish legs
Colour on wings	Infuscate	Hyaline	Infuscate	Hyaline but slightly infuscate distally
Areolet shape	Quadrangular	Quadrangular	Quadrangular	Triangular
Shape of T1 posteriorly	Rounded/convex	Slightly elevated, rounded/convex	With a median knob	Truncate
Notauli	Weakly impressed, indicated only by narrow depressions postero-laterally	Well defined anteriorly but indistinct posteriorly	Well defined throughout	Weakly impressed, indicated only by narrow depressions postero-laterally
Medial furrow of mesoscutum	Absent	Present and incomplete	Present and complete	Absent
Setae in head and mesosoma	Moderately to sparsely setose	Moderately to sparsely setose	Densely setose	Moderately to sparsely setose
Distribution in the KSA	Faifa (Jazan Province)	Hofuf (Eastern Province)	Khamis Mushyat (Asir Province)	Abha, Almanaf (Asir Province)
Elevation (m)	906	154	1988	2226
Microplitis species to which it most resembles	*M. hova* (Granger, 1949) from Madagascar	*M. albipennis* (Abdinbekova, 1969) *M. hispalensis* (Marshall 1898), *M. mandibularis* (Thomson 1895), and *M. spectabilis* (Haliday, 1834) from the Palaeartic	*M. bambusanus* (de Saeger, 1944) from Congo and Rwanda	*M. isis* (de Saeger, 1944) from Congo

Black/white line drawings of some structures are available on Papp 1984 (fig. 73, p. 123; figs 146, 147, p. 129).

Microplitis idreesae **and** ***M. hispalensis.*** In both species the first antennal flagellomere is thrice longer than broad, further flagellomeres gradually shorten so that the penultimate is twice longer than broad; the precoxal sulcus is crenulate; and with gregarious lifestyle.

Microplitis idreesae can be separated from *M. hispalensis* by the following characters: 1) female body size: in *M. hispalensis* the length is 3 mm, whereas in *M. idreesae* is 2.6–2.9 mm; 2) position of the r vein concerning the pterostigma: in *M. hispalensis* the vein r is perpendicular to the pterostigma, whereas in *M. idreesae* the vein r is oblique to the pterostigma; 3) colour on the body: in *M. hispalensis* is completely black, whereas in *M. idreesae*, females with T2 completely pale and T3 bicoloured (half anterior pale, half posterior dark), contrasting with the colour on the males, where the pale coloration is confined only to a small area, anterior corners of T2; 4) colour on the wings: in *M. hispalensis* is weakly smoky (famous), whereas in *M. idreesae* is hyaline; 5) colour on the legs: in *M. hispalensis* is black although, in males, the legs show a light pattern and more infuscation, whereas in *M. idreesae* the legs are completely dark yellow-brown, except the hind coxa with basal third dark brown, second third black, and distal third yellow-brown ; 6) and in *M. hispalensis* the antenna is as long as the body, while in *M. idreesae* is antenna is longer than the body.

Microplitis hispalensis has been reported in France and Spain (Fernandez-Triana et al. 2020). Black/white line drawings of some structures are available on Papp 1984 (figs 141–144, p. 129).

***Microplitis idreesae* and *M. mandibularis*.** In both species, the fore and middle coxae are entirely yellow, and the hind coxa is frequently splashed with yellow, and with gregarious lifestyle.

Microplitis idreesae can be separated from *M. mandibularis* by the following characters: 1) colour on T2 and T3: in *M. mandibularis*, sometimes the females display the T2 and the T3 very marked with yellow, whereas in *M. idreeasae*, the females with the T2 completely pale and the T3 bicoloured (half anterior pale, half posterior dark); 2) colour on the male antennal flagellomeres: in *M. mandibularis* they are pale throughout though this is sometimes more obvious on the underside, whereas in *M. idreesae* the pale colouration (yellow-brown) is clear in the first eight proximal antennal flagellomeres and gets gradually darker in the next two flagellomeres (9th and 10th) and become dark (dark brown or black) in the remaining flagellomeres; 3) the body length: in *M. mandibularis*, specimens are variable in size (2.4–3.2 mm), whereas in *M. idreesae* is 2.5–2.9 mm.

Microplitis mandibularis has been reported in 19 countries from the Palaeartic and one country (Greenland) from the Nearctic region (Fernandez-Triana et al. 2020). A black/white line drawing of the T1 is available in Nixon 1970 (fig. 1, p. 6).

***Microplitis idreesae* and *M. spectabilis*.** In both species the wings are often almost uniformly hyaline; the scutellum becoming strongly shining over most of its median surface and only vaguely sculptured; on the hind wing, the vannal lobe is small; the hind tibia without apical infuscation; gregarious lifestyle; the cocoon is oval, lacking any kind of remarkable ornament, the silk fibers look disordered and fluffy, the body length in *M. spectabilis* ranges between 2.6 to 2.8 mm, and in *M. idreesae* is between 2.5 to 2.9 mm; and setae of the metasoma somewhat inconspicuous, often restricted to a single row on the tergites.

The two species can be separated by the following characters: 1) colour on the tegula: in *M. spectabilis* is yellow, whereas in *M. idreesae* is dark yellow-brown, 2) antennal flagellomeres length: in *M. spectabilis* are rather thick and somewhat smooth looking towards apex, whereas in *M. idreesae* are longer than wider and the pubescence are present along its entire surface; 3) length of the penultimate antennal flagellomere: in *M. spectabilis* it varies from one and one third to one and a half times longer than wide, whereas in *M. idreesae* is at least 2 times longer than wide, 4) antennal flagellomeres in the males: in *M. spectabilis* they are apparently always at least slightly paler beneath, whereas in *M. idreesae* the pale colouration (yellow-brown) is clear in the first eight proximal antennal flagellomeres and gets gradually darker in the next two flagellomeres (9th and 10th) and become dark (dark brown or black) in the remaining flagellomeres; 4) apex of the hind tibia: in *M. spectabilis*, seen from the side the hind tibia is a little broaden before apex, whereas in *M. idreesae* the apex is not broaden, and 5) position of the r vein concerning the pterostigma: in *M. spectabilis* the r is perpendicular to the pterostigma, whereas in *M. idreesae* the r is oblique to the pterostigma.

Microplitis spectabilis has been reported in 36 countries from the Palaeartic region and there is also been recorded in the Oriental region (Pakistan) (Fernandez-Triana et al. 2020). Black/white line drawings of some structures are available in Nixon 1970 (fig. 11, p. 9; fig. 25, p. 11) and Papp 1984 (figs 64–67, p. 123).

Comments. As mentioned before, in 2017 one morpho-species was reported in the KSA (Fernandez-Triana and van Achterberg 2017), but the only data associated were morpho-species number (*Microplitis* sp. 6), numbers of females and males (2 females, 1 male), the collecting date (only the year, 1959), and the collecting site (Riyadh, the administrational center of Riyadh Province, located in the center of the country). Specimens are old, and not in particularly look conditions, without molecular data, and are currently deposited in the Canadian National Collection of Insects (CNC), Ottawa, Ontario, Canada (Fernandez-Triana, pers. commun.).

Discussion

Microplitis from the KSA

The Kingdom of Saudi Arabia is located at the intersection of three biogeographic regions, Palaearctic, Afrotropical, and Oriental. The previous three *Microplitis* species reported were caught in the southwestern part of the country. This is a mountainous region that runs parallel to the Red Sea, includes areas near the Yemeni border, and consists of mountains, plains, and valleys. The area is divided by steep rocky mountains into two distinct topographical zones: Tihama a lowland coastal plain at the west, and the Asir mountains range at the east (Ghramh et al. 2020). On the other hand, the new species, reported here, was collected in Hofuf, which is located on the opposite side of the country at least 1,000 km to the northeast, and is characterized by a hot desert climate.

Some tropical microgastrine genera (e.g., *Beyarslania* Koçak & Kemal, *Miropotes* Nixon, *Venanides* Mason, *Wilkinsonellus* Mason) have been reported from the southwestern part of the Arabian Peninsula (mainly Yemen), showing a clear faunal similarity with the Afrotropical region (Fernandez-Triana and van Achterberg 2017). This pattern has been also revealed in other groups of insects (e.g., Diptera, Lepidoptera, and Hymenoptera mainly Formicidae) (D'entrèves and Roggero 2004, Alahmed et al. 2010, Sharaf et al. 2014). In contrast, the fauna from the southeastern part of the Arabian Peninsula (Oman and UAE) collected in temperate climate localities show more affinity with the Palearctic region (Fernandez-Triana and van Achterberg 2017). On account of that, *M. faifaicus*, *M. khamisicus*, and *M. tihamicus* likely have a close affinity with the fauna of the Afrotropical region (Table 1) whereas *M. idreesae*, the new species here described, would have more affinity with the Palaearctic fauna. Furthermore, the accidental discovery of a new species without mass sampling from the field may indicate the presence of several new species of agricultural importance. *Microplitis*, as well as the status of the insect biodiversity of the eastern region of the KSA, is yet scarcely known and it is a niche to be explored by taxonomists. It is expected that the diversity of *Microplitis*, as well as Microgastrinae for the entire country, will certainly be much higher when more material becomes available for study.

Gene sequence data

The first DNA sequence data for a *Microplitis* species from the KSA is presented here. A fragment of the mitochondrial Cyt-b gene (381 bp) was obtained instead of the traditional standardized portion of the mitochondrial Cytochrome Oxidase I (COI) gene. Several attempts were made to amplify the COI following the standard protocols and primers but without success, for unknown reasons. Increasing the coverage of the gene sequence data library for the region would allow for comparisons with other regions, which already have genetic information of specimens and species of Microgastrinae (e.g., Smith et al. 2013).

Mythimna Ochsenheimer

This moth caterpillar genus is commonly known as armyworm. Their name refers to the habit of spreading in a line across a lawn or pasture, and marching slowly forward, consuming the foliage they encounter on their path. The genus *Mythimna* was also known as *Cirphis* or *Pseudaletia* previously.

As aforementioned, the usual lepidopteran hosts for *Microplitis* are larvae from Noctuoidea and Bombycoidea, both superfamilies belong to Macrolepidoptera. This is a traditional term used to refer to butterflies and moths which tend to exhibit large body sizes (Mason 1981), but it is an artificial group. In both superfamilies, the caterpillars are large and live fully exposed to vegetation throughout their larval stages (Shaw and Huddleston 1991). Those characteristics make them more suited to support gregariousness, a lifestyle that is much more expressed in *Microplitis* (Fernandez-Triana et al. 2020).

Before the rearing reported here, three species of *Microplitis* had been reported parasitizing *Mythimna. Microplitis leucaniae* (Xu & He), a species presents in the Palaearctic and Oriental regions (Fernandez-Triana et al. 2020), had been associated parasitizing *Mythimna separata* (Walker) (Xu and He 2002; Ranjith et al. 2015). As for the Middle East, *Microplitis eremitus* Reinhard (from Iran and Turkey) parasitizes *Mythimna unipuncta* (Haworth), *M. mediator* (Haliday) (from Iran and Turkey) parasitizes *M. straminea* (Treitschke), and an undetermined species of *Microplitis* (from Iran) parasitizes *M. loreyi* (Whitfield et al. 2022).

Biological control

Armyworms are pests of rice, corn, and other agricultural products and have an economic impact on farmers. Using insecticides to control armyworms is becoming less popular due to health-related concerns and due to the risk of the development of resistant strains (Zhao et al. 2018). Accordingly, employing natural enemies such as the currently identified parasitoid is a green solution that reduced the environmental contamination of pesticides. *Microplitis idreesae* hence can act as a biological control agent to combat moth caterpillars that are considered pests on local crops in the eastern region of the KSA. All known microgastrines are obligate endoparasitoids of larval Lepidoptera and practically every higher taxon of Lepidoptera is used as a host, making the subfamily one of the principal groups of natural enemies of caterpillars feeding on plants (Whitfield et al. 2018). Nonetheless, using natural enemies as agents of biological control requires wider identification of local species that can strive in ambient conditions and at the same time serve candidates for mass production in the labs.

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Sexual dimorphism in excess power index of four North American native bees (Hymenoptera, Andrenidae, Apidae, and Halictidae)

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Abstract

A multitude of hymenopteran species exhibit sexual dimorphism for simple traits, such as color, size, or antennal segment number. These differences can reflect selection for specialized biological roles, many of which have not been documented for the majority of bee and wasp species. The excess power index (EPI) is an estimate of insect flight performance that is inferred by the combination of several morphological characteristics. We compared the female and male EPIs in four species of native bees: *Agapostemon virescens* Fabricius, *Andrena carlini* Cockerell, *Melissodes bimaculata* Lepeletier and *Xylocopa virginica* L.. While females of each species had a significantly larger whole body mass, males had a significantly larger EPI. A larger body mass for females is associated with egg laying abilities and foraging behavior. Male fitness may be dependent on EPI; males that have greater flight capacity can travel further or remain in flight for longer time periods in search of mates.

Keywords

excess power index, flight machinery, sexual dimorphism, wing loading

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[*] These authors contributed equally.

Introduction

In North America, it is estimated that there are 4,000 different species of native bees (Michener 2007). Native bees are important pollinators for a multitude of crops (Allen-Perkins et al. 2022) and non-crop plants alike (Ollerton et al. 2011). However, native bees have been in decline due to numerous anthropogenic activities (Cameron et al. 2011; Abbate et al. 2019). Despite their economic and ecological importance, the basic biology and life history of the vast majority of native bee species have remained unstudied. Observational field studies of bees can be challenging, time consuming, and often unsuccessful at finding species of interest. One indirect method of learning about native bee biology is through the use of preserved specimens. Museum specimens have been used to assess population declines of native bees (Colla et al. 2012), pollen sources utilized (Kleijn and Raemakers 2008; Scheper et al. 2014), phylogenetics (Vaudo et al. 2018), and species determination via morphometrics and DNA barcoding (Ndungu et al. 2017).

Previous studies have used flight-relevant morphological features of bees to predict an individual's flight performance potential that is described in a composite value called Excess Power Index (EPI). Excess Power Index has been used to calculate the maximum power that an individual bee has in order to maintain a steady flight at equilibrium in relation to the bee's body proportions and wing dimensions (Hepburn et al. 1998). These measurements have been used to compare flight mechanics of workers from different honey bee subspecies (*Apis mellifera* subsp. L.), honey bee species (*Apis* spp. L.), and castes (Hepburn et al. 1998; Hepburn et al. 1999; Radloff et al. 2003). Additionally, EPI has been used to examine relationships among native and non-native bumble bees (*Bombus* spp. Latreille) (Polidori and Nieves-Aldrey 2015), compare progeny size of *Osmia bicornis* L. (Seidelmann 2014) and *Osmia lignaria* Say (Helm et al. 2021) via provision studies, and explore flight morphology and metabolic rates of *Megachile rotundata* Fabricius (Grula et al. 2021). EPI is a composite variable that includes the ratio of mesosomal mass/whole body mass (r) and wing loading (L), which is a ratio of whole body mass/total wing area.

In this study, we calculated EPI for four native bee species from three different families (Andrenidae, Apidae, and Halictidae). Our objectives were to determine if EPI varied among sexes of solitary bees and whether these morphological measurements could be used to predict flight behavior. We hypothesized that EPI would differ between the sexes due to the variable ecological and social roles that male and female bees play.

Materials and methods

Bee collection

Agapostemon virescens Fabricius (N = 20 ♀ and 20 ♂) and *Andrena carlini* Cockerell (N = 12 ♀ and 12 ♂) were collected by Sam Droege at the USGS Patuxent Wildlife Research Center. *Melissodes bimaculata* Lepeletier (N = 72 ♀ and 21 ♂) were captured near Scooba, Mississippi (Campbell et al. 2016). *Xylocopa virginica* L. (N = 19 ♀ and 18 ♂) were captured in St. Louis, Missouri in May 2015. All bees were either collected with sweep nets or colored pan traps. Additionally, all bees were collected from small locales to limit geographical/environmental differences in body size. These four species were chosen due to their commonness and easily distinguishable features.

Specimen preparation and trait measurements

Whole specimens were dried for 72 hours at 45 °C prior to determination of whole body mass (WBM) and mesosomal mass (MM) via a digital scale. One forewing and one hind wing were removed and flattened between glass microscope slides (Darveau 2005). Each mounted wing was photographed with a 5mm size standard in the frame using a dissecting microscope (Zeiss). Images were assembled using Tps Utility software (Rohlf 2012), and wing area was determined with the TpsDIG software package (Rohlf 2005). We assumed symmetry between the paired wings, and therefore, we calculated total wing area (TWA) by doubling the forewing and hindwing areas that were measured from each specimen: TWA = (forewing area*2) + (hindwing area*2).

Excess power index calculation and statistical analysis

The excess power index (EPI) was calculated with the following formula:

$$\mathrm{EPI} = \sqrt{\frac{(\text{Mesosomal Mass}/\text{Whole Body Mass})^2}{\text{Whole Body Mass} \,/\, \text{Total Wing Area}}}$$

We performed pairwise comparisons of single and composite variables between males and females of each species using the Mann-Whitney U test. To better understand the relative contributions of each portion of the EPI formula to differences between sexes, we compared two additional composite variables: 1. the ratio of mesosomal mass/whole body mass (r) and 2. the ratio of whole body mass/total wing area or wing loading (L). We judged statistical significance to be $p < 0.05$.

Results

The whole body mass of females was significantly larger than males in all four bee species (Table 1). For *A. virescens* and *X. virginica*, the r and L values were both significantly different between females and males. Males had both an elevated r and lower L compared to females, both contributing positively to a male-biased dimorphism in EPI (Fig. 1, Table 1). In contrast, both *M. bimaculata* and *A. carlini* r values were not significantly different between male and female cohorts (Table 1). However, male L was significantly lower than females in both species, resulting in a male-biased dimorphism in EPI (Fig. 1, Table 1). Wing surface area was significantly different between sexes in all bee species except *X. virginica*. See Table 2 for all test statistics.

Table 1. Mean morphological measurements (±SE) for four male and female native bee species that were used to calculate Excess Power Indices (EPI). An * indicates statistical significance between male and female of each bee species at P = 0.05.

Bee Species/Sex	WBM (mg)	MM (mg)	r	WSA (mm^2)	L (mg/mm^2)
Agapostemon virescens ♀, N = 20	15.76 (0.76)*	5.98 (0.28)*	0.38 (0.005)*	50.65 (1.06)*	0.31 (0.009)*
Agapostemon virescens ♂, N = 20	8.25 (0.36)	3.61 (0.17)	0.44 (0.006)	36.20 (0.75)	0.23 (0.007)
Andrena carlini ♀, N = 12	36.64 (3.03)*	11.18 (.64)*	0.31 (0.01)	67.32 (1.60)*	0.54 (0.04)*
Andrena carlini ♂, N = 12	11.02 (0.40)	3.30 (0.30)	0.30 (0.03)	44.66 (1.47)	0.25 (0.007)
Melissodes bimaculata ♀, N = 72	41.40 (0.90)*	14.21 (0.30)*	0.34 (0.003)	87.14 (0.80)*	0.47 (0.008)*
Melissodes bimaculata ♂, N = 21	27.66 (1.37)	9.50 (0.44)	0.35 (0.006)	76.05 (1.53)	0.36 (0.01)
Xylocopa virginica ♀, N = 19	259.17 (14.44)*	68.96 (2.22)	0.27 (0.01)*	188.52 (3.72)	1.36 (0.06)*
Xylocopa virginica ♂, N = 18	152.15 (4.97)	62.29 (3.23)	0.41 (0.02)	196.69 (3.93)	0.77 (0.02)

WBM = whole body mass, MM = mesosomal mass, r = mesosomal/body mass ratio, WSA = wing surface area, L = wing loading.

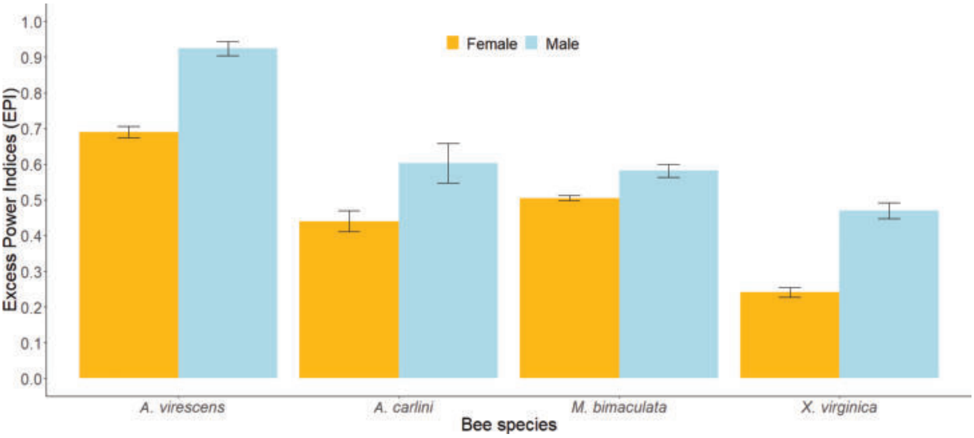

Figure 1. Excess Power Indices (EPI) (±SE) of four native bee species (*Agapostemon virescens*, *Andrena carlini*, *Melissodes bimaculata*, *Xylocopa virginica*) and their corresponding sex. All Mann-Whitney U tests found that all males of each species had a significantly higher EPI compared to females at $p < 0.05$.

Discussion

Differences in body size of male and female insects can result in different thermoregulatory and flight abilities (Gilchrist 1990). In general, total wing area in bees has been shown to be positively related to body mass (Bullock 1999) as might be expected. Body mass differences and wing loading in these four bee species were probably due to mating and foraging behaviors. Male bees invest no energy into their offspring; their activities are primarily directed to finding mates. Thus, male bee activity is driven by (1) the need to thermoregulate flight muscles, (2) finding enough nectar to power flight, and (3) find and mate with females (Willmer and Stone 2004). Thus, having a smaller body but increased wing loading should allow males to fly longer distances or remain in flight for longer time periods in search of females but also limit the amount of nectar

Table 2. Mann-Whitney U test statistics for morphological parameters and Excess Power Indices.

	WBM	MM	r	WSA	L	EPI
Andrena carlini	$z = 4.13$, $P < 0.00001$	$z = 4.13$, $P < 0.00001$	$z = 0.14$, $P = 0.89$	$z = 4.13$, $P < 0.00001$	$z = 4.13$, $P < 0.00001$	$z = 2.45$, $P = 0.014$
Melissodes bimaculata	$z = 5.87$, $P < 0.00001$	$z = 5.93$, $P < 0.00001$	$z = 0.11$, $P = 0.91$	$z = 5.22$, $P < 0.00001$	$z = 5.80$, $P < 0.00001$	$z = 3.92$, $P = 0.001$
Agapostemon virescens	$z = 5.26$, $P < 0.00001$	$z = 4.93$, $P < 0.00001$	$z = 4.65$, $P < 0.00001$	$z = 5.37$, $P < 0.00001$	$z = 4.75$, $P < 0.00001$	$z = 5.32$, $P < 0.00001$
Xylocopa virginica	$z = 4.85$, $P < 0.00001$	$z = 1.84$, $P = 0.066$	$z = 4.60$, $P < 0.00001$	$z = 1.14$, $P = 0.25$	$z = 5.18$, $P < 0.00001$	$z = 4.60$, $P < 0.00001$

needed to sustain themselves. Additionally, many male bee species (e.g., *A. carlini*) will 'patrol' flowers in search of females (Schrader and LaBerge 1978). Male bees, including *A. virescens* and *M. bimaculata* will sleep inside flowers (Rau 1938; Abrams and Eickwort 1981). This male-biased dimorphism in EPI, a composite variable that describes the predicted flight capacity of an individual based on mass and morphological attributes, can be used to predict flight behavior between bee sexes.

Female bee activities are primarily driven by the need to collect floral resources (e.g., pollen and nectar) to provision themselves and for their offspring. Unlike social bee species, solitary females complete all nest construction and provisioning on their own. Although some species in this study are considered communal nesters, each individual female only provisions her own nest(s). Solitary bees provision each brood cell sequentially and must provide enough food resources for each one (mass provisioning), which will take multiple foraging trips per brood cell (Danforth et al. 2019). Having a larger body mass may enable females to better thermoregulate body temperature enabling them to forage in less than optimal conditions (Stone 1993). Additionally, a larger body size should also allow for carrying larger loads of pollen and nectar and the ability to fly to farther flower patches (Skandalis et al. 2009). Indeed, larger-bodied female bee species have been correlated with increased foraging ranges (Greenleaf et al. 2007). However, female bees may be faced with an evolutionary tradeoff; larger body sizes can carry more provisions but have reduced flight capacity (Seidelmann 2014). Alternatively, larger body size in female bees has not always shown consistent patterns when relating body size to fecundity (Tepedino et al. 1984) and may contribute to higher parasitism rates by parasitoids (Müller et al. 1996). Thus, multiple evolutionary pressures may contribute to bee body size.

Among the bee species utilized for this study, *X. virginica*, a cavity nesting species, is probably the most thoroughly studied. Males often compete in intrasexual aggression which is mediated primarily through the body size of the males (Barthell and Baird 2004). The interactions between these males are often done in the form of aerial pursuits, which indicates the necessity for the males to have a better EPI in order to fly more efficiently for these male aggression encounters (Barthell and Baird 2004). Interestingly, despite the difference in EPI between male and female *X. virginica*, wing area did not significantly differ. The ecologies of the other three bee species in this study are poorly documented. However, they are all ground nesters but include a range of nesting habits from communal nesters for *A. virescens* (Eickwort 1981) to solitary nests for *A. carlini* (Schrader and LaBerge 1978). All four bee species feed on a variety of plants for pollen and nectar and, thus, are considered polylectic (Mitchell 1960, 1962).

Conclusion

The four bee species utilized for this study comprised three ground-nesting species (*A. carlini*, *M. bimaculata*, *A. virescens*) and one cavity nesting bee (*X. virginica*). Despite the differences in nesting and the wide taxonomic differences, the morphological measurements between the sexes showed similar trends. Although we only assessed four species, this proof of concept would also be expected for other solitary bees that have similar life histories and ecologies. To our knowledge, this is the first report of EPI measurements on non-*Apis*/*Bombus* bees other than *O. bicornis*, *O. lignaria*, and *M. rotundata* (Seidelmann 201; Grula et al. 20214; Helm et al. 2021) and the only wild bee species utilized from the Nearctic for this type of study. Utilizing EPI for other wild bee species may allow for inferences to be made regarding male/female behaviors but also comparative studies across landscapes and environmental conditions.

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Braconid imagobionts from the tribe Cosmophorini (Hymenoptera, Braconidae, Euphorinae) in the fauna of South Korea

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Abstract

Two euphorine taxa from the tribe Cosmophorini, the genus *Cryptoxilos* Viereck, 1911 and the subgenus *Eucosmophorus* Belokobylskij, 2000 (genus *Cosmophorus* Ratzeburg, 1848) are recorded for the first time for the Korean Peninsula. Three species from South Korea, *Cosmophorus* (*Eucosmophorus*) *jejuensis* **sp. nov.**, *C.* (*Eu.*) *wandoensis* **sp. nov.**, and *Cryptoxilos* (*Cryptoxiloides*) *ulleungus* **sp. nov.**, are described and illustrated. Keys to the described species of *Cosmophorus* (*Eucosmophorus*) and *Cryptoxilos* (*Cryptoxiloides*) are provided. Digital photographs of the type species of the subgenus *Eucosmophorus*, *Cosmophorus undulatus* Belokobylskij, 2000, are published for the first time.

Keywords

Cosmophorini, descriptions, diagnosis, Ichneumonoidea, Korean Peninsula, new records, new species, parasitoid

Introduction

For a long time, the euphorine tribe Cosmophorini Muesebeck & Walkley, 1951 of the braconid subfamily Euphorinae included only one morphologically distinctive genus, *Cosmophorus* Ratzeburg, 1848, whose distribution was restricted to the Palaearctic and

Nearctic regions (Muesebeck and Walkley 1951; Čapek 1958; Shenefelt 1969). However, recent extensive collects along subtropical and tropical regions that were carried out with different techniques showed an almost worldwide distribution for this genus, with the apparent exception of the Neotropics. The genus *Cosmophorus* currently contains three subgenera, *Cosmophorus* s. str., *Eucosmophorus* Belokobylskij, 2000, and *Regiphorus* van Achtergberg, 2000, and 39 valid species (van Achterberg and Quicke 2000; Yu et al. 2016).

The latest molecular phylogenetic study of the maximum possible genera of the subfamily Euphorinae (Stigenberg et al. 2015), which was based on four molecular markers, significantly redefined the composition of this tribe including five morphologically different genera, *Cosmophorus* (together with the subgenus *Eucosmophorus* Belokobylskij), *Cryptoxilos* Viereck, 1911, *Plynops* Shaw, 1996, *Ropalophorus* Curtis, 1837, and *Tuberidelus* Chen & van Achterberg, 1997.

The Cosmophorini taxa with known life history strategies are imagobionts (sensu Shaw, 2004), specifically koinobiont endoparasitoids of adult bark-beetles, (Coleoptera, Curculionidae, Scolytinae) (Čapek and Capecki 1979; Shaw 1985, 2004; Chen et al 2001; Yang et al. 2003; Yu et al. 2016). Females of *Cosmophorus*, and perhaps also those of other related genera, use their enlarged mandibles for seizure and fixation to the host adults for their infestation (Hedqvist, 1998).

Two species of the tribe Cosmophorini have been already found in the fauna of the Korean Peninsula, *Cosmophorus* (*Cosmophorus*) *cembrae* Ruschka, 1925 and *C.* (*C.*) *klugii* Ratzeburg, 1848 (Belokobylskij and Ku 1998; Ku et al. 2001; An et al. 2015). In this paper, the genus *Cryptoxilos* and subgenus *Cosmophorus* (*Eucosmophorus*) of this tribe are recorded for the first time in South Korea, and three new species belonging to these genera are described.

Materials and methods

The terminology employed for the morphological features, sculpture, and body measurements follows Belokobylskij and Maetô (2009). The wing venation nomenclature follows Belokobylskij and Maetô (2009), with the terminology of van Achterberg (1993) shown in parentheses. The specimens were examined using an Olympus SZ51 stereomicroscope. Photographs were taken with an Olympus OM-D E-M1 digital camera mounted on an Olympus SZX10 microscope (Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia). Image stacking was performed using Helicon Focus 5.0. The figures were produced using the Adobe Photoshop CS6 program. In the keys, additional features useful for separating species are listed after the dash (–).

The specimens examined in this study were deposited in the collections of the National Institute of Biological Resources (Incheon, Republic of Korea; **NIBR**) and the Science Museum of Natural Enemies (Geochang, Republic of Korea; **SMNE**).

Taxonomic part

Class Hexapoda Blainville, 1816
Order Hymenoptera Linnaeus, 1758
Family Braconidae Nees, 1811
Subfamily Euphorinae Foerster, 1863
Genus *Cosmophorus* Ratzeburg, 1848

Subgenus *Eucosmophorus* Belokobylskij, 2000

Cosmophorus (*Eucosmophorus*) Belokobylskij, 2000b: 372; Stigenberg et al. 2015: 583; Yu et al. 2016.

Sinuatophorus van Achterberg, in van Achterberg and Quicke 2000: 286 (Type species: *Sinuatophorus maximus* van Achterberg, 2000); Stigenberg et al. 2015: 583 (as synonym of *Eucosmophorus*); Yu et al. 2016.

Type species. *Cosmophorus* (*Eucosmophorus*) *undulatus* Belokobylskij, 2000.

The subgenus *Eucosmophorus* Belokobylskij of the genus *Cosmophorus* Ratzeburg is a small braconid taxon of the tribe Cosmophorini (Euphorinae) includes six East Asian (Palaearctic-Oriental) species, *C.* (*Eu.*) *acutidentatus* (van Achterberg, 2000) (Indonesia), *C.* (*Eu.*) *breviceps* (Quicke & van Achterberg, 2000) (Malaysia: Sabah), *C.* (*Eu.*) *constrictus* (van Achterberg, 2000) (Malaysia: Sabah), *C.* (*Eu.*) *longiceps* (Quicke & van Achterberg, 2000) (Brunei), *C.* (*Eu.*) *maximus* (van Achterberg, 2000) (Indonesia), and *C.* (*Eu.*) *undulatus* (Belokobylskij, 2000) (Japan: Ryukyus) (Belokobylskij 2000a; van Achterberg and Quicke 2000). Most of species of this subgenus (five species) were described from the Greater Sunda Islands, and only a single species, *C.* (*Eu.*) *undulatus*, which previously had the northernmost distribution, was recorded from the Ryukyu Islands (Ishigaki I.) in Japan. Two additional new species of the subgenus *Eucosmophorus* were found in the south of the Korean Peninsula (Wando and Jeju Islands). Now these localities are the northernmost habitat of the *Eucosmophorus* species.

Key to described species of the subgenera *Eucosmophorus*

1 Mandible mainly horizontal, its second tooth situated at inner side of mandible and in same plane as apical (upper) tooth, small or obsolescent (Figs 1C, 3B, 5E). Ovipositor of female distinctly twice sinuate apically (Figs 1J, 3H, 5K). Posterior half of second metasomal tergite entirely or mainly sculptured and with complete lateral crease (Figs 2C, 4B, 6B). Anterior ocellus situated below level of posterior ocelli. – Vertex usually distinctly depressed medially and often with wide longitudinal medial groove (Figs 1D, 3C). POL 2.5–4.0 times diameter of posterior ocellus. Antenna with 19–23 segments. Third abscissa of costal vein (2-SC+R) of hind wing long (Figs 2B, 4A,

6A) .... **Subgenus *Eucosmophorus* Belokobylskij, 2000 (type species *Cosmophorus undulatus* Belokobylskij, 2000)**

– Mandible more vertical, its second tooth situated ventrally to apical tooth of mandible (not in same plane) and medium-sized or small. Ovipositor of female straight or sometimes somewhat curved apically. Posterior half of second tergite usually largely or entirely smooth, and without lateral crease. Anterior ocellus situated at same level as posterior ocelli **2**

2 Vertex with deep median longitudinal groove. POL ~ 2.5 times diameter of posterior ocellus and at least twice distance between anterior and posterior ocelli. Third abscissa of costal vein (2-SC+R) of hind wing comparatively long........................ .... **Subgenus *Regiphorus* van Achterberg, 2000 (type species *Cosmophorus regius* Niezabitowski, 1910)**

– Vertex without median longitudinal groove. POL 1.5–2.0 times diameter of ocellus and at most 1.5 times distance between anterior and posterior ocelli. Third abscissa of costal vein (2-SC+R) of hind wing variable, but usually medium-sized or short.. **Subgenus *Cosmophorus* Ratzeburg, 1848 (type species *Cosmophorus klugii* Ratzeburg, 1848)**

The hosts of this relatively rare subgenus are unknown. However, since members of the genus *Cormophorus* with known mode of life are endoparasitoids (imagobionts: Shaw 2004) of adults of bark-borer beetles (Curculionidae, Scolytinae), we presume that species of *Eucosmophorus* also attack imagoes of the same beetle group.

***Cosmophorus* (*Eucosmophorus*) *jejuensis* sp. nov.**

https://zoobank.org/21C0184D-3CF3-4AC5-94A4-C345E7DDC3D1
Figs 1, 2

Type material. ***Holotype*:** female, "Korea (JJ), Muljangori, Bonggae-dong, Jeju-si, Jeju-do, VIII.12–VIII.29.2017 (Malaise Trap) [Hyung-Keun Lee leg.]" (NIBR).

***Paratypes*:** 1 female, "Korea (JJ), Mulyeongari, Sumang-ri, Namwon-up, Seoqwipo-si, Jeju-do, VI.03–VI.17.2017 (Malaise Trap) [Hyung-Keun Lee leg.]" (SMNE).

Description. Female. Body length 2.4–3.0 mm; fore wing length 1.7–2.2 mm.

***Head*:** Width of head 1.3–1.4 times its median length, equal to its maximum length, 1.35–1.45 times its maximum height (without mandible), 1.3 times width of mesoscutum. Vertex with wide and shallow medial longitudinal depression. Occiput strongly concave. Temples behind eyes weakly convex in anterior 1/2–3/5, than weakly and roundly narrowed, 1.1–1.3 times longer than transverse diameter of eye. Frons medially distinctly concave, with distinct, relatively low, but higher anteriorly, median longitudinal carinae, which distinctly divergent anteriorly at short distance on antennal sockets. Ocelli medium-sized, arranged in triangle with base 1.4–1.5 times its lateral sides; posterior margin of anterior ocellus placed weakly before line between anterior margins of lateral ocelli. POL 2.8–3.0 times Od, 1.3–1.4 times OOL. Eye subround, Eye with rather sparse and short setae, 1.05–1.15 times as high as broad. Malar suture invisible. Malar space very narrow, 0.10–0.15 times height of eye, 0.1–0.2 times basal width of mandible. Antennal protuberances with one wide, relatively long and acuminate apical antero-medial tooth. Clypeus very narrow, almost straight ventrally. Upper tentorial pit rather distinct, situated between eye and antennal socket and almost connected with socket its outer border. Face 2.0–2.4 times wider than its medial height with antennal protuberances. Mandible wide, widened towards basal 3/5–2/3 and then strongly narrowed towards apex, with distinct submedial ventral corner and small tubercle on lower margin, with small but wide corner in upper margin, with two apical teeth, upper tooth short and obtuse, lower tooth longest and acuminate. Length of mandible 2.0 times its maximum submedial width. Occipital carina present only in ventral 1/3, absent widely upper and upper-laterally, below fused with distinct hypostomal carina.

***Antenna*:** Antenna slender, almost filiform, 18–20-segmented, flagellum weakly compressed and segment concave below (if antenna directed posteriorly). Scape subcylindrical, distinctly widened towards apex (lateral view), not depressed, with two distinct and acuminate teeth on its anterior apical side; length of scape 1.5–1.6 times its maximum width (lateral view), 1.3–1.5 times longer than rather narrow pedicel. First flagellar segment 3.3–3.8 times longer than its apical width, 1.1–1.3 times longer than widened second segment. Second flagellar segment 2.2 times longer than its maximum width. Length of penultimate segment 2.5–3.0 times its width, 1.2–1.3 times longer than shortened apical segment; the latter weakly acuminate or obtuse.

***Mesosoma*:** Length of mesosoma 1.9–2.1 times its maximum height. Dorsal part of mesosoma weakly convex (lateral view). Oblique short and crenulate notauli present only on vertical part of mesoscutum, completely absent on its horizontal part. Prescutellar depression short, with six–seven carinae, smooth between carinae, 0.2–0.3 times as long as scutellum. Scutellum without posterior transverse depression, completely smooth. Subalar depression distinct but shallow, rather narrow, densely reticulate-rugose and sometimes with oblique striation. Precoxal sulcus distinct, long, narrow, crenulate-rugulose, strongly curved up in posterior 2/3 and prolonged towards mesopleural pit and pleural suture. Prepectal carina present but fine.

***Wings*:** Length of fore wing 2.6–2.9 times its width. Length of pterostigma 2.7–3.1 times its maximum width. Metacarp (1-R1) strongly desclerotised and lost distally. Radial (marginal) cell strongly shortened, open apically; anterior margin of radial (marginal) cell 0.9–1.0 times as long as pterostigma and 1.7–2.4 times as long as distance from apex of radial (marginal) cell to apex of wing. Radial vein (r) arising behind middle of pterostigma, its first abscissa (r) more or less distinctly thickened and short, 0.3–0.4 times as long as maximum width of pterostigma. Second abscissa of radial vein (3-SR + SR1) evenly regularly curved and transparent (discolored), absent apically at short distance. Parallel vein (CU1a) straight and unsclerotised, interstitial to mediocubital vein (2-CU1). Recurrent vein (m-cu) forming usually weak obtuse corner with first radiomedial vein (2-SR). Nervulus (cu-a) short and postfurcal, distance from basal vein (1-M) to nervulus (cu-a) almost equal to nervulus (cu-a) length. Hind wing 4.2–4.8 times longer than wide. Second abscissa of costal vein (1-SC+R)

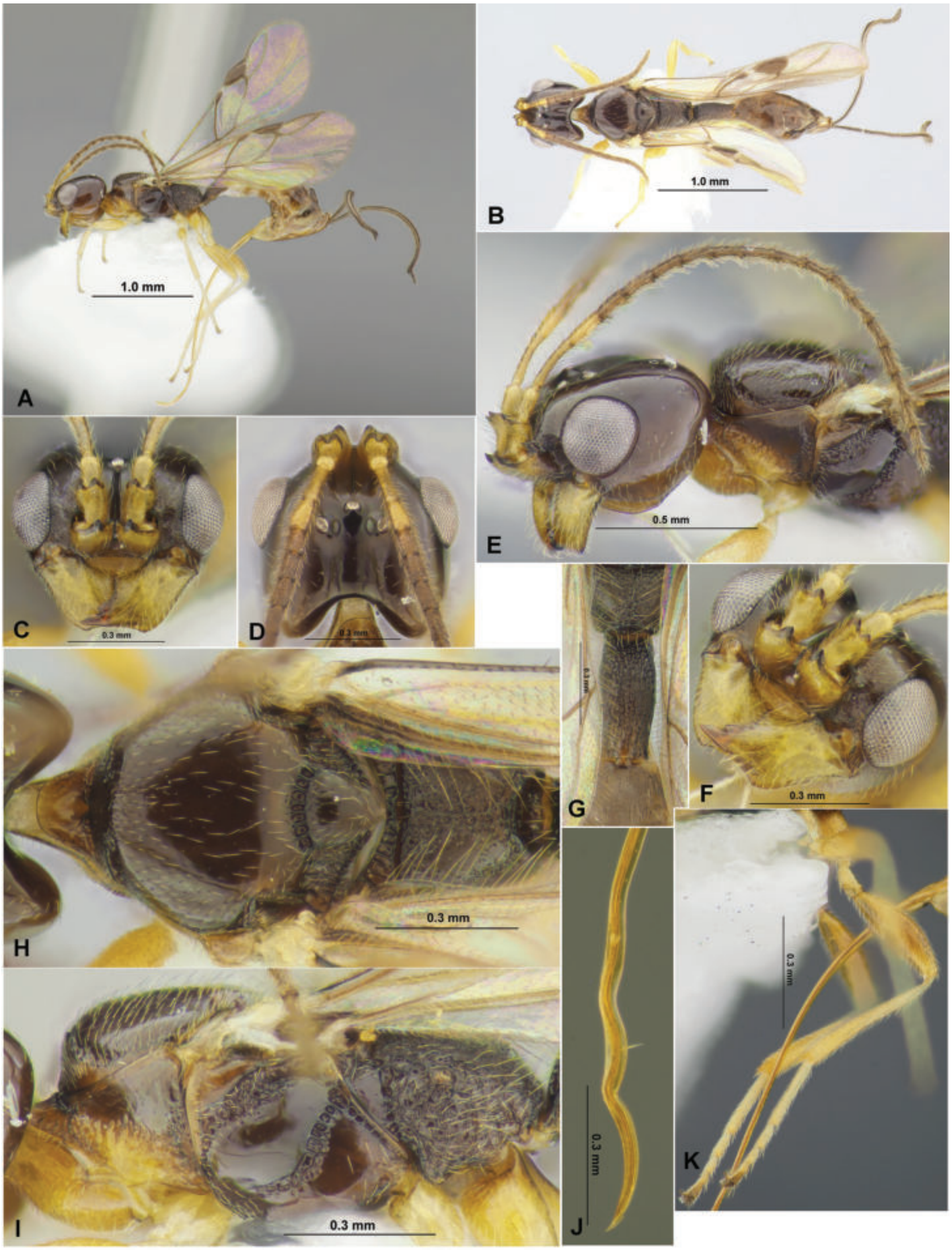

Figure 1. *Cosmophorus* (*Eucosmophorus*) *jejuensis* sp. nov. (female, holotype) **A** habitus, lateral view **B** habitus, dorsal view **C** head, front view **D** head, dorsal view **E** head and antenna, lateral view **F** face and mandible, front view **G** propodeum, first and second metasomal tergites, dorsal view **H** mesosoma, dorsal view **I** mesosoma, lateral view **J** tip of ovipositor, lateral view **K** hind leg.

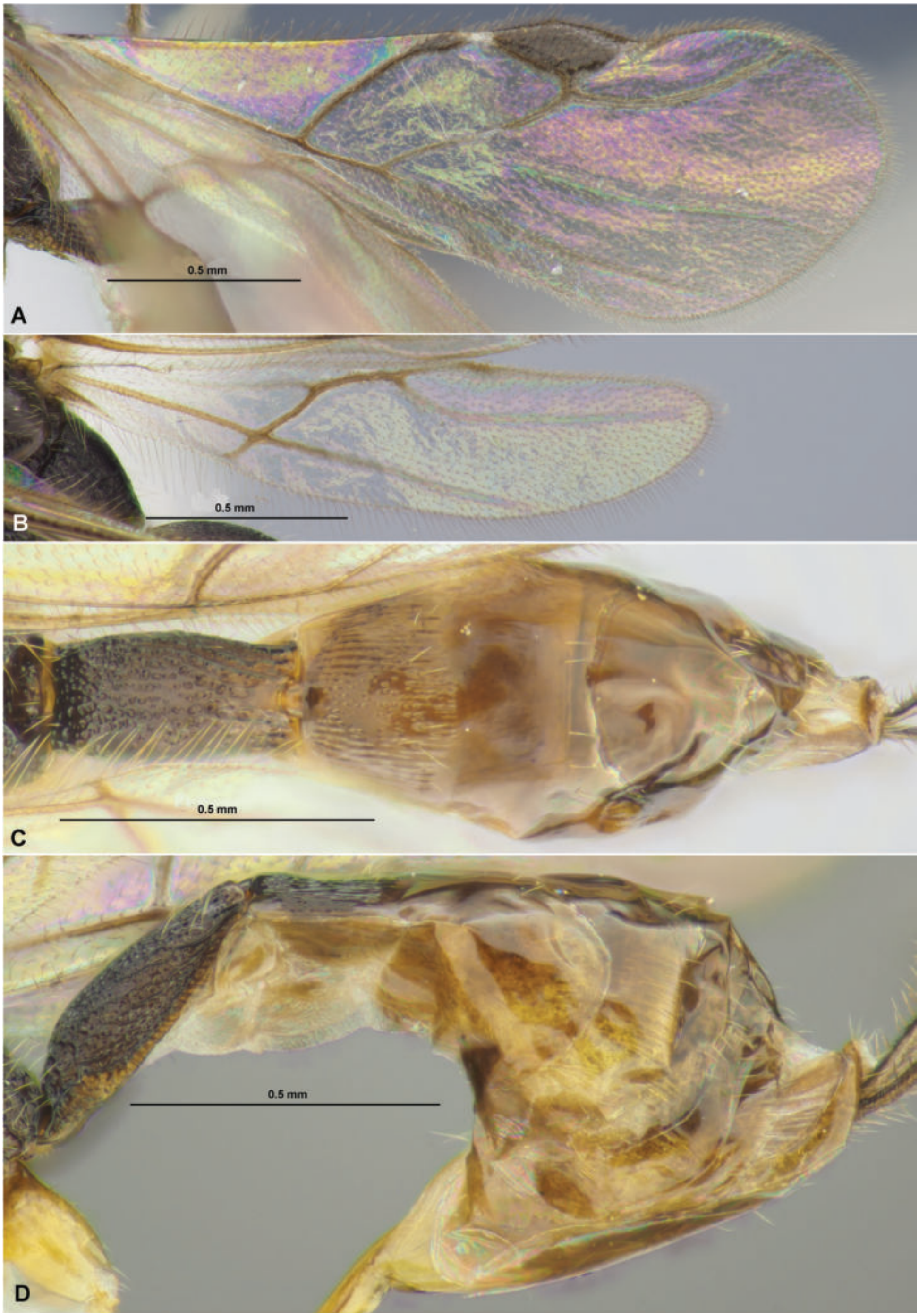

Figure 2. *Cosmophorus* (*Eucosmophorus*) *jejuensis* sp. nov. (female, holotype) **A** fore wing **B** hind wing **C** metasoma, dorsal view **D** metasoma, lateral view.

almost absent in basal 1/3 and present but strongly desclerotised in apical 2/3; fourth abscissa of costal vein (SC+R1) strongly desclerotised in distal 4/5. Submedial (subbasal) cell distally open. Recurrent vein (m-cu) straight, sclerotised, mainly pigmented and almost interstitial.

***Legs*:** Hind femur 3.2–3.3 times longer than wide. Hind tarsus almost equal to hind tibia, its second segment 0.4 times as long as first segment, approximately as long as fifth segment (without pretarsus).

***Metasoma*:** First tergite of metasoma relatively long, weakly curvedly widened to middle and then narrowed (sometimes weakly) towards apex, spiracular tubercles absent, dorsope almost absent. Apical width of first tergite 0.85–0.90 times its maximum medial width, almost equal to or 1.2 times large than its minimum width, length 1.9–2.0 times its apical width and 1.2–1.4 times length of propodeum. Suture between second and third tergites present, but very shallow. Length of second tergite approximately equal to its basal width, 1.0–1.1 times length of third tergite. Ovipositor compressed, with 3 arcuate and not equivalent sections in apical 1/5 (missing in holotype), distal section longest and crescent. Ovipositor sheath not widened in apical quarter, approximately as long as metasoma, 1.5–1.7 times longer than mesosoma, 0.7 times as long as fore wing.

***Sculpture and pubescence*:** Head entirely smooth. Sides of pronotum coarsely reticulate-rugose in lower half or medially and in posterior 1/5, smooth on remaining upper and lower parts. Mesoscutum finely and densely punctate on anterior vertical part, entirely smooth on posterior horizontal surface; scutellum entirely smooth. Mesopleuron mainly smooth. Propodeum entirely reticulate-rugulose or reticulate-punctate, with small and almost smooth areas latero-posteriorly or submedially, with longitudinal medial carina in basal 1/2–3/5 and almost semi-circular areola in posterior 2/5. Legs smooth. First metasomal tergite entirely densely reticulate-rugulose. Second tergite mainly longitudinally striate, with sparse fine punctation medially, sometimes almost smooth in small antero-lateral areas. Remaining tergites smooth. Vertex medially widely glabrous, laterally with sparse, short and semi-erect pale setae directed laterally; mesoscutum almost entirely with short and relatively densely white setae.

***Colour*:** Body mainly dark reddish brown to dark brown, metasoma ventrally brown to partly pale brown; mandible, antennal socket (sometimes only their lower part) and lower half of prothorax yellow to yellowish brown. Antennae mainly dark brown to black, four basal segments yellow to brownish yellow. Palpi pale yellow. Legs yellow to pale brown, femora mainly brown or pale reddish brown. Ovipositor sheath dark brown to black. Wings very faintly evenly infuscate, subhyaline. Pterostigma dark brown, pale basally at short distance.

Male. Unknown.

Comparative diagnosis. The new species is similar to *C.* (*Eu.*) *constrictus* (van Achterberg, 2000) from Malaysia (Sabah) (van Achterberg and Quicke 2000) in their shape of the head in dorsal view and shape of the first metasomal tergite, but differ from each other by having the first flagellar segment 1.2 times longer than the second segment (1.6 times in *C. constrictus*), second flagellar segment in front view 2.5 times longer than its width and only weakly wider than the first segment (2.0 times longer

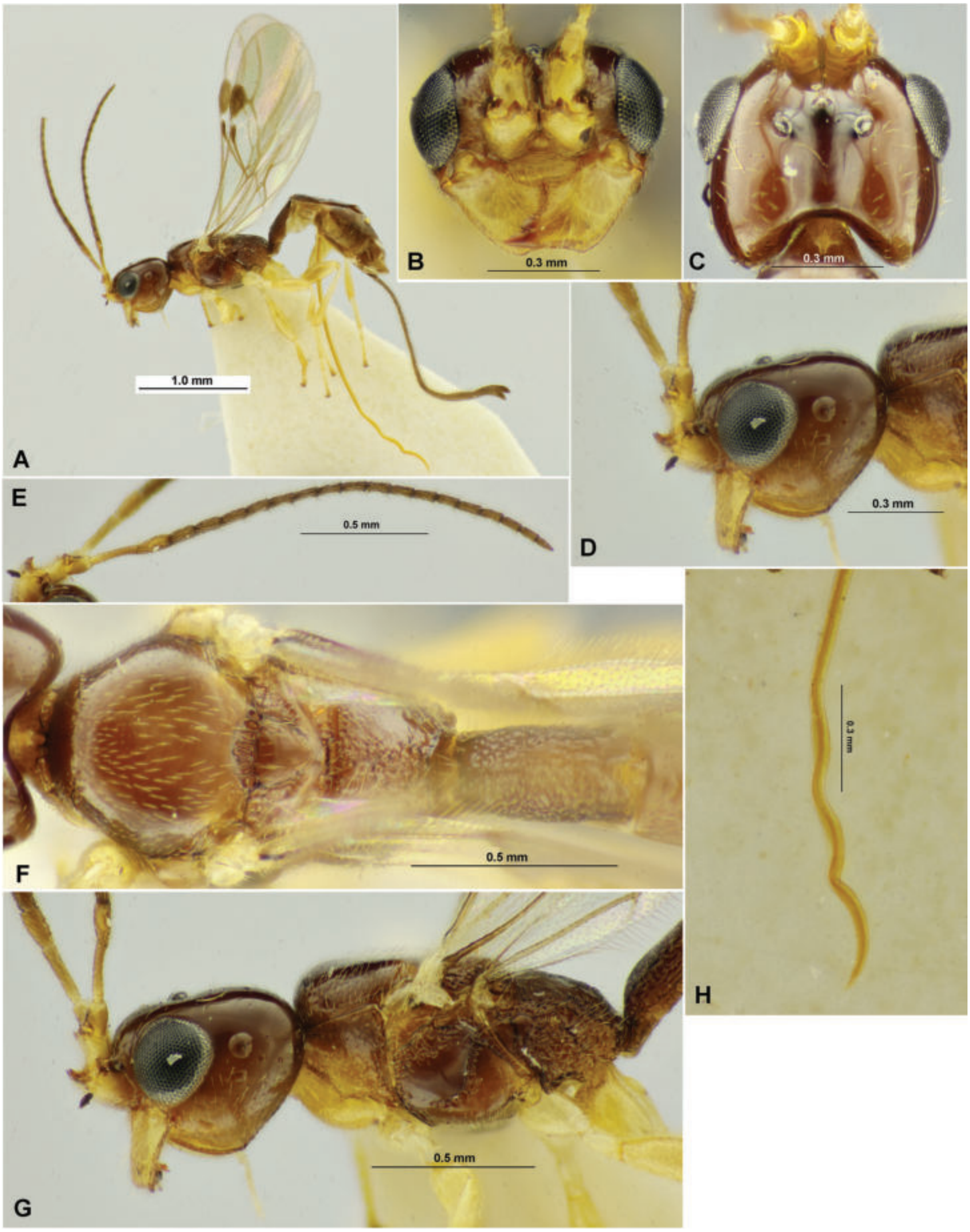

Figure 3. *Cosmophorus* (*Eucosmophorus*) *undulatus* (Belokobylskij, 2000) (female, holotype) **A** habitus, lateral view **B** head, front view **C** head, dorsal view **D** head, lateral view **E** antenna, lateral view **F** mesosoma and first tergite, dorsal view **G** head and mesosoma, lateral view **H** tip of ovipositor, lateral view.

and twice wider in *C. constrictus*), first and second flagellar segments yellow (dark brown in *C. constrictus*), upper teeth of the scape subpointed apically (obtuse apically in *C. constrictus*), mandible practically not twisted apically with the first tooth large

Figure 4. *Cosmophorus* (*Eucosmophorus*) *undulatus* (Belokobylskij, 2000) (female, holotype) **A** wings **B** metasoma, dorsal view **C** propodeum and metasoma, lateral view.

(strongly twisted apically and with a small first tooth in *C. constrictus*), mesosoma 2.1 times longer than the height (1.8 times in *C. constrictus*), precoxal sulcus distinctly crenulate (finely crenulate in *C. constrictus*), prescutellar depression distinctly crenulate (finely crenulate in *C. constrictus*), radial vein (r) arising weakly behind the middle of pterostigma (weakly before middle in *C. constrictus*), and second metasomal tergite shorter, 1.1 times longer than anterior width (longer, 1.3 times longer in *C. constrictus*).

Cosmophorus (*Eucosmophorus*) *jejuensis* sp. nov. is also very similar to the South Japanese *C.* (*Eu.*) *undulatus* Belokobylskij, 2000 (Belokobylskij 2000a: 24; 2000b: 372; Yu et al. 2016) (Figs 3, 4), but differs from the latter species by having the first flagellar segment 1.1–1.3 times longer than the second segment (1.6 times in *C. undulatus*), the first tergite widened to its middle and then narrowed towards the apex, apical width of this tergite 1.05–1.20 times large than its minimum width (evenly widened towards apex, and its apical width 1.5 times large than its minimum width in *C. undulatus*), the ovipositor sheath 1.5–1.7 times longer than mesosoma and 0.7 times as long as the fore wing (1.2 and 0.9 times correspondingly in *C. undulatus*).

Etymology. This species is named after its type locality, Jeju Island

Distribution. Korean Peninsula (Jeju Island).

***Cosmophorus* (*Eucosmophorus*) *wandoensis* sp. nov.**

https://zoobank.org/8C8964FD-657E-4F31-B839-BC27F3A82C0E
Figs 5, 6

Type material. ***Holotype***: female, "Korea (JN), Jangjoa-ri, Wando-eup, Wando-gun, VIII.29–IX.12.2020 (Malaise Trap), Ku Deokseo, Lee Jaehyeon " (NIBR).

Description. Female. Body length 2.6 mm; fore wing length 2.0 mm.

***Head*:** Width of head 1.8 times its median length, 1.5 times its maximum length, 1.6 times its height, 1.3 times width of mesoscutum. Vertex without medial longitudinal depression. Occiput distinctly concave. Temples behind eyes distinctly and roundly narrowed, ~1.2 times longer than transverse diameter of eye. Frons medially very weakly concave, with low double longitudinal carinae, which are fused medially and distinctly divergent anteriorly. Ocelli medium-sized, arranged in triangle with base 1.4 times its lateral sides; posterior margin of anterior ocellus placed distinctly before line between anterior margins of lateral ocelli. POL 2.0 times Od, 0.8 times OOL. Eye subround, without setae, 1.1 times as high as broad. Malar suture present and distinct. Malar space narrow, 0.2 times height of eye, 0.4 times basal width of mandible. Antennal protuberances with one wide and long acuminate apical anteromedial tooth. Clypeus narrow, straight ventrally. Upper tentorial pit distinct, situated between eye and antennal socket and connected with socket outer border. Face 2.3 times wider than its medial height. Mandible wide, widened towards subapex and then narrowed towards apex, with small but distinct ventral tubercle on lower margin, with two wide apical teeth, anterior (upper) tooth longest and acuminate, posterior (lower) tooth short and less acuminate. Length of mandible 2.7 times its maximum width. Occipital carina present only laterally, absent widely upper, below fused with hypostomal carina.

***Antenna*:** Antenna weakly thickened, almost setiform, 21-segmented, flagellum not compressed. Scape subcylindrical, not depressed, without pointed apical teeth in anterior side; length of scape 1.1 times its maximum width, almost as long as pedicel. First flagellar

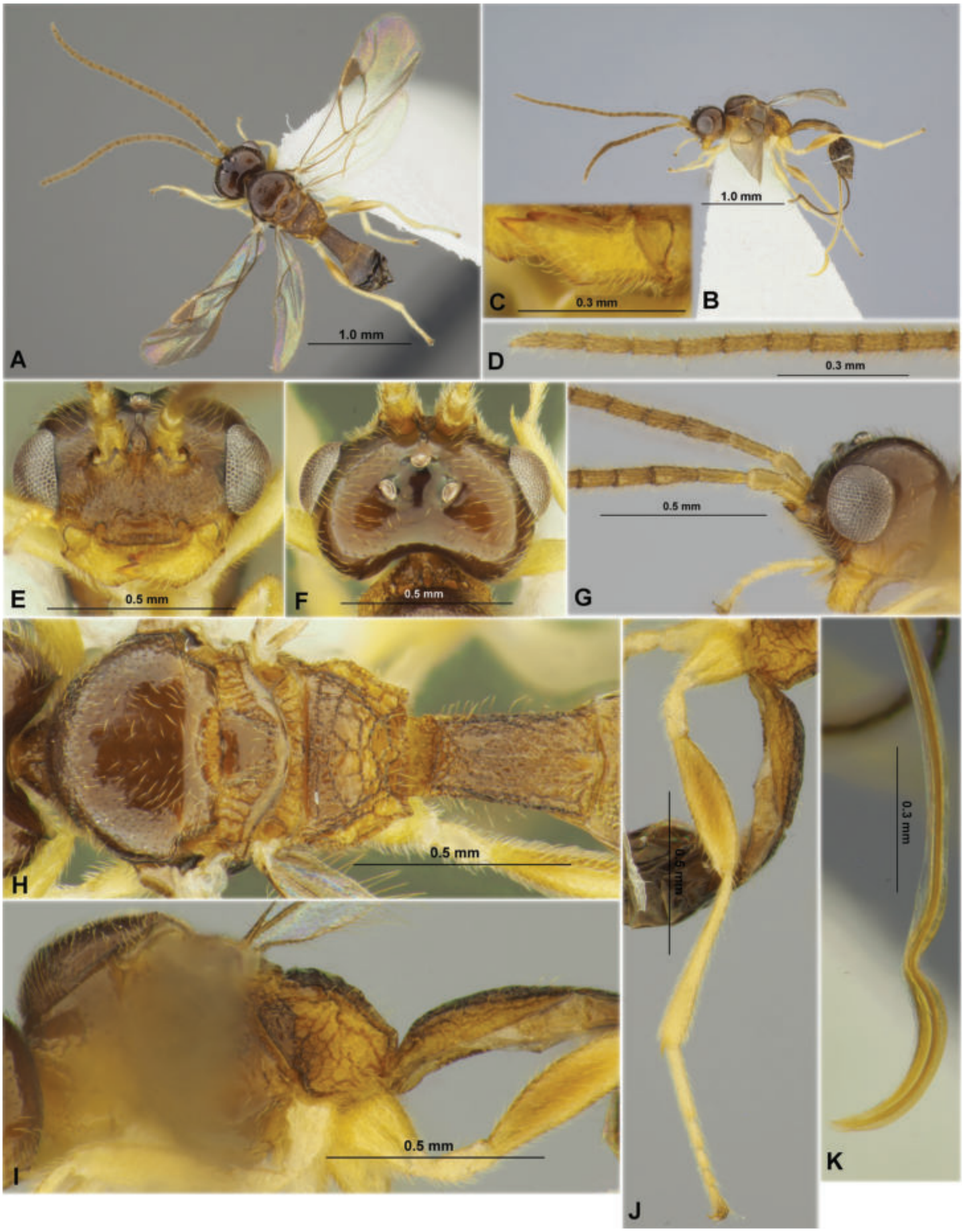

Figure 5. *Cosmophorus* (*Eucosmophorus*) *wandoensis* sp. nov. (female, holotype) **A** habitus, dorsal view **B** habitus, lateral view **C** mandible **D** apical segments of antenna **E** head, front view **F** head, dorsal view **G** head and basal segments of antenna, lateral view **H** mesosoma and first tergite, dorsal view **I** mesosoma and first tergite, lateral view **J** hind leg **K** tip of ovipositor, lateral view.

segment 3.7 times longer than its apical width, 0.9 times as long as second segment. Second flagellar segment 3.0 times longer than apical width. Length of penultimate segment 2.7 times its width, 1.1 times longer than apical segment; the latter weakly acuminate.

Figure 6. *Cosmophorus* (*Eucosmophorus*) *wandoensis* sp. nov. (female, holotype) **A** wings **B** propodeum and metasoma, dorsal view **C** propodeum and metasoma, lateral view.

***Mesosoma*:** Length of mesosoma 1.6 times its maximum height. Dorsal part of mesosoma weakly convex. Notauli present on vertical part of mesoscutum only and crenulate, completely absent on its horizontal part. Prescutellar depression rather short, with four carinae, almost smooth between carinae, 0.3 times as long as scutellum. Scutellum without transverse posterior depression, weakly sculptured in posterior 1/3. Subalar depression shallow, wide and densely rugose-areolate. Precoxal sulcus distinct, long, rather wide, crenulate-rugulose, curved up posteriorly and prolonged towards mesopleural pit and pleural suture (fused with additional oblique crenulate furrow). Prepectal carina absent. Mesosternal furrow narrow and shallow, rugulose.

***Wings*:** Length of fore wing 2.6 times its width. Length of pterostigma 2.3 times its maximum width. Metacarp (1-R1) strongly desclerotised and lost distally. Radial (marginal) cell strongly shortened, open apically; anterior margin of radial (marginal) cell 0.9 times as long as pterostigma and 2.5 times as long as distance from apex of radial (marginal) cell to apex of wing. Radial vein (r) arising slightly behind middle of pterostigma, its first abscissa (r) strongly thickened and very short, 0.2 times as long as maximum width of pterostigma. Second abscissa of radial vein (3-SR + SR1) evenly regularly curved and transparent, absent apically at short distance. Parallel vein (CU1a) almost straight and unsclerotised, subinterstitial to mediocubital vein (2-CU1). Recurrent vein (m-cu) forming weak obtuse corner with first radiomedial vein (2-SR). Nervulus (cu-a) short and strongly postfurcal, distance from basal vein (1-M) to nervulus (cu-a) twice nervulus (cu-a) length. Hind wing 4.7 times longer than wide. Second abscissa of costal vein (1-SC+R) completely absent; fourth abscissa of costal vein (SC+R1) almost absent in distal half. Medial (basal) cell antero-distally and submedial (subbasal) cell distally open. Recurrent vein (m-cu) sclerotised, pigmented and almost interstitial.

***Legs*:** Hind femur 3.6 times longer than wide. Hind tarsus 0.9 times hind tibia, its second segment 0.4 times as long as first segment, 0.9 times as long as fifth segment (without pretarsus).

***Metasoma*:** First tergite rather long, weakly and almost linearly widened posteriorly, spiracular tubercles absent, dorsope very small. Apical width of first tergite 1.7 times its minimum width, length approximately 1.6 times its apical width and length of propodeum. Suture between second and third tergites present, but fine, distinct medially and almost absent laterally Length of second tergite almost equal to its basal width, 1.4 times length of third tergite. Ovipositor compressed, with three arcuate and not equivalent sections in its apical 1/3, distal section longest and crescent. Ovipositor sheath weakly widened to apical quarter, ~ 1.2 times longer than metasoma, 1.5 times longer than mesosoma, 0.7 times as long as fore wing.

***Sculpture and pubescence*:** Head mainly smooth, face weakly rugulose-punctate. Sides of pronotum coarsely reticulate-areolate in lower half and in posterior quarter, mainly smooth on remaining part. Mesoscutum finely rugulose-granulate on anterior vertical part, entirely smooth on posterior horizontal surface; scutellum mainly smooth, rugulose in narrow posterior quarter. Mesopleuron smooth medially and below, rugulose-reticulate anteriorly and ventro-posteriorly. Propodeum entirely reticulate-areolate, areas enlarged posteriorly, without mediolateral areas and posterior transverse carina. Legs smooth. First metasomal tergite densely reticulate-rugulose. Second tergite mainly small reticulate-areolate, smooth on rather large latero-posterior areas. Remaining tergites smooth. Vertex entirely with relatively dense, short and semi-erect yellow setae directed laterally; mesoscutum almost entirely with short and rather densely yellowish setae.

***Colour*:** Body reddish brown to dark reddish brown, metasoma in latero-posterior half almost black; propodeum dorsally and first metasomal tergite paler; mandible, lower median part of prothorax, and metapleuron yellow to yellowish brown. Antennae mainly brown to dark brown, three basal segments brownish-yellow. Palpi pale yellow. Legs yellow to pale brown, hind femur mainly brown. Ovipositor sheath dark brown to black. Wings faintly evenly infuscate. Pterostigma dark brown, pale basally at very short distance.

Male. Unknown.

Comparative diagnosis. The new species is similar to *C.* (*Eu.*) *breviceps* (Quicke & van Achterberg, 2000), which was described from Malaysia (Sabah) (van Achterberg and Quicke 2000), but differs from the latter species by having the eye in dorsal view ~1.2 times longer than the temple (1.5 times in *C. breviceps*), temple distinctly convex in dorsal view (weakly convex in *C. breviceps*), teeth of the scape distinctly protruding dorsally (weakly protruding in *C. breviceps*), frons with distinct but not high carinae divergent anteriorly (without carinae in *C. breviceps*), mandible with two apical teeth (only with one tooth in *C. breviceps*), area below and behind the mandibular base smooth (rugose-striate in *C. breviceps*), and the second metasomal tergite densely reticulate-areolate (sparsely longitudinally rugose in *C. breviceps*).

Etymology. This species is named after its type locality, Wando Islands

Distribution. Korean Peninsula.

Key to the Asian species of the subgenus *Eucosmophorus*

(Transformed and update after van Achterberg and Quicke 2000)

1 Temple short and distinctly narrowed posteriorly in dorsal view; eye 1.2–1.5 times longer than temple (Fig. 5F). First metasomal tergite robust, its length ~ 1.6 times apical width (Fig. 6B). Depression of vertex shallow or very shallow (Fig. 5F)..... **2**

– Temple long and weakly narrowed posteriorly in dorsal view; eye 0.6–1.0 times as long as temple (Figs 1D, 3C). First metasomal tergite slender, its length 2.4–2.7 times its apical width (Figs 2C, 3F). Depression of vertex deep (Figs 1D, 3C). – Area behind mandibular base largely smooth (Figs 1E, 3D) **3**

2 Eye in dorsal view 1.5 times longer than temple; temple weakly convex. Teeth of scape minute, slightly protruding dorsally. Frons without carinae. Mandible only with one tooth. Area behind and below mandibular base rugose-striate. Second tergite of metasoma sparsely longitudinally rugose. Body length 1.9 mm. Malaysia (Sabah) .... ***Eu. breviceps* (Quicke & van Achterberg, 2000)**

– Eye in dorsal view 1.2 times longer than temple (Fig. 5F). Teeth of scape medium-sized, distinctly protruding dorsally (Fig. 5E). Frons with distinct but not high carinae divergent anteriorly (Fig. 5E). Mandible with two apical teeth (Fig. 5E). Area below and behind mandibular base smooth (Fig. 5G). Second tergite of metasoma densely reticulate-areolate (Fig. 6B). Body length 2.6 mm. South Korea ....***Eu. wandoensis* sp. nov.**

3 Head in dorsal view comparatively slender, rather distinctly flat in lateral view. Length of fore wing 1.5 mm. Shape of fused discoidal-radiomedial (disco-submarginal) cell of fore wing comparatively slender, parallel-sided. – Body brown. Body length 2.3 mm. Brunei ....***Eu. longiceps* (Quicke & van Achterberg, 2000)**

– Head in dorsal view less slender, less flattened in lateral view (Figs 1E, 3D). Length of fore wing 1.8–2.5 mm. Shape of fused discoidal-radiomedial (disco-submarginal) cell of fore wing variable (Figs 2A, 4A) **4**

4 Scape with pair of minute teeth dorsally. Third antennal segment ~ 1.2 times longer than fourth segment. Antennal socket with relatively short acute tooth. Mandible comparatively slender. Mesoscutum largely glabrous medio-anteriorly. Mesosternal sulcus nearly smooth. Body length 2.7 mm. Indonesia (Sulawesi) .... ***Eu. acutidentatus* (van Achterberg, 2000)**

– Scape with pair of large lobe-shaped teeth dorsally (Figs 1C, 3B). Third antennal segment 1.4–1.6 times longer than fourth segment (except *C. jejuensis* sp. nov.) (Fig. 3E). Antennal socket with large lobe-shaped tooth (Figs 1C, 3B). Mandible wide (Figs 1C, 3B). Mesoscutum largely setose medio-anteriorly (Figs 1H, 3F). Mesosternal sulcus distinctly rugose-reticulate.. **5**

5 First metasomal tergite distinctly constricted posteriorly and comparatively short (Fig. 2C). Second costal vein (1-SC+R) of hind wing largely absent (Fig. 2B). Discoidal-radiomedial (disco-submarginal) cell of fore wing subparallel-sided (Fig. 2A). Antennal sockets brown (Fig. 1C) **6**

– First metasomal tergite almost parallel-sided or weakly widened posteriorly, not constricted posteriorly and comparatively long (Fig. 3F). Second costal vein (1-SC+R) of hind wing at least faintly pigmented (Fig. 4A). Discoidal-radiomedial (disco-submarginal) cell of fore wing more or less distinctly widened anteriorly (Fig. 4A). Antennal sockets mainly pale yellowish (Fig. 3B) **7**

6 Head rather bulbous above (lateral view). Upper teeth of scape obtuse apically. First flagellar segment 1.6 times longer than second segment. Second flagellar segment in front view 2.0 times longer than its width and on half wider than first segment. First and second flagellar segments dark brown. Mesosoma 1.8 times longer than its height. Prescutellar depression and precoxal sulcus finely crenulate. Radial vein (r) of fore wing arising weakly before middle of pterostigma. Second metasomal tergite longer, 1.3 times longer than anterior width. Body length 3.5 mm. Malaysia (Sabah)... ***Eu. constrictus* (van Achterberg, 2000)**

– Head not distinctly bulbous above (lateral view). Upper teeth of scape subpointed apically (Fig. 1C, E). First flagellar segment 1.2 times longer than second segment (Fig. 1E). Second flagellar segment in front view 2.5 times longer than its width and only weakly wider than first segment (Fig. 1E). First and second flagellar segments yellow (Fig. 1E). Mesosoma 2.1 times longer than its height (Fig. 1I). Prescutellar depression and precoxal sulcus distinctly crenulate (Fig. 1H, I). Radial vein (r) of fore wing arising weakly behind middle of pterostigma (Fig. 2A). Second metasomal tergite shorter, 1.1 times longer than anterior width (Fig. 2C). Body length 3.0 mm. South Korea (Jeju) .... ***Eu. jejuensis* sp. nov.**

7 First flagellar segment in lateral view 4.7 times longer than its apical width. Apical teeth of scape long. Eye in dorsal view 0.6 times as long as temple. Length of mesosoma 1.5 times its height. Prescutellar depression entirely narrow. Areola of propodeum subconical-oval shape. First metasomal segment long, 2.7 times longer than distal width. Second metasomal segment 1.3 times longer than its basal width. Body mainly black. Body length 4.2 mm. Indonesia (Sumatra)......***Eu. maximus* (van Achterberg, 2000)**

– First flagellar segment in lateral view 3.5 times longer than its apical width (Fig. 3E). Apical teeth of scape relatively short (Fig. 3B). Eye in dorsal view 0.85 times as long as temple (Fig. 3C). Length of mesosoma 1.9 times its height (Fig. 3G). Prescutellar depression wide medially and narrow laterally (Fig. 3F). Areola of propodeum semi-round shape. First metasomal segment short, 2.2 times longer than distal width (Fig. 3F). Second metasomal segment as long as its basal width (Fig. 4B). Body mainly brown to dark brown (Fig. 3A). Body length 3.1 mm. Japan (Ryukyus) .... ***Eu. undulatus*** **(Belokobylskij, 2000)**

Genus *Cryptoxilos* Viereck, 1911

Type species. *Cryptoxilos dichromorphus* Viereck, 1911.

This is a relatively small and rare euphorine genus that belong to the tribe Cosmophorini, and currently contains seven described species (Stigenberg et al. 2015; Yu et al. 2016). Members of *Cryptoxilos* are koinobiont endoparasitoids (imagobionts) of bark-boring beetle adults (Curculionidae, Scolytinae) (Shaw 1985; Yu et al. 2016). Species of this genus have been recorded in the Nearctic (2), Neotropical (1), Oceanic (Fiji) (1), Australasian (New Zealand) (1), and Palaearctic (2) regions (Shaw 1985; Chen et al. 2001; Shaw and Berry 2005).

The two species of *Cryptoxilos* previously known for the Palaearctic region belong to the Old World subgenus *Cryptoxiloides* Čapek & Capecki, 1979, and were described from Europe (Poland) and the Eastern Palaearctic (China: Zhejiang) (Čapek and Capecki 1979; Chen et al. 2001). A third species of *Cryptoxilos* (*Cryptoxiloides*) is described here from South Korea (Ulleung Island), with the first record of this genus for the Korean Peninsula.

Cryptoxilos **(*Cryptoxiloides*)** ***ulleungus*** **sp. nov.**

https://zoobank.org/9C12BF12-8214-4F16-B3FB-A04CEC609414

Figs 7, 8

Type material. ***Holotype*****:** female, "Korea (GB), Dosolam, Naesujeon-gil, Ulleung-up, Ulleung-gun, V.27.2017 (Sweeping), Ku Deokseo" (NIBR).

Paratype**:** 1 female, same label as in holotype (SMNE).

Description. Female. Length of body 1.6–1.8 mm, length of fore wing 1.4–1.6 mm.

Head**:** Width of head (dorsal view) 1.7–1.9 times its medial length, 1.1 times width of mesoscutum. Occipital carina complete and rather distinct, joining with hypostomal carina weakly upper base of mandible. Temple behind eyes (dorsal view) weakly convex in anterior 1/3–1/2, than distinctly evenly narrowed. Length of eye in dorsal view 1.3–1.4 times length of temple. Ocelli arranged in almost equilateral triangle; POL 1.4–1.6 times OD, 0.4 times OOL. Eye covered by rather long and dense setae. Face narrow and convex, its minimum width 0.6 times width at level of antennal sockets, almost equal to medial height (without clypeus). Clypeus narrow, its width 3.8 times maximum height; ventral margin of clypeus weakly concave. Distance between tentorial pits almost 8.0 times distance between pit and margin of eye. Malar

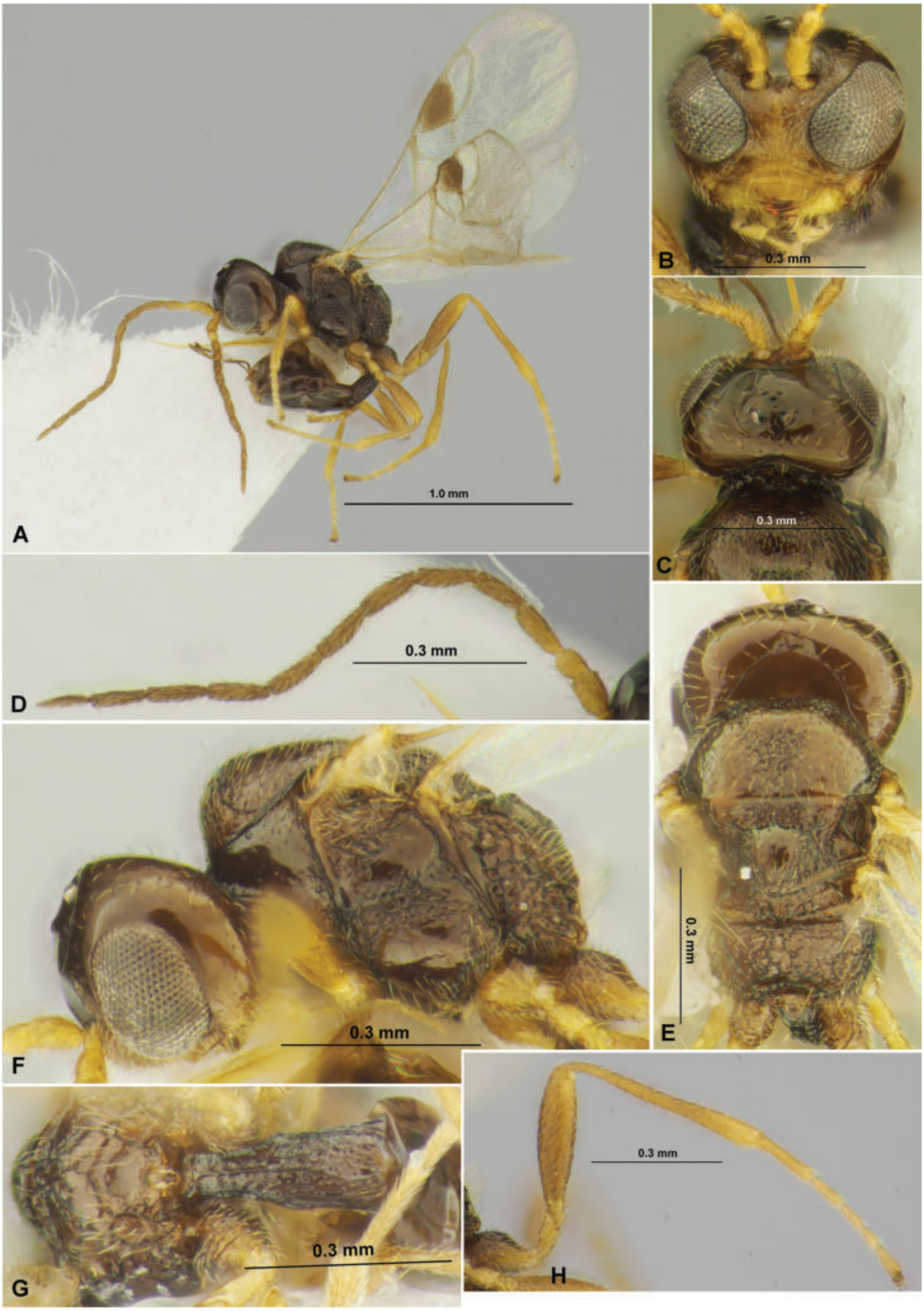

Figure 7. *Cryptoxilos* (*Cryptoxiloides*) *ulleungus* sp. nov. (female, holotype **A, C–H**; paratype **B**) **A** habitus, lateral view **B** head, front view **C** head, dorsal view **D** antenna, lateral view **E** mesosoma, dorsal view **F** head and mesosoma, lateral view **G** propodeum and first tergite of metasoma, dorsal view **H** hind leg.

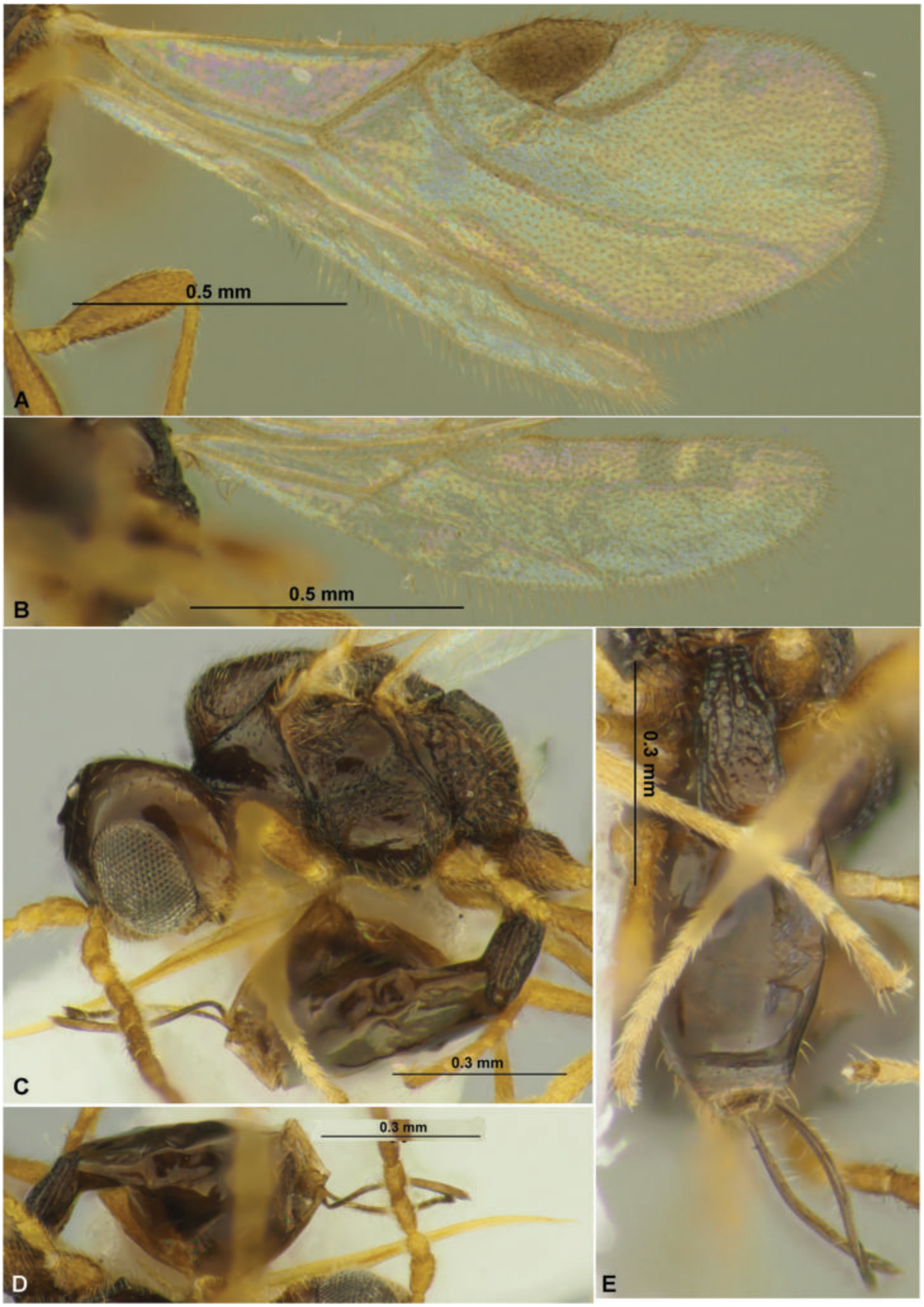

Figure 8. *Cryptoxilos* (*Cryptoxiloides*) *ulleungus* sp. nov. (female, holotype) **A** wings **B** hind wing **C** body, lateral view **D** metasoma, lateral view **E** metasoma, dorsal view.

space 0.4 times basal width of mandible. Mandible relatively slender, distinctly twisted in apical half. Length of maxillary palp 0.8 times height of head; maxillary palp with 5 segments, third, fourth and fifth segments almost same length.

Antenna**:** Antenna 12-segmented, weakly thickened, weakly setiform, 0.7 times as long as body. Scape 1.4–1.5 times longer than wide, 1.3–1.5 times longer than pedicel. First flagellar segment 2.4–2.7 times longer than its maximum width, approximately as long as second segment and wider than it. Length of second flagellar segment 2.8–3.2 times its width. Penultimate segment 3.6–3.7 times longer than wide, almost as long as first and apical segments; apical segment slender and acuminated.

Mesosoma**:** Length of mesosoma 1.6 times its height. Mesoscutum transverse, weakly protruding anteriorly, 0.6 times as long as maximum width. Notauli distinct, complete, shallow, crenulate-rugulose. Prescutellar suture relatively wide, with six carinae and with dense and fine rugosity between carinae. Scutellum slightly convex, rugose laterally and posteriorly. Precoxal sulcus distinct, wide, long, weakly evenly curved or almost straight, posteriorly fused with mesopleural suture, entirely widely crenulate-rugose. Propodeum postero-medially weakly and widely concave.

Wings**:** Fore wing 2.6 times longer than wide. Pterostigma wide, 2.0–2.4 times longer than maximum width. Metacarp (1-R1) 0.5 times length of pterostigma. Radial vein (r) arising from middle of pterostigma. First radial abscissa (r) present but very short, first radiomedial vein (2-SR) arising from radial vein (r) closely to pterostigma. First radiomedial vein (2-SR) strongly desclerotised and mainly discolored, incomplete and visible in anterior half only. First abscissa of medial vein (1-SR+M) mainly discolored and curved. Mediocubital vein (M+CU1) sclerotized but distinctly discolored, strongly curved. Nervulus (cu-a) discolored, distinctly postfurcal. Recurrent (m-cu), cubital (1-CU1, 2-CU1, 3-CU1), parallel (CU1a) and second abscissa of longitudinal anal (2-1A) veins absent or strongly desclerotised. Hind wing 4.0–4.3 times longer than wide, its hind margin with long and dense setae. Second abscissa of costal vein (1-SC+R) practically absent. Radial vein (SR) discolored, distinctly curved basally; radial (marginal) cell narrowed distally.

Legs**:** Hind femur elongate-oval, 3.5–3.7 times longer than its maximum width. Hind tibia rather distinctly widened posteriorly. Hind tarsus almost as long as hind tibia. Basitarsus of hind leg 0.5–0.6 times as long as second to fifth segments combined; second segment 0.5–0.6 times as long as basitarsus, 0.9–1.0 times as long as fifth segment (without pretarsus).

Metasoma**:** First tergite of metasoma weakly widened distally, its ventral margins not connected below and with distinct gape, 2.3 times longer than its apical width, almost 2.0 times longer than propodeum; maximum apical width 2.0–2.3 times its minimum subbasal width; its spiracular tubercles weakly or distinctly protruding and situated submedially, dorsope and laterope absent. Suture between second and third tergites absent medially on wide distance, shortly present laterally. Combined second and third tergites large, almost complete or mostly covered all posterior tergites; medial length of these tergites 1.8–1.9 times basal width of second tergite, 1.3 times their maximum width. Ovipositor weakly curved in posterior half, compressed, distinctly narrowed towards apex. Ovipositor sheath relatively long, covered by sparse, long and almost erect setae, 0.45–0.50 times as long as metasoma, 0.6 times as long as mesosoma, 0.25 times as long as fore wing.

***Sculpture and pubescence*:** Temple, vertex and frons smooth, face finely and rather densely punctate. Side of pronotum almost smooth in upper half, remainder distinctly rugose. Mesoscutum densely punctate-granulate anteriorly on vertical surface, mainly smooth on horizontal surface, with wide and dense rugosity in subtriangular medio-posterior area. Scutellum widely smooth. Mesopleuron smooth in large oval upper area below rugose subalar depression and large area below precoxal sulcus. Propodeum entirely rugose-reticulate, sculpture weak in basolateral 1/3. Hind coxa dorsally distinctly coarsely rugose with transverse curved striation; hind femur smooth. First metasomal tergite longitudinally striate, with dense and coarse rugosity between striae; following tergites smooth and glabrous. Vertex almost entirely covered by rather dense, semi-erect pale setae directed in sides, usually glabrous medio-posteriorly. Mesoscutum entirely with dense, semi-erect pale setae. Fore wing entirely densely setose.

***Colour*:** Body dark brown to black, face, clypeus, lower and lateral parts of head dark reddish brown. Palpi and ovipositor yellow. Antenna mainly brown to dark brown, basal three–four segments paler, reddish brown or brownish yellow. Fore and middle coxae yellowish brown, hind coxa dark reddish brown; all femora reddish brown or partly dark reddish brown and paler distally; tibiae and tarsi yellowish brown or pale brown. Wing membrane hyaline with dense dark setae; pterostigma brown or dark brown with short pale basal and apical areas; veins pale brown to nebulose. Ovipositor sheaths dark brown to black.

Male. Unknown.

Comparative diagnosis. This new species is similar to the Chinese *Cryptoxilos* (*Cryptoxiloides*) *pallipes* Chen, He, van Achterberg & Ma, 2001 (Chen et al. 2001), but differs from it by having the eye in dorsal view 1.3–1.4 times longer than the temple (1.8 times in *C. pallipes*), POL 1.4–1.6 times OD (equal to OD in *C. pallipes*), clypeus width 3.8 times its maximum height with its ventral margin weakly concave (only 2.8 times and with its ventral margin straight in *C. pallipes*), first flagellar segment 2.4–2.7 times longer than its maximum width and approximately as long as the second segment (4.0 times longer than its maximum width and 1.2 times longer than second segment in *C. pallipes*), prescutellar suture with dense rugosity between carinae (without rugosity in *C. pallipes*), first radial abscissa (r) of the fore wing present but very short and the first radiomedial vein (2-SR) arising from radial vein (r) very close to the pterostigma (first radial abscissa (r) not developed and the first radiomedial vein (2-SR) arising from pterostigma in *C. pallipes*), first metasomal tergite 2.3 times longer than its apical width (1.8 times in *C. pallipes*), and ovipositor weakly curved in posterior half (straight in *C. pallipes*).

Etymology. This species is named after its type locality, the Ulleung Island in the East Sea.

A key to known species of *Cryptoxilos* (*Cryptoxiloides*)

(Updated after Chen et al. 2001)

1 Face of female strongly narrowed submedially and with minimum distance between eyes less than distance between outer margins of antennal sockets. Metacarp (1-R1) of fore wing approximately as long as pterostigma. Shape of last abscissa of radial vein (SRI) of fore wing variable, often partly straight. New World, Australasia, Oceania .... **Subgenus *Cryptoxilos* Viereck, 1911 (type species: *C. dichromorphus* Viereck, 1911)**

– Face of female moderately narrowed submedially, and with minimum distance between eyes approximately equal to distance between outer margins of antennal sockets (Fig. 7B). Metacarp (1-R1) of fore wing 0.3–0.5 times length of pterostigma (Fig. 8A). Shape of last abscissa of radial vein (SRI) of fore wing distinctly evenly curved (Fig. 8A). Old World. (Subgenus *Cryptoxiloides* Čapek & Capecki, 1979) **2**

2 Anterior tentorial pits enlarged and oval. Mesoscutum without rugose subtriangular medio-posterior area. Mesopleuron largely smooth above and below precoxal sulcus. First radiomedial vein (2-SR) of fore wing far separated from base of radial vein (RS). Radial (RS) vein of hind wing less curved basally. Body length 1.7 mm. West Palaearctic (Poland) .... ***C.*(*C.*) *cracoviensis* (Čapek & Capecki, 1979)**

– Anterior tentorial pits normal and round (Fig. 7B. Mesoscutum with wide and densely rugose subtriangular medio-posterior area (Fig. 7E). Mesopleuron largely sculptured with narrow smooth areas above and below precoxal sulcus (Fig. 7F). First radiomedial vein (2-SR) of fore wing situated closely to base of radial vein (RS) or arising from developed first radial abscissa (r) (Fig. 8A). Radial (RS) vein of hind wing distinctly curved basally (Fig. 8B) **3**

3 Eye in dorsal view 1.8 times longer than temple. POL equal to OD. Width of clypeus 2.8 times its maximum height and its ventral margin straight. First flagellar segment 4.0 times longer than its maximum width, 1.2 times longer than second segment. First abscissa of radial vein (r) of fore wing not developed, first radiomedial vein (2-SR) arising from pterostigma. First metasomal tergite 1.8 times longer than its apical width. Body length 2.1 mm. East Palaearctic (China) .... ***C.*(*C.*) *pallipes* Chen, He, van Achterberg & Ma, 2001**

– Eye in dorsal view 1.3–1.4 times longer than temple (Fig. 7C). POL 1.4–1.6 times OD (Fig. 7C). Width of clypeus 3.8 times its maximum height, its ventral margin weakly concave (Fig. 7B). First flagellar segment 2.4–2.7 times longer than its maximum width, approximately as long as second segment (Fig. 7D). First abscissa of radial vein (r) of fore wing developed but short, first radiomedial vein (2-SR) arising from radial vein (r) closely to pterostigma (Fig. 8A). First metasomal tergite 2.3 times longer than its apical width (Fig. 7D). Body length 1.6–1.8 mm. East Palaearctic (Korea)....................... ***C.*(*C.*) *ulleungus* sp. nov.**

Discussion

The cosmopolitan subfamily Euphorinae is one of the most morphologically diverse groups of koinobiont braconid parasitoids, which have a wide range of the host taxa and host developmental stages used for infestation (Tobias 1965, 1966; Shaw 1985; Stigenberg et al. 2015; Yu et al. 2016). The most recent molecular phylogenetic study this subfamily (Stigenberg et al. 2015) recognized 14 tribes in the Euphorinae, though the placement of the genera *Asiacentistes* Belokobylskij, 1995 and *Tainiterma* van Achterberg & Shaw, 2001 within this subfamily was not supported.

Despite the number of publications regarding the Euphorinae parasitoids of the Korean Peninsula (Papp 1990, 1992, 1994, 2003; Belokobylskij and Ku 1998a, 1998b; Belokobylskij 2000a, 2000b; Ku et al. 2001, 2020, An et al. 2014, 2015a, 2015b; Lee et al. 2016, 2018), the knowledge of the fauna of this group is incomplete and new euphorine records together with descriptions of the species new for science continue increasing regularly. Currently, the following tribes and genera were already recorded in the fauna of Korean Peninsula: Centistini (*Allurus* Foerster, 1863, *Asiacentistes* Belokobylskij, 1995 and *Centistes* Haliday, 1835); Cosmophorini (*Cosmophorus* Ratzeburg, 1848 and *Cryptoxilos* Viereck, 1911); Dinocampini (*Dinocampus* Foerster, 1863); Euphorini (*Euphorus* Nees, 1834, *Leiophron* Nees, 1819, *Mama* Belokobylskij, 2000 and *Peristenus* Foerster, 1863); Helorimorphini (*Aridelus* Marshall, 1887, *Chrysopophthorus* Goidanich, 1948 and *Wesmaelia* Foerster, 1863); Meteorini (*Meteorus* Haliday, 1835 and *Zele* Curtis, 1832); Myiocephalini (*Myiocephalus* Marshall, 1898); Neoneurini (*Neoneurus* Haliday, 1838); Perilitini (*Microctonus* Wesmael, 1835, *Orionis* Shaw, 1987, *Perilitus* Nees, 1819, *Rilipertus* Haeselbarth, 1996 and *Spathicopis* van Achterberg, 1977); Pygostolini (*Pygostolus* Haliday, 1833), Syntretini (*Syntretus* Foerster,1863), and Townesilitini (*Marshiella* Shaw, 1985, *Streblocera* Westwood, 1833 and *Townesilitus* Haeselbarth & Loan, 1983). On the other hand, some additional euphorine genera previously recorded in the faunas of the Russian Far East, Japan and China also could be found in the fauna of this peninsula, namely *Ropalophorus* Curtis, 1837 (Cosmophorini), *Centistina* Enderlein, 1912 (Dinocampini), *Holdawayella* Loan, 1967 (Helorimorphini), *Elasmosoma* Ruthe, 1858 (Neoneurini) and *Proclithrophorus* Tobias & Belokobylskij, 1981 (Townesilitini).

The current generic composition of the euphorine tribe Cosmophorini is very polymorphic and does not have the combined morphological criteria (diagnostic features) for tribe characteristic and delimitation. Currently, only molecular data (Stigenberg et al. 2015) has allowed union of the following genera, *Cosmophorus*, *Cryptoxilos*, *Plynops*, *Ropalophorus* and *Tuberidelus*, inside this morphologically diverse taxonomic group.

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Melipona beecheii (Hymenoptera, Apidae) foragers deposit a chemical mark on food to attract conspecifics

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Abstract

Stingless bees have a sophisticated system of chemical communication that helps conspecifics find food sources. In this study, we investigated whether *Melipona beecheii* foragers deposit a chemical mark on food to recruit conspecifics. Our results showed that foragers preferred to visit the feeders visited previously by conspecifics over clean feeders. We also found that foragers preferred visiting feeders baited with labial gland extracts over those baited with mandibular extracts or hexane. Labial gland extracts elicited higher forager antennal responses compared with those evoked by the mandibular gland extracts or hexane. Labial gland extracts and extracts from feeders visited by foragers contain a mixture of unsaturated hydrocarbons, followed by straight chain hydrocarbons and small quantities of esters. The main component is a mixture of alkene isomers C27:1.

Keywords

CG-MS, cuticular hydrocarbons, labial gland, stingless bees

Introduction

Eusocial bees, such as *Apis mellifera* and stingless bees, use communication mechanisms such as vision, smell for food search and mechanical signals (Dyer 2002; Nieh 2004; Barth et al. 2008; Dyer et al. 2016). These mechanisms are species-specific and make social bees highly efficient in locating and exploiting food resources. For example, several bee species can recognize whether the flower resources have been exhausted and if so, reduce their searching time (Stout and Goulson 2001).

A typical method of communication happens when stingless bee foraging workers arrive at their nest with food; then they release chemical signals to stimulate other workers to go out to the field in search of food sources (Nieh 2004). *Trigona* and *Scaptotrigona* species display another form of communication. Here, foragers use chemicals from the labial glands as a tracking pheromone to mark the paths to food sources (Jarau et al. 2004a, 2006; Schorkopf et al. 2007; Hemmeter 2008; Stangler et al. 2009; Jarau et al. 2011). When marking the paths, the bee extends its proboscis and rubs it against the substrate to deposit the chemical trail produced by the labial glands (Jarau et al. 2004a). In contrast, *Melipona* foragers do not lay out chemical paths to recruit conspecifics to the food site (Hrncir et al. 2004); they deposit chemical marks on the food source to attract conspecifics (Jarau et al. 2004b). However, the source of these marks is unclear and is occasionally controversial. For instance, *Melipona favosa* foragers deposit anal excretions on food sources (Aguilar and Sommeijer 2001), while *Melipona panamica* and *Melipona scutellaris* foragers deposit chemical marks that influence the conspecifics orientation toward a food source. Notwithstanding the precise source is known, the chemical identity of these signals has been reported only in a few species (Nieh 1998; Hrncir et al. 2004; Jarau et al. 2004b; Roselino et al. 2016), such as, *Melipona solani* which foragers leave a mixture of hydrocarbons from their cuticle and methyl oleate from the labial gland as an odor mark on the food source (Alavez-Rosas et al. 2017). However, it is not known if this communication mechanism occurs in other *Melipona* species. Consequently, we investigated whether *Melipona beecheii* foragers deposit marks on food to attract their conspecifics. Our hypothesis is that *M. beecheii* foragers deposit chemical marks on food to attract their conspecifics. *M. beecheii* is one of the stingless bees species with high ecological, economical, and cultural importance in Mexico. Particularly, *M. beecheii* stingless bees are highly valuable in meliponiculture and crop pollination in Mexico. In spite of this, little is known of its chemical ecology (Ayala et al. 2013).

Materials and methods

Biological material

We used five *M. beecheii* (Hymenoptera, Apidae, Meliponini) colonies obtained from a meliponary in Tuxtla Chico (14°56'25"N, 92°10'08"W), Chiapas, Mexico. The experiments were conducted from April to October 2021 at El Colegio de la Frontera

Sur gardens, Tapachula (14°54'39.86"N, 92°15'51.55"W), Chiapas, Mexico. Annual rainfall in this region is approximately 3843 mm, with September as the wettest month and February as the driest month. The temperature normally ranges between 29 °C and 35 °C. The colonies were free of fungi and parasites.

Training

The forager bees were trained to collect a solution of 3 M sucrose *ad libitum* from an artificial feeder, consisting of a Petri dish (100 × 10 mm) containing a small cotton ball drenched in the sucrose solution in the center. The feeder was placed 5 m from the beehives. The training was conducted between 08:00 and 13:00 h.

Collection of chemical marks

We extracted the compounds deposited by *M. beecheii* foragers on a glass feeder (100 × 10 mm) (Hrncir et al. 2004) by washing the feeders with 4 mL hexane (HPLC grade, Aldrich, Toluca, Mexico). The amount of compounds left by 40 or 50 foragers on the food source was considered as a biological active mark. The hexane extracts were concentrated to 50 µL using a gentle flow of N_2 and stored at -20 °C until their analysis. Five different extracts were obtained.

Gland extracts

To prepare the gland extracts, we captured foragers bees that arrived at the feeder during training. Bees were frozen at -20 °C before dissection and analysis. The glands of the foragers were carefully dissected in distilled water with two pairs of fine tweezers under a stereoscopic microscope. The gland extracts were prepared by carefully dissecting the labial and mandibular glands of 10 foragers in 1000 µL of solution. So, 100 µL of the prepared solution is the amount corresponding to 1 labial gland equivalent (LGE), 50 µL of solution corresponds to 0.5 LGE and 10 µL to 0.1 LGE; and 100 µL of the prepared solution is the amount corresponding to 1 mandibular gland equivalent (MGE), 50 µL of solution corresponds to 0.5 MGE and 10 µL to 0.1 MGE. Five gland extracts were prepared.

Behavioral bioassays

In a first experiment, we evaluated whether the forager bees leave odor marks on the feeders in a two-choice tests. We offered to foragers two feeders: one with chemical marks (previously visited by foragers) and the other clean (not visited by foragers). The feeders were placed at the site where the bees were trained. Feeders were placed 30 cm from each other. We placed a few drops of the 3M sucrose solution in the entrance to stimulate the visits. We recorded the number of bees that visited the marked feeder and the clean feeder. A visit was counted when the bee landed and extended its proboscis to feed. All bees were marked with a fine brush with acrylic paint not toxic and captured on their first visit to avoid counting the same bee more than once (Alavez-Rosas et al. 2017). To prevent the phenomenon of social facilitation (influence in the bee election due to the presence of a conspecific at the feeding site), care was taken not to count the bees that visited the feeders while other bees were there. The position of the feeders was interchanged every 5 min to prevent position bias. At the end of the trial, the bees were freed near the colony. All trials were conducted between 08:00 and 13:00 h. In a total, 10 replications were performed.

In a second experiment, we assessed the effect of the labial gland extracts on food searching in two choice tests. Here, using pieces of 1cm^2 filter paper placed on feeders, one feeder was sprinkled with 10 μL of labial gland extract at the beginning of the experiment and the other feeder was sprinkled with 10 μL of hexane as a control. The gland extracts were evaluated at 0.1, 0.5, and 1 LGE. In total, 10 replications were performed for each gland equivalent extract.

In a third experiment, we evaluated foragers preference for labial gland extract, mandibular gland extract, or solvent in three-choice tests. Three feeders were placed in the training site: control (hexane), labial gland extract, and mandibular gland extract. The feeders were placed 20 cm from each other. Care was taken not to count bees that visited the feeder while other bees were there to avoid the phenomenon of social facilitation. The position of the feeders was interchanged every 5 min to avoid position bias. The gland extracts were evaluated at 0.1, 0.5, and 1 LGE or MGE. In total, 10 replications were performed for each gland equivalent extract.

Electroantennography (EAG)

We collected forager bees from three established colonies, bees were frozen for one minute to numb them before dissection, subsequently their antennae were carefully removed. The base of the antenna was inserted into the tip of the glass capillary logging electrode. The signals generated by the antenna passed through a high impedance amplifier (NL 1200; Syntech, GmbH) and visualized with the software Syntech to process the EAG signals. We used a stimulus Flow controller (CS-05, Syntech) to generate stimuli at intervals of one minute. A constant current of pure humidified air (0.7 L min^{-1}) was directed toward the antenna (Malo et al. 2004).

The experimental procedure consisted of depositing the treatment (1 LGE extract, 1 MGE extracts or solvent, in this order) onto 1.5 × 1.5 mm pieces of filter paper (Whatman no. 1, Whatman, Maidstone, England) exposed to air for 20 s to allow the solvent to evaporate, inserted into a glass Pasteur pipette, and left for 40 s before applying. The application of the stimulus consisted of inserting the tip of the pipette that contained the piece of filter paper in a hole at the end of the glass tube through which the current of air blew continuously on the antenna. The waiting time between one stimulus and the next was one minute. The treatment was carried from the filter paper to the antenna on the controlled air current (0.5 L/min). The duration of the stimulus was 1 s. The continuous flow of pure air was maintained through the tube to assure that the odors were removed immediately. We used one antenna of the bee per treatment, and at least thirty five bees were used.

Chemical analysis

Extracts were analyzed in a gas chromatograph (Shimadzu GC-2010 Plus) coupled with a quadrupole mass spectrometer (Shimadzu, TQ8040), using a capillary column of non-polar silica SPB-1 (30 m long × 0.25 mm interior diameter) (Supelco, Toluca, Mexico). The initial temperature was 50 °C (held for 2 min), increased 15 °C/min up to 280 °C (held 10 min). Helium was the carrier gas and the injector temperature was 250 °C. Ionization was achieved by electron impact at 70 eV. The compounds were identified by comparison with those registered in the NIST 2014 library (software GCMS-solution), the retention index, the mass spectra, and retention times of available synthetic standards. The relative percentage of the components was calculated from the sum of the recorded peaks.

Bioassay with synthetic compounds

We evaluated the mixture of synthetic compounds with some compounds identified in the labial gland secretion. The synthetic blend evaluated was prepared in accord with the natural proportions of the *M. beecheii* labial gland using hexane as solvent. The compounds evaluated were heneicosane (100 ng), tricosane (100 ng), and pentacosane (25 ng). These compounds were chosen as they were available in supplies. Unfortunately, C27:1 isomers the main components in the labial gland secretion were not commercially available. We recorded the number of bees that visited a feeder baited with the synthetic blend, or a feeder with solvent. The feeders were placed where the bees were trained to visit. The distance between the feeders was 30 cm. The position of the feeders was changed every 5 min to avoid position bias. In total, 10 replications were performed in this experiment.

Statistical analysis

All data were analyzed using R software (R Core Team 2020). The EAG data were natural logarithm transformed and analyzed by a one-way analysis of variance (ANOVA), followed by a Tukey test. Behavioral data were transformed to satisfy the assumptions of normality and homoscedasticity and analyzed by generalized linear model (GLM) to the Poisson or negative binomial models.

Results

Behavioral bioassays

M. beecheii foragers preferred the feeders visited previously by their conspecifics over the clean feeder ($\chi 2$ = 56.783, df = 1, p < 0.001) (Fig. 1).

In the two-choice bioassays, foragers preferred to visit the feeders marked with extracts of 0.5 LGE ($\chi 2$ = 134.38, df = 1, p < 0.001) and 1 LGE ($\chi 2$ = 71.676, df = 1,

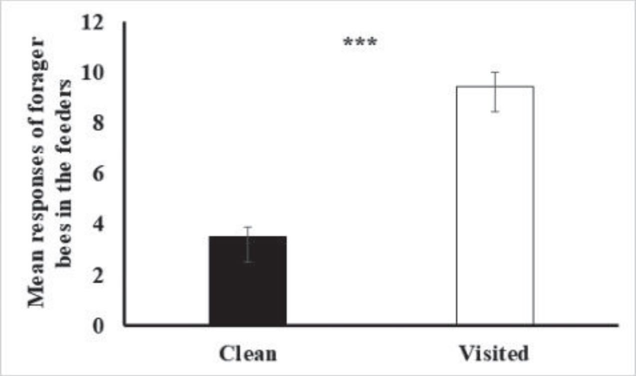

Figure 1. Mean (± SEM) responses of *M. beecheii* foragers to marked and clean feeders (*** P< 0.001). Ten replications were performed.

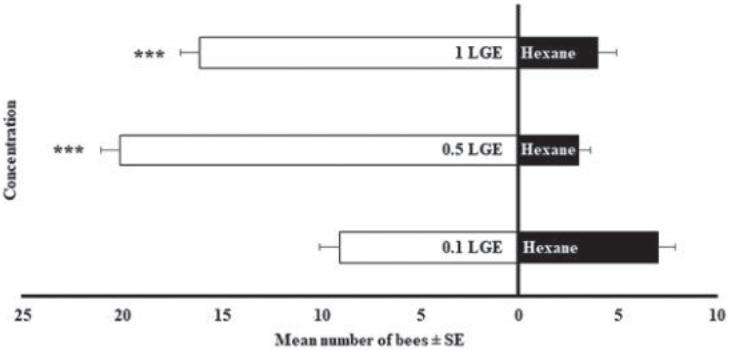

Figure 2. Mean (± SEM) responses of foraging *M. beecheii* worker bees to labial gland extract from conspecific worker bees at different concentrations (LGE=labial gland equivalent, *** P< 0.001, ** P<0.01, * P< 0.05). Ten replications were carried out for each gland equivalent extract.

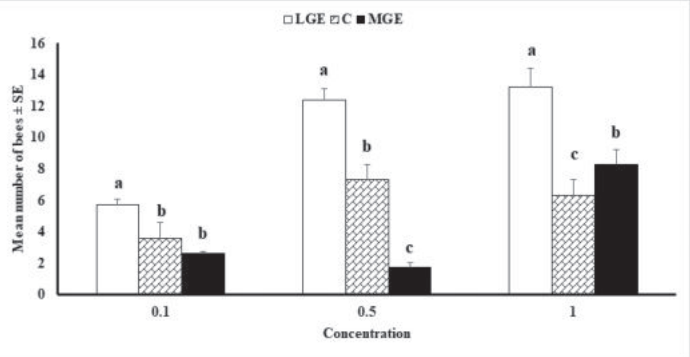

Figure 3. Mean (± SEM) responses of *M. beecheii* foragers to labial gland and mandibular gland extracts at different concentrations. Different small letters ($P<0.05$) indicate significant differences between treatments. Ten replications were performed for each gland equivalent extract. LGE=labial gland equivalent, MGE=mandibular gland equivalent, C=control.

$p < 0.001$) over those treated with hexane. However, they did not show a preference for the 0.1 LGE or the control ($\chi2 = 0.53236$, df = 1, $p = 0.4656$) (Fig. 2).

In the three-choice bioassays, more foragers preferred visiting feeders with labial gland extracts (0.1 LGE: $\chi2= 13.335$, df = 2, $p<0.01$; 0.5 LGE: $\chi2= 81.747$, df = 2, $p < 0.001$; 1 LGE: $\chi2 = 23.929$, df = 2, $p < 0.001$) over other feeders with mandibular extracts or the control (Fig. 3).

Electroantennography

Analysis of EAG data revealed significant differences in the antennal response of forager bees to the different extracts evaluated and to the solvent (control) ($F = 13.24$, df = 2, $P > 0.001$). The antennal responses of the foragers was greater with 1 eq/µL of labial gland extract than with the mandibular gland extract or with the control (Fig. 4).

Chemical analysis

Chemical analysis showed that the labial gland extracts and extracts from feeders visited by foragers contain a mixture of unsaturated hydrocarbons, followed by straight chain hydrocarbons and small quantities of esters. The main components are a mixture of alkene isomers C27:1 (Table 1).

The chromatographic profile of the hexane feeder wash was similar to the labial gland extract profile, but different from that of the mandibular gland extract (Fig. 5).

Bioassay with synthetic compounds

Foragers did not show a preference for the feeders treated with a three-component blend and those treated with hexane.

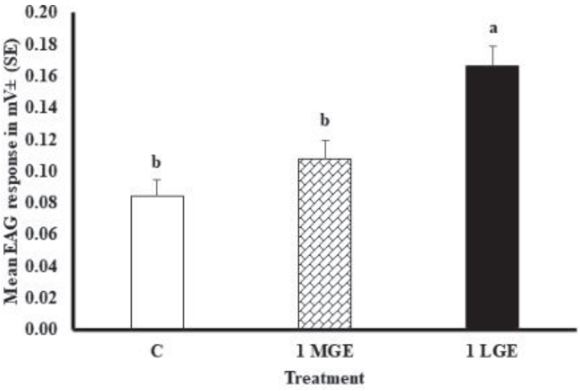

Figure 4. Electroantennographic (EAG) response in mV of *M. beecheii* forager bee antennae to labial gland extract, mandibular gland extract and the control (C). Different small letters ($P<0.05$) indicate significant differences between treatments. N=35. LGE=labial gland equivalent, MGE=mandibular gland equivalent, C=control.

Table 1. Average value (%) ± standard error of the proportion of the compounds found in the labial glands of *M. beecheii* forager bees. N=Five gland extracts.

Peak	RT	RI	Compound	Proportion in labial gland	Proportion on feeder
1	13.53	1778.50	Alcohol	2.07±0.40	ND
2	15.57	2100.00	Heneicosane (C21)*	0.26±0.15	ND
3	15.85	2124.75	Methyl stearate *	0.4±0.07	ND
4	15.97	2143.48	Geranyl palmitate **	2.79±0.48	ND
5	16.11	2166.93	2,3-Dihydro farnesyl hexanoate**	1.89±0.31	ND
6	16.25	2189.90	Unknown 1	1.28±0.22	ND
7	16.33	2202.45	Farnesyl butanoate**	1.88±0.30	ND
8	16.74	2274.56	Alkene C23:1 (1)	0.63±0.26	0.81±0.47
9	16.78	2281.22	Alkene C23:1 (2)	0.61±0.18	0.12±0.07
10	16.88	2300.00	Tricosane (C23)*	0.26±0.07	0.30±0.18
11	17.90	2474.00	Alkene C25:1 (1)	7.09±0.60	0.74±0.42
12	17.94	2481.16	Alkene C25:1 (2)	2.17±0.20	0.19±0.11
13	18.04	2500.00	Pentacosane (C25)*	0.6±0.05	0.24±0.14
14	18.20	2570.25	Unknown 2	3.37±0.75	ND
15	19.29	2672.08	Alkene C27:1 (1)	8.33±0.87	1.21±0.70
16	19.33	2684.35	Alkene C27:1 (2)	8.05±0.81	1.38±0.80
17	19.39	2698.00	Alkene C27:1 (3)	11.2±1.10	1.37±0.79
18	19.51	2700.00	Heptacosane (C27)*	2.89±0.27	5.52±3.19
19	21.07	2853.12	Alkene C29:1 (1)	3.95±0.34	ND
20	21.14	2875.78	Alkene C29:1 (2)	1.92±0.17	0.61±0.35
21	21.34	2883.39	Alkene C29:1 (3)	5.52±0.58	3.02±1.74
22	21.43	2897.22	Alkene C29:1 (4)	7.93±0.96	1.06±0.61
23	21.58	2900.00	Nonacosane (C29)*	1.23±0.14	1.21±0.70
24	23.86	3065.26	Unknown 3	2.81±2.13	ND
25	24.05	3076.78	Alkene C31:1 (1)	0.95±1.76	0.08±0.5
26	24.19	3089.48	Alkene C31:1 (2)	1.01±0.12	0.60±0.35
27	24.35	3096.23	Alkene C31:1 (3)	1.92±0.21	1.14±0.66

ND = Not detected; * = Confirmed with synthetics; ** = Compared with the NIST library; RT = retention time; RI = retention index; Number in parenthesis = number of isomer.

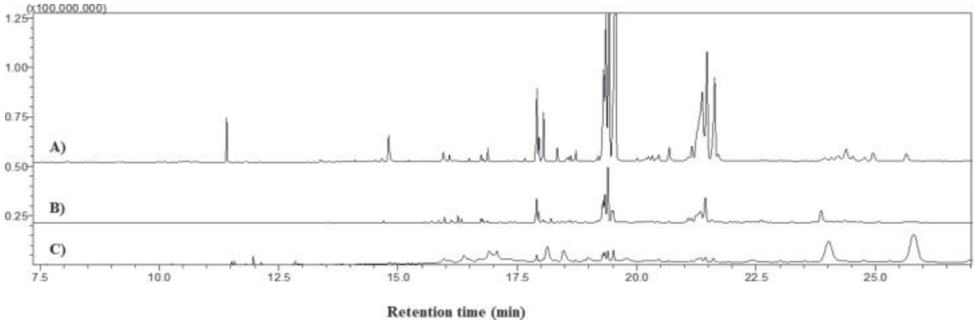

Figure 5. Chromatographic analysis of the extracts from *M. beecheii* **A** hexane wash of the Petri dish feeder **B** hexane extract of the labial gland **C** hexane extract of the mandibular gland.

Discussion

In this study, we demonstrated that *M. beecheii* foragers preferred to visit feeders that had been previously visited by their conspecifics over a clean feeder. This behavior has been observed in several species of the genus *Melipona*, such as *M. favosa* (Aguilar and Sommeijer 2001), *Melipona mandacaia* (Nieh et al. 2003), *Melipona seminigra* (Jarau et al. 2004b; Jarau et al. 2005), *M. panamica*, *M. scutellaris* (Nieh 1998; Roselino et al. 2016), and *M. solani* (Alavez-Rosas et al. 2017). Therefore, the main mechanism that stingless bees of the genus *Melipona* use is leaving chemical markers to guide their conspecifics to food sources, which could be considered as a clear proof that the chemicals are not signals with a specific meaning for the receiver but rather cues that have to be learned according to context specific meanings (Barth et al. 2008; Roselino et al. 2016). For example, it is known that *M. favosa* foragers constantly deposit anal excretions on food sources (Aguilar and Sommeijer 2001), while *M. mandacaia* foragers deposit anal droplets and a ventro-abdominal odor, an event not previously described (Nieh et al. 2003). *M. seminigra* foragers deposit a pheromone secreted by their claw retractor tendons on food sources (Jarau et al. 2004b; Jarau et al. 2005). *M. panamica* and *M. scutellaris* deposit and associate olfactory marks that influence the orientation of conspecifics to a source food (Nieh 1998; Roselino et al. 2016), and *M. solani* uses the secretion of its labial gland (Alavez-Rosas et al. 2017). Through behavioral experiments, we showed that *M. beecheii* foragers prefer to visit feeders that contain extracts of labial gland secretion and, moreover, exhibited antennal responses to these extracts. By washing the food container, we also demonstrated that foragers, indeed, deposit the labial gland secretion on food. The chemical composition of the extracts from the hexane wash corresponds to the chemical composition of the labial gland extract, suggesting that labial gland secretion may contribute to chemicals left behind by foraging bees at food sources. Regarding the chemical composition of the deposited marks, there is no information (Nieh 1998; Roselino et al. 2016), except for *M. solani*, whose foragers deposit a mixture of hydrocarbons and methyl oleate (Alavez-Rosas et al. 2017). In our study, we found that in the secretion from the *M. beecheii* labial gland the most abundant compounds were alkene C25:1 (1), alkene C27:1 (1), alkene C27:1 (2), alkene C27:1 (3), alkene C29:1 (4), and unknown 3. Heneicosene, methyl stearate, and tricosane are found in small amounts. The main composition of the labial gland includes hydrocarbon-type compounds; we believe that the function of this type of compounds is short-range recognition. In the field, *M. beecheii* foragers deposit their labial gland secretions to mark feeding sites and which might help to promote visits by their conspecifics; the presence of these compounds likely indicates to the bees that it is a food-rich resource, while flower volatiles attract the bees to the food source.

Interestingly, during the analysis of the labial gland extracts (data no shown) we found a group of samples with the same composition but in different proportions. According to the literature, *M. beecheii* bees first fly at the age of 33 days, probably to orient themselves in the environment; the first foraging flight is at 40-days-old, although at 20 days of age, a constant proportion of bees leave the hive to feed (Biesmeijer and Tóth 1998; Medina-Medina et al. 2014), and thus it is concluded that age is not a factor for initiating the search for food. For this reason, we can infer that, although the profiles found here are not significant, there are foragers of different ages that search for food.

When the mandibular gland extract was evaluated, foragers behavior was more aggressive. Bee antennae responded to the labial and mandibular gland extracts similarly. The responses to the labial gland were stronger, while responses to the mandibular gland were weak, but stronger than the control. The *M. beecheii* mandibular gland possesses rose oxide isomers, which cause high levels of defense behavior, as do geraniol and farnesyl acetate that, when used at levels similar to those of the mandibular extract, cause more pronounced defense reactions than the rose oxide isomer (Cruz-López et al. 2005). These compounds were possibly detected by the worker bee antennae and induced a stronger response to the mandibular extract than to the control.

Conclusion

In sum, our results indicate that *M. beecheii* foragers prefer to visit feeders have been previously visited by their conspecifics. Labial gland secretion may contribute to chemicals left behind by foraging bees at food sources, and more sophisticated analyses are needed to come to a definite conclusion. The secretion found at feeding sites is composed of a mixture of unsaturated hydrocarbons, straight chain hydrocarbons, and small quantities of esters. The main components are a mixture of alkene C27:1 isomers. Further studies are needed to identify and synthetize if required the compounds used by *M. beecheii* foragers to recruit conspecifics toward the food resources.

Acknowledgments

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Revision of Bethylinae from Dominican amber, with description of a new genus (Hymenoptera, Bethylidae)

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Abstract

Fossil species of bethyline wasps from Dominican amber are revised. Based on a cladistic analysis of female morphological data we recognize a new genus and species, †*Crassibethylus dominicanus* **gen. et sp. nov.**, which came out as sister group of the clade *Odontepyris* + *Prosierola*. We also transfer to Bethylidae a fossil taxon originally described in Sclerogibbidae, placing †*Pterosclerogibba* Olmi as a new junior synonym under *Goniozus* Förster, in the new combination †*Goniozus antiquus* (Olmi). Additionally, the third species of Bethylinae known from Dominican amber, †*Goniozus respectus* Sorg, is diagnosed and illustrated with color images of the holotype. An identification key to the species of Bethylinae from Dominican amber is provided.

Keywords

Aculeata, aptery, Chrysidoidea, Lepidoptera, Miocene

Introduction

Bethylinae have their diversity represented by 540 species distributed into 11 genera, and recorded around all zoogeographical regions (Azevedo et al. 2018; Ramos and Azevedo 2020). Their fossil diversity is represented by 20 species distributed in seven genera, †*Cretabethylellus* Rasnitsyn, from Russia, Transbaikalia; *Eupsenella* Westwood, from Baltic, Oise French, and Rovno amber; *Goniozus* Förster, from Baltic, Rovno, Mexican and Dominican amber; *Lytopsenella* Kieffer, from Baltic and Rovno amber;

†*Nucifrangibulum* Cockx, McKellar & Perrichot, from Charentese French amber; *Prosierola* Kieffer, from Baltic amber; and *Sierola* Cameron, from Baltic, Rovno and Zhangpu amber (Azevedo et al. 2018; Brazidec and Perrichot 2022, in press).

The females of Bethylinae are idiobiont ectoparasitoids mostly of lepidopterous mature larvae. The majority of host records are based on species of *Goniozus*, and according to Hardy and Blackburn (1991) and Bentley et al. (2009) they have gregarious life histories and exhibit a subsocial behavior with maternal care and defense of the developing brood. The males of Bethylinae, as in the other bethylid wasps, emerge before their sibling females and have the capacity to inseminate all of them, the sex ratio being female biased with a low degree of variation (Khird et al. 2014).

In Bethylinae, there is a reduced sexual dimorphism, thus being easy to establish sex associations in most groups. The genera belonging to Bethylinae are recognized based on the following combination of characteristics: antenna with 10 or 11 flagellomeres; mandible thick, short, with four sharp apical teeth; clypeus extending posterad into frons, with clypeal carina strongly outcurved in profile; dorsal pronotal area with posterior margin outcurved medially; legs with tarsal claws bifid and strongly angled; forewing with first abscissa of vein Rs+M tubular, minimally as a stub; sting with posterior area of second valvifer with anterior slender projection (Azevedo et al. 2018; Barbosa et al. 2021).

The phylogenetic relationships within Bethylinae have received the attention from previous studies conducted by Sorg (1988), Polaszek and Krombein (1994), Terayama (1995), Carpenter (1999), De Ploëg and Nel (2004) and Ramos and Azevedo (2020). The latter investigation avoided some of the shortcomings of the former studies, using a broader representation both in terms of geographic distribution and morphological diversity within the subfamily. Ramos and Azevedo's (2020) results recovered three main clades: *Lytopsenella* + *Eupsenella*; *Odontepyris* + *Prosierola*; "*Goniozus*" + (*Sierola* + (*Afrobethylus* + *Bethylus*)). There is good support for the monophyly of the constituent genera in Bethylinae, except for *Goniozus*.

In the present work we revise the fauna of Bethylinae known from Dominican amber. Our starting point was an intriguing fossil inclusion that at first sight suggested a female sclerogibbid wasp due to its distinctly swollen profemora. Further study revealed that instead it represented a Bethylinae, showing many features in common with *Odontepyris* and *Prosierola*, and which is described here as new genus. During our investigations we also concluded that †*Pterosclerogibba antiqua*, a Dominican amber fossil described by Olmi (2005) in Sclerogibbidae, represents a bethyline wasp as well.

Materials and methods

Examined material

The amber piece containing the fossil inclusion that prompted this study is deposited in the Departament of Zoology, of the Universidade Federal do Paraná, Curitiba, Brazil (**DZUP**). It is from Miocene deposits from the Dominican Republic and was obtained from a dealer established in USA. Additional institutions containing

Dominican amber taxa mentioned in the text are as follows: GPCO, George Poinar's collection, Department of Entomology, Oregon State University, Corvallis, USA; SGN, Senckenberg Gesellschaft für Naturforschung, Frankfurt, Germany. Dominican amber has been estimated to be around 15–20 million years old, from the Burdigalian, in the Early Miocene (Iturralde-Vinent and MacPhee 2019).

Terminology

Morphological terminology follows mainly Huber and Sharkey (1993), including for wing venation, except for some terms taken from Lanes et al. (2020). Those related to the integument follow Harris (1979).

Identification

We used the key proposed by Azevedo et al. (2018) for genus-level identifications. The species were identified through comparison with original descriptions in Sorg (1988) and Olmi (2005), and with illustrations in Martynova et al. (2019) and Perkovsky et al. (2020).

Phylogenetic analysis

In order to establish the phylogenetic position of the bethyline taxon under investigation, we used Ramos and Azevedo's (2020) matrix for females, keeping their same selection of ingroup and outgroup taxa (see Suppl. material 1). The two additional bethyline taxa treated here were not included in the analysis because we were not able to directly examine them.

The tree searches followed all parameters used by Ramos and Azevedo (2020). For choice of concavity value (*K*) we used the TNT script setk.run, proposed by Salvador Arias (Instituto Miguel Lillo, Argentina). Tree visualization and character optimization were carried out in Winclada 1:00:08 (Nixon 2002).

Specimen illustrations

The specimen images were obtained by a LEICA DFC295 digital camera, and the stacking was carried using the software Zerene Stacker. The figures were prepared in GIMP (2.10.18). The images of the type specimen of †*Goniozus respectus* Sorg were provided by the depositary institution.

Results

Phylogenetic relationships

The implied weighting analysis, under K=13.3, resulted in six most parsimonious trees, whose strict consensus is shown in Fig. 1 (complete tree with all taxa shown as Suppl. material 2). The monophyly of the subfamily Bethylinae, as well as all

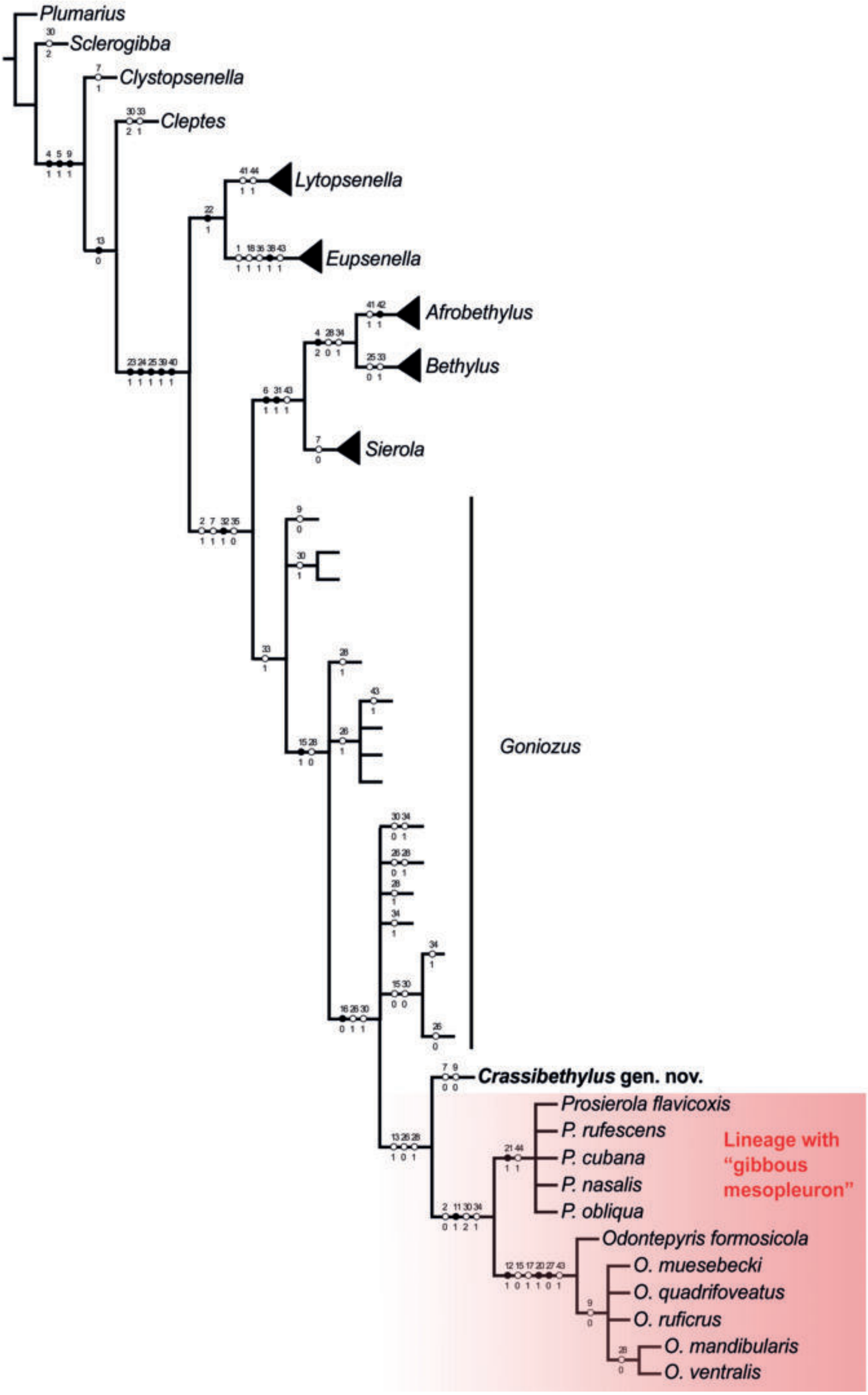

Figure 1. Simplified cladogram of the relationships within the bethylid subfamily Bethylinae; strict consensus of six most parsimonious trees under implied weighting. Original data matrix from Ramos and Azevedo (2020), for species represented by female specimens. See text for further details.

clades retrieved by Ramos and Azevedo (2020), were also recovered here. Additionally, the fossil bethyline under investigation came out as sister-group of the clade *Prosierola* + *Odontepyris*, supported by the mesoscutellar groove present as sulcus (character 13:1), ventral carina of metasomal petiole straight (26:0) and forewing vein 2Cu present (28:1). The fossil taxon was supported by two transformations: maxillary palp with four articles (7:0) and prosternum smaller than area of procoxa (9:0). Moreover, the clade *Prosierola* + *Odontepyris* was supported by four transformations: frontal unsculptured streak present (2:0), gibbous mesopleuron (11:1), forewing with vein 1Rs longer than M (30:2) and Rs+M shorter than 1Rs (34:1). *Prosierola* was supported by two transformations: propodeum with a pair of conspicuous anterior pits on the propodeal disc (21:1) and distal region of dorsal area of the tergite 9 enlarged (44:1). And *Odontepyris* was supported by six transformations: mesopleuron with a dentate process (12:1), metapostnotum not marked dorsally as a smooth triangular area (15:0), median metapostnotal carina present (17:1), propodeum with a pair of pits in basal outer portion (20:1), forewing bula absent (27:0) and proximal margin of first valvifer angled (43:1).

Although we did not code the fossil bethyline under investigation as possessing a gibbous mesopleuron, it has a considerably swollen mesopleuron, therefore reinforcing its similarity to the clade *Prosierola* + *Odontepyris*. Also, it shares with *Prosierola* the posterior margin of the pronotum slightly produced backward medially (8:1). Considering its unique position and close relationship with *Prosierola* and *Odontepyris*, we propose a new fossil genus to accommodate this Dominican amber bethyline.

Taxonomy

Order Hymenoptera Linnaeus, 1758
Superfamily Chrysidoidea Latreille, 1802
Family Bethylidae Haliday, 1839
Subfamily Bethylinae Haliday, 1839

†*Crassibethylus* gen. nov.

https://zoobank.org/4384DCD2-34B3-420A-A564-A50148001CE3
Figs 2, 3

Type species. †*Crassibethylus dominicanus* sp. nov.

Diagnosis. Maxillary palp with four articles; prosternum shorter than area of procoxa; pro- and metafemora strongly swollen, profemur lenticular-shaped, about 0.6× as wide as long; posterior margin of pronotum slightly produced backward medially; mesoscutellar groove present as a narrow sulcus; forewing vein 2Cu present; insertion of metacoxae displaced anteriorly between mesocoxal insertion; ventral carina of metasomal petiole straight.

Description. Female. ***Head.*** Head as long as wide; antenna with 11 flagellomeres; clypeus with median clypeal carina continuous with frontal carina, lateral lobe not evident; anterior margin of frons projected anteriorly. Eye large, occupying most of lateral

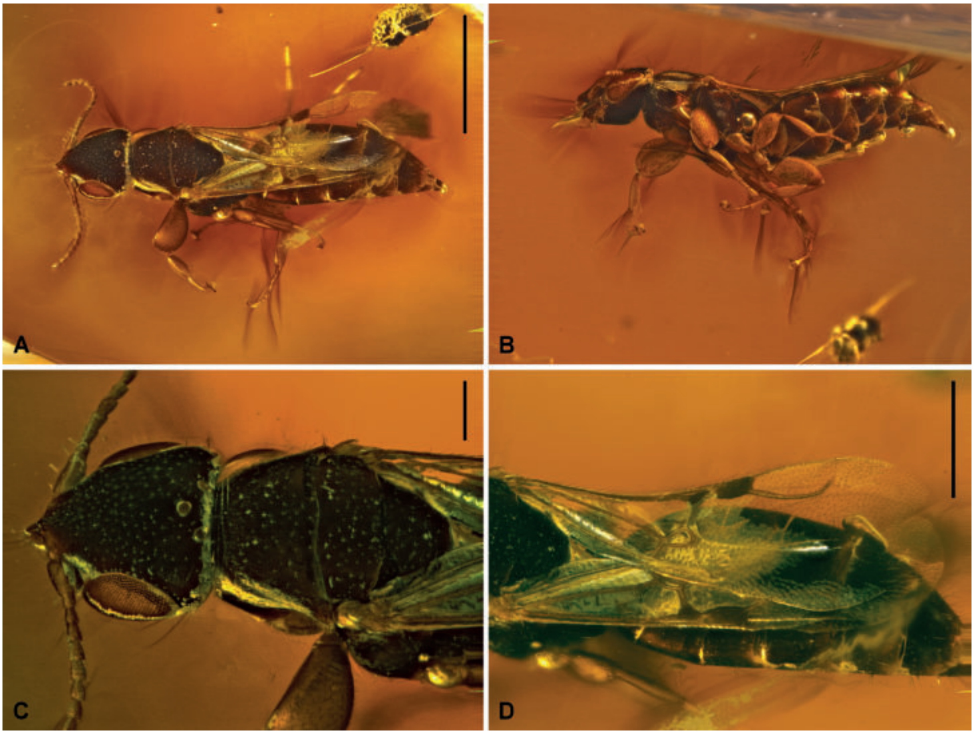

Figure 2. †*Crassibethylus dominicanus* gen. et sp. nov. Female holotype **A** dorsal habitus **B** lateral habitus **C** head and mesosoma, in dorsal view **D** wings and metasoma, in frontal view. Scale bars: 1 mm (**A**); 0.2 mm (**C**); 0.5 mm (**D**). **A, B** at same scale.

portion of head. Ocelli located close to vertex crest; anterior angle of ocellar triangle obtuse. Vertex straight. ***Mesosoma.*** Pronotum with dorsal pronotal area longer than mesoscutum, its posterior margin slightly produced backward medially. Mesoscutum without notaulus; parapsidal signum absent. Mesoscutellar groove as a narrow sulcus, lacking enlarged lateral pits. Metapectal-propodeal complex coriaceous; metapostnotum indistinct, apparently without metapostnotal median carina and metapostnotal-propodeal suture; posterior transverse carina present. Mesopleuron somewhat swollen in dorsal view, coriaceous, not sculptured; mesopleural pit shallow. Prosternum relatively large, somewhat rhombic-shape. ***Wings.*** Forewing with costal cell conspicuous; second radial cell closed, short, almost triangular; length of vein Rs2 as long as vein M2; length of vein Rs2+M2 as long as vein 1Rs2; stigma well developed, bula present. ***Legs.*** Pro- and metafemora strongly swollen, profemur lenticular-shaped, about 0.6× as wide as long. Insertion of metacoxae displaced anteriorly between mesocoxal insertion. Tarsal claws strongly curved, with a large basal expansion. ***Metasoma.*** Sting with 3vv narrow and long.

Etymology. The genus name is an allusion to the strongly swollen profemora, from Latin *crassus*, thick, fat, stout, and *Bethylus*, the type genus of Bethylinae.

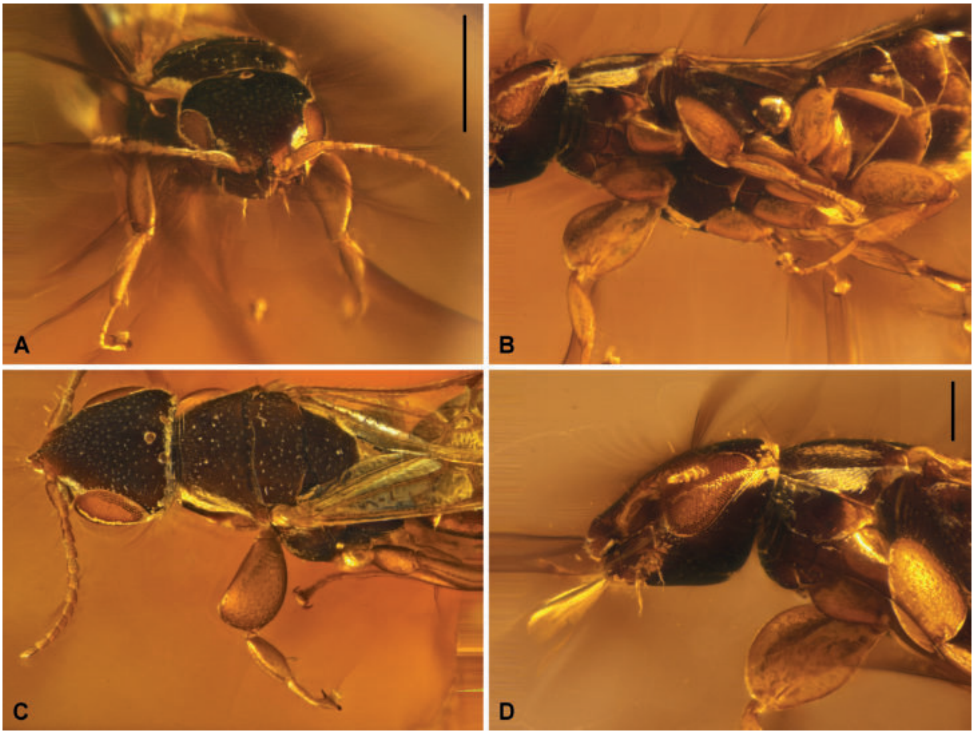

Figure 3. †*Crassibethylus dominicanus* gen. et sp. nov. Female holotype **A** head, in frontal view **B** mesosoma, in lateroventral view **C** head and mesosoma, in dorsal view **D** head and protórax, in lateroventral view. Scale bars: 0.5 mm (**A**); 0.2 mm (**D**). **A–C** at same scale.

†*Crassibethylus dominicanus* sp. nov.

https://zoobank.org/42715AFA-4B46-4853-A25C-2D83FEE9A57D
Figs 2, 3

Type material. ***Holotype*** female, amber inclusion from the Dominican Republic (DZUP Dom-024). Specimen complete and very well preserved. Syninclusions: one small spider and a springtail.

Description. Holotype. Female. Body length 3.2 mm; forewing 1.95 mm long. ***Color.*** Wings clear hyaline; antenna, mandible, palpi, tegula, legs, and wing venation light castaneous; metasoma castaneous; head and mesosoma dark castaneous. ***Head.*** Head as long as wide in dorsal view, triangular-shaped in both frontal and lateral views. Mandible narrow and evenly wide along its extension. Clypeus with median lobe rounded, well projected; median carina well developed, continuous with frontal carina; lateral lobe inconspicuous. Antenna with flagellar pubescence sparse, with few outstanding erect setae; scape 3.0× longer than pedicel; pedicel as long as first flagellomere; flagellomeres subequal in length. Eye not protruding, elliptical, large, and glabrous; area between anterior margin of eye and demarcation of median clypeal lobe clearly concave. Frons coriaceous and finely punctate. Posterior ocelli close to vertex crest; anterior angle of ocellar triangle obtuse; anterior ocellus aligned with upper tangent of eyes. Vertex crest straight, sparse thick setae at corner. Hypostomal carina straight. ***Mesosoma.*** Pronotum wider than long, coriaceous and finely punctate; anterior corner angled. Metapectal-propodeal complex with lateral marginal carina. ***Wings.*** Forewing with R2 cell longer than 1Cu2 cell; only one longitudinal flexion line present, not forming rectangular area. ***Metasoma.*** About 2.3× longer than wide, polished, whole surface glabrous. Genitalia with 3vv narrow and longer than wide.

Male. unknown.

Etymology. The specific epithet *dominicanus* is an allusion to the Dominican Republic, country from the where the amber piece originated.

Goniozus Förster

Goniozus Förster, 1856: 95. Type species: *Bethylus claripennis* Förster, 1851.
Parasierola Cameron, 1883: 197. Type species: *Parasierola testaceicornis* Cameron, 1883.
Progoniozus Kieffer, 1905: 105. Type species: *Perisemus floridanus* Ashmead, 1905.
Perisierola Kieffer, 1914: 533. Type species: *Parasierola gallicola* Kieffer, 1905.
†*Pterosclerogibba* Olmi, 2005: 186. Type species: †*Pterosclerogibba antiqua* Olmi, 2005, syn. nov.

Remarks. *Goniozus* Förster is the second most speciose genus in Bethylinae, being composed by 174 described species, three of them representing fossil taxa, two from Baltic amber and one from Dominican amber (Azevedo et al. 2018). Its species are distributed around all zoogeographic regions. The taxonomic efforts for this genus are represented by a species revision for the Nearctic region (Evan, 1978), in which nine species groups were recognized; and a species revision for the Sino-Japanese region (Terayama 2006). The latest phylogenetic work for this group, published by Ramos and Azevedo (2020), included the largest representation of the diversity within *Goniozus*, and retrieved it as a paraphyletic group, a result also found here. Based on this result, Ramos and Azevedo (2020) reinforced the necessity to further investigate its constituent groups in order to better delimit the genus, based on the morphological evidence.

The fossil fauna of Dominican amber is interpreted here as containing two species of *Goniozus*. In addition to †*G. respectus*, described by Sorg (1988), we also transfer the taxon †*Pterosclerogibba antiqua*, described by Olmi (2005) as a sclerogibbid wasp, to *Goniozus* (see below).

†*Goniozus antiquus* (Olmi) comb. nov.

†*Pterosclerogibba antiqua* Olmi, 2005: 186. Female holotype. Dominican Republic: amber from La Toca mine (GPCO, not examined).

Diagnosis. Antenna, tibia, and tarsi light castaneous; head and mesosoma castaneous; metasoma dark-castaneous to nearly black. Head longer than wide, not punctured; clypeal carina strong, but not extending over frons; antenna relatively short, apical portion moniliform; malar space as long as eye length; eye small, without pilosity; ocellar triangle with a right anterior angle; vertex concave, apparently without thick setae. Mesosoma without conspicuous setae; posterior margin of dorsal pronotal area concave posteriorly; mesoscutum shorter than dorsal pronotal area, not punctured, notaulus absent; mesopleuron not gibbous; mesoscutellum as long as mesoscutum, not punctured; metapectal-propodeal complex as long as mesonotum. Forewing with clearly developed pterostigma, venation apparently reduced. Proleg with a swollen femur, almost 2.0× longer than wide, metafemora not distinctly swollen. Metasoma without visible setae; sting curved downward.

Remarks. Olmi (2005) described †*Pterosclerogibba antiqua* as the first fully winged female of Sclerogibbidae, and postulated that this species has a great importance for evolutionary studies of the family. However, the photographs of the holotype provided in Martynova et al. (2019: 1797) and Perkovsky et al. (2020: 3) clearly indicate to us that it represents a Bethylidae. The following features, which according to Azevedo et al. (2018) are useful for the identification of bethylid wasps, can be observed in the holotype: head elongate, depressed, and prognathous; clypeus with vertical carina extending between antennae; antenna placed close to the clypeus and with 11 flagellomeres in both sexes; clypeus partially covered by antennal base; occipital carina present and complete; dorsal pronotal area always present and at least as long as wide; mesoscutum-mesoscutellar suture always represented either by sulcus or pits, or both; metapostnotum well developed and invading propodeum; propleuron covered by pronotal collar in dorsal view; mesopleural pit always present centrally or nearly so; forewing with pterostigma present and well developed. Moreover, additional features observed in the holotype of †*Pterosclerogibba antiqua* indicate that it belongs to Bethylinae, as follows: head triangular-shaped, in lateral profile; swollen profemur; and strongly curved tarsal claws. Although both Olmi (2005) and Martynova et al. (2019) outlined what they interpreted as the wings, these represent small cracks in the amber around the inclusion. The true wings are folded over the specimen, as can be seen in Perkovsky et al. (2020).

Within Bethylinae, Olmi's species can be accommodated in *Goniozus* based on its general morphology and especially for lacking diagnostic features found in other genera of Bethylinae. Considering that *Goniozus*, as currently defined (see Ramos and Azevedo 2020), represents a paraphyletic assemblage, future work should focus in better positioning †*Goniozus antiquus* among the many species groups found within this genus.

†*Goniozus respectus* Sorg

Fig. 4

†*Goniozus respectus* Sorg, 1988: 86. Female holotype. Dominican Republic: amber from unknown mine (SGN, examined through photographs).

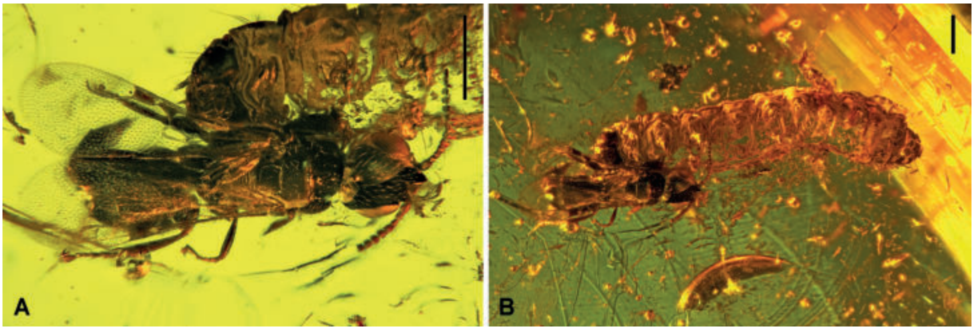

Figure 4. †*Goniozus respectus* Sorg. Female holotype **A** dorsal habitus **B** view of the amber inclusions, showing the female holotype and a microlepidopteran larva (putative host). Scale bars: 0.5 mm.

Diagnosis. Antenna, clypeus and legs light castaneous; head and mesosoma dark-castaneous nearly black. Head as long as wide, sparsely punctured; antenna with flagellomeres with large sensilla, distinctly moniliform; malar space shorter than eye length; eye large, without pilosity; ocellar triangle with anterior angle obtuse; vertex straight, with few scattered setae. Mesosoma setae as long as head setae; posterior margin of dorsal pronotal area concave; mesoscutum shorter than dorsal pronotal area, punctured, notaulus absent; mesoscutellum as long as mesoscutum, punctured; metanotum with metascutellum visible; metapectal-propodeal complex longer than mesonotum, lateral marginal carina of the metapectal-propodeal complex present. Forewing with clearly developed pterostigma, 1M2 cell, Rs2 vein not reach margin. Legs with profemur almost 3.0× longer than wide, metafemora not distinctly swollen. Metasoma with setae slightly longer than those on mesosoma.

Remarks. The species was described by Sorg (1988) based on a single female specimen. In addition to the description, the author also illustrated the head and forewing. We were able to study this taxon based also on color photographs kindly provided by Dr. Solórzano Kraemer. As already emphasized by Sorg (1988), the wasp is preserved together with a microlepidopteran larva (see Fig. 4). Considering that all Bethylinae are known to parasitize larvae of Lepidoptera, except for the unusual *Goniozus* attacking *Microstigmus* wasps (Melo and Evans 1993), one can deduce that the larva entombed together with †*Goniozus respectus* likely represents its host.

Key to the species of Bethylinae from Dominican amber

1 Profemur and metafemur strongly swollen, profemur about 0.6× as wide as long; mesopleuron swollen; insertion of metacoxae displaced between mesocoxae.................................... **†*Crassibethylus dominicanus* gen. et sp. nov.**

– Profemur and metafemur not as swollen, profemur much less than 0.6× as wide as long; mesopleuron not swollen; metacoxae inserted posteriorly to mesocoxal insertion.. **2 (*Goniozus*)**

2 Head longer than wide, with malar space as long as eye length; eye small; ocellar triangle with anterior angle right; vertex concave; notauli absent; metapectal-propodeal complex as long as mesonotum; profemur almost 2.0× longer than wide.. **†*G. antiquus* (Olmi)**

– Head as long as wide, with malar space shorter than eye length; eye large; ocellar triangle with anterior angle obtuse; vertex straight; mesoscutum with notauli; metapectal-propodeal complex longer than mesonotum; profemur almost 3.0× longer than wide.. **†*G. respectus* Sorg**

Discussion

The discovery of an enigmatic bethylid wasp in Dominican amber has provided us with an opportunity to reassess the taxa currently known from this fossil deposit. The inclusion of the new fossil in the dataset assembled by Ramos and Azevedo (2020) recovered its sister-group relationship with the clade *Odontepyris* + *Prosierola*, a position supported by some unequivocal morphological features present in these three lineages. In addition to these characters, their phylogenetic affinity is also reinforced by the morphology of the mesopleuron. The clade *Odontepyris* + *Prosierola* is notable for their swollen mesopleuron, giving it a "gibbous" appearance in dorsal view (see Ramos and Azevedo 2020). Although we did not code †*Crassibethylus* gen. nov. as having a swollen mesopleuron, it has a condition reminiscent of that seen in species of *Odontepyris* and *Prosierola*. These three taxa have a broad mesosoma, with the foramina of their mesocoxae placed considerably apart from each other. It is possible that the mesopleuron in this group became enlarged to accommodate the musculature associated with the mesocoxae.

Our phylogenetic results also shed light on the age and biogeography of the *Odontepyris* + *Prosierola* clade. While the species of *Odontepyris* are distributed in the Old World, being presently recorded from the Afrotropical, Australian, Oriental and Palearctic regions, *Prosierola* is restricted to the New World, including the Greater Antilles (Azevedo et al. 2018). The discovery of †*Crassibethylus* gen. nov. and its placement as sister to *Odontepyris* + *Prosierola* could indicate a New World origin for the entire group. Improved resolution of the biogeographic pattern, however, will require further study of the relationships involving the species groups in *Goniozus*.

Although recognition of a new taxon at genus level in Bethylinae does not solve the paraphyletic condition of *Goniozus*, we think that simply subsuming *Odontepyris* and *Prosierola* (and for that matter †*Crassibethylus* gen. nov. as well) within *Goniozus* is not a reasonable solution to the problem. These taxa have distinct morphologies and occupy distinct regions of the globe. Future work on Bethylinae should focus on establishing the limits of the species groups within *Goniozus*, so that a new genus-level classification could be proposed on more solid ground. There are already some genus-group names available, currently synonymized under *Goniozus*, that could be reinstated for some of these lineages.

It is also important to call attention to additional contributions of our work to the understanding of the evolution within Sclerogibbidae. The removal of †*Pterosclerogibba* from Sclerogibbidae to Bethylidae, placed here as a synonym of *Goniozus*, makes the fauna of Sclerogibbidae known from Dominican amber restricted to †*Probethylus poinari*, a taxon described from an apterous female and exhibiting a condition similar to that found in the extant species (Olmi 2005). Therefore, presence of fully developed wings in female sclerogibbid wasps is restricted to those taxa known only from the Cretaceous (see Perkovsky et al. 2020).

Acknowledgements

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Supplementary material 1

Character matrix

Authors: Diego N. Barbosa, Gabriel A. R. Melo

Data type: Morphogical (Excel spreadsheet)

Explanation note: Morphological character matrix.

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Supplementary material 2

Phylogenetic tree

Authors: Diego N. Barbosa, Gabriel A. R. Melo

Data type: (PDF file)

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Synopeas maximum Awad & Talamas (Hymenoptera, Platygastridae): a new species of parasitoid associated with soybean gall midge, *Resseliella maxima* Gagné (Diptera, Cecidomyiidae)

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Abstract

Synopeas maximum Awad & Talamas, **sp. nov.**, the first reported parasitoid associated with the soybean gall midge, *Resseliella maxima* Gagné, is described based on morphological and molecular data. Parasitoids were reared from soybean stems infested by *R. maxima* in Minnesota. A phylogenetic reconstruction of the genus *Synopeas* Förster was performed with COI sequences (n=2412) available on the Barcode of Life Data System (BOLD). Phylogenetic and barcode gap analyses suggest 279 *Synopeas* species in this dataset, with *S. maximum* sequences forming a monophyletic clade that is distinct from relatives. The *Synopeas maximum* clade was close to specimens from Canada and the United States, suggesting it is native to North America. We present a taxonomic treatment of *S. maximum* to facilitate its identification, including comparison to morphologically similar species. This project provides baseline data for further ecological study of *R. maxima* parasitism, and its management in soybean.

Keywords

gall midge, parasitism, phylogenetic reconstruction, soybean

Introduction

Gall midges (Diptera: Cecidomyiidae) are a hyper-diverse lineage, representing 30% of dipteran diversity in some ecosystems (Huang et al. 2022). Similarly diverse are parasitoids in the subfamily Platygastrinae (Hymenoptera: Platygastridae), (Chen et al. 2021). Platygastrines are larval or egg-larval parasitoids of Cecidomyiidae, and development of the parasitoid is often suspended until the host is in the last instar or prepupal stage (Kim et al. 2011; Abram et al. 2012; Chen et al. 2021). For both Cecidomyiidae and Platygastrinae, the diversity of species far exceeds what has been described (Srivathsan et al. 2022). However, a recent treatment of the genus *Synopeas* from Papua New Guinea, using morphology, DNA barcoding, and available data on host associations, has set a new standard for making inroads into both the taxonomy and ecology of gall midge parasitoids (Awad et al. 2021). The diversity of species and trophic interactions between Cecidomyiidae and Platygastrinae are large and complex. However, agricultural ecosystems can provide excellent opportunities to investigate these relationships within much simpler systems.

In 2018, larvae of an unknown species of cecidomyiid were found associated with dying soybean plants, *Glycine max* (L.) Merr., in the midwestern United States (Gagné et al. 2019). In 2019, this species of unknown origin was described as *Resseliella maxima* Gagné, the soybean gall midge (Gagné et al. 2019). Soybean plants become susceptible to *R. maxima* attack when the plants have two or three expanded trifoliate leaves, which is when the plant stems present natural fissures below the cotyledonary node (McMechan et al. 2021). Adult female midges oviposit in these fissures and the larvae feed within the stem at the base of the plant, resulting in necrotic lesions that can cause lodged, wilted, and dead plants (McMechan et al. 2021; Helton et al. 2022).

Efforts to reduce *R. maxima* injury to soybeans have focused primarily on chemical control, but have so far provided insufficient protection of soybean plants (Hodgson and Helton 2021; McMechan 2021). Therefore, additional tactics for more effective and sustainable management are needed. One potential management approach is biological control, which has yet to be examined for *R. maxima*. Other pestiferous Cecidomyiidae have been successfully managed using biological control agents, including *Aprostocetus epicharmus* (Walker) (Hymenoptera: Eulophidae) that parasitized up to 38% of raspberry cane midge, *Resseliella theobaldi* (Barnes) (Vétek et al. 2006), and *Synopeas myles* (Walker) (Hymenoptera: Platygastridae) that parasitized up to 28% of swede midge, *Contarinia nasturtii* (Kieffer) (Abram et al. 2012b; Ferland 2020).

The present work investigates potential parasitism of *R. maxima* by rearing parasitoids from field-collected soybean stems. We present a taxonomic and molecular description of the *R. maxima*-associated parasitoid, *Synopeas maximum* Awad & Talamas, sp. nov., and a phylogenetic analysis of *Synopeas* sequences available on the Barcode of Life Data System (BOLD).

Methods

Field collection and emergence cages

Soybean stems presenting symptoms of infestation by *R. maxima* (i.e., darkened swollen lesions at the base of the stems) were collected during the summer of 2021 in two fields on one farm near the city of Luverne (Rock County), Minnesota, USA. Field collection started on 30 June 2021, when soybean plants started to show symptoms of infestation, and continued every other week until *R. maxima* larval infestation was no longer detected on 01 September 2021. On each sampling date, 10 randomly selected symptomatic plants were collected per eight sampling locations per field by pulling the entire plant from the soil. These plants were trimmed above the first pair of unifoliate leaves, placed in zipper-locking plastic bags (17.7 × 18.8 cm, Ziploc), and held in coolers until brought to the laboratory (approximately five hours).

In the laboratory, the stems were prepared for placement in emergence cages. The cut end of each stem was wrapped with a small piece of PARAFILM to slow plant dehydration. Soybean roots were trimmed to a length of five centimeters. Ten trimmed stems were placed together in one emergence cage per location. Emergence cages consisted of 5-liter clear plastic paint-mixing buckets with lids (TCP Global Corporation, Lakeside, California, USA). A 6-cm diameter hole was cut in the side of each bucket approximately 6 cm from the bottom of the bucket. A white fine-mesh (0.02 cm mesh size, 100% polyester, Quest Outfitters, Sarasota, Florida, USA) sleeve 30 cm long was attached to the hole with hot glue to allow access to the contents of the cages. The sleeves were tied to prevent insects from escaping. In each cage, the stems were placed vertically into a 3 cm deep layer of potting soil (BM2 Seed Germination and Propagation Mix, Berger, Saint-Modeste, Quebec, CA). The emergence cages were maintained at room temperature in 16h light:8h dark, watered as needed to maintain soil moisture, and checked daily for emergence of insect adults. Adult insects were collected manually into microcentrifuge tubes, freeze-killed in -20 °C for 24 hours and preserved in 95% ethanol for taxonomic and molecular identification.

DNA extraction

Non-destructive DNA extraction from individual specimens followed a modified HotSHOT protocol (Truett et al. 2000). Each specimen was placed in a 0.2 mL PCR tube (Olympus plastic, Cat# 27-125) with 100 µL of the lysis reagent (25 mM NaOH: 0.2 mM disodium EDTA) and incubated at 95 °C for 30 minutes on a Mastercycler nexus PCR cycler (Eppendorf). Samples were cooled to 4 °C and 100 µL of neutralizing reagent (40 mM Tris-HCl) was added to each sample (a final volume of 200 µL). The aqueous solution containing DNA was moved to a fresh tube and 95% Ethanol was added to the specimen for preservation.

DNA barcoding

We barcoded all *Synopeas* (n=16) as well as six adult specimens of *R. maxima* randomly selected from the emergence cages. The cytochrome oxidase subunit I (COI) gene was amplified alongside negative controls using the universal primer pair LCO-1490/HCO-2198 for *S. maximum* and COIA/J-1718 for *R. maxima* (Folmer et al. 1994; Simon et al. 1994; Funk et al. 1995; Gagné et al. 2019). PCR reactions were prepared in a final volume of 20 µL with 1 µL of DNA template, Q5 Hot Start High-Fidelity 2X Master Mix (New England BioLabs), and 500 nM of each primer. Thermalcycling was performed on a Mastercycler nexus PCR cycler (Eppendorf) with an initial denaturation of 2 min at 98 °C, followed by 40 cycles of amplification (10 s at 98 °C, 30 s at 60 °C, and 20 s at 72 °C), and a final elongation of 2 min at 72 °C. The annealing temperature was determined using NEB Tm calculator (version 1.15.0, https://tmcalculator.neb.com/). PCR-products were separated by gel electrophoresis on a 1% agarose gel and imaged under ultraviolet light after staining with GelRed 3X in water (Biotium). PCR-products were cleaned with the Exo-CIP Rapid PCR Cleanup Kit (New England BioLabs) according to manufacturer's instructions and Sanger sequenced in both directions at the University of Minnesota Genomics Center (Saint Paul, Minnesota, USA). Sequences were inspected for peak quality, aligned, and trimmed of priming regions in SnapGene (SnapGene5.3.2).

Synopeas maximum-specific primer design and DNA barcoding

We designed a *Synopeas maximum*-specific forward primer after finding that (1) not all *Synopeas* samples were compatible with the LCO-1490/HCO-2198 primer set, and (2) *Synopeas* samples that were amplified with LCO-1490/HCO-2198 primers typically generated low sequence quality when sequencing from the LCO-1490 primer (these sequences were ~50% of the amplicon length and were low quality, with average quality scores around 20, rather than a typical mean of ~40). Using the preliminary data from the reverse reads, we selected a new forward primer targeting a region that was conserved across our samples (SYN_F: 5'-CGATTAGAAGTTGGAACTCC-3') and generated a 550-bp amplicon when combined with the HCO-2198 reverse primer. A new PCR reaction mix was prepared for all wasps (n=16) as described in the section above, using the new primer pair (SYN_F/HCO-2198). Thermal cycling was performed on a Mastercycler nexus PCR cycler (Eppendorf) with an initial denaturation of 2 min at 98 °C, followed by 35 cycles of amplification (10 s at 98 °C, 30 s at 61 °C, and 20 s at 72 °C), and a final elongation of 2 min at 72 °C.New PCR-products were separated, purified, and sequenced as described above. Resulting sequences were uploaded to BOLD and are listed in Table 1.

Phylogenetic reconstruction

A phylogenetic analysis was performed with *Synopeas* sequences available on BOLD (Suppl. material 1) along with *S. maximum* sequences, and selected outgroups (n=2412). Amino acid sequences were aligned with MAFFT version 7.475 (Katoh and Standley 2013) using default parameters for downstream use in phylogenetic analyses.

Table 1. Specimens of *Synopeas maximum* reared from emergence cages.

Lab code†	Collecting unit identifier	Sex	BOLD ID
PG01	FSCA 00095876	Male	SYMAX005-23
PG02	FSCA 00095877	Male	SYMAX006-23
PG03	FSCA 00095878	Male	SYMAX011-23
PG04	FSCA 00095879	Male	SYMAX010-23
PG05	FSCA 00095880	Female	SYMAX009-23
PG06	FSCA 00095881	Female	SYMAX001-23
PG07	FSCA 00095882	Male	SYMAX002-23
PG08	FSCA 00095883	Female	SYMAX003-23
PG10	FSCA 00095885	Female	SYMAX012-23
PG11	FSCA 00060750	Male	SYMAX013-23
PG12	FSCA 00060752	Female	SYMAX014-23
PG13	FSCA 00060751	Male	SYMAX004-23
PG17	FSCA 00060754	Female	SYMAX016-23
PG18	FSCA 00060755	Male	SYMAX007-23
PG20	FSCA 00060756	Male	SYMAX008-23
PG21	FSCA 00060757	Female	SYMAX017-23

†Codes used in phylogenetic tree (Suppl. material 3 and Fig. 7).

The alignment was trimmed in SnapGene (SnapGene5.3.2) to remove sequences from outside of the SYN_F/HCO-2198 amplicon. A reduced version of the alignment, which excluded identical sequences (n=1459, 518 bp in length), was submitted to maximum likelihood analysis in RAxML version 8.2.11 using a GTRGAMMA substitution model and 1000 bootstrap replicates (Stamatakis 2014). Tree topology was rooted and visualized in FigTree version 1.4.4 and annotated in Inkscape version 1.2.1. Species delimitation was performed with the ASAP web server and default settings (https://bioinfo.mnhn.fr/abi/public/asap/) including the full aligned FASTA file containing all sequences (n=2412) and a JC69 Jukes-Cantor substitution model (Puillandre et al. 2021). The best scoring partition was selected for downstream processing as per ASAP guidance.

Imaging

Photography was performed using a Macropod microphotography system (Macroscopic Solutions) using 10X and 20X Mitutoyo objective lenses, with image stacks rendered in Helicon Focus. Images of primary types were deposited in Zenodo (Table 2), and images of molecular voucher specimens were deposited in BOLD.

Institutional abbreviations

Specimens examined during this study are deposited in the following institutions and abbreviated as follows:

CNCI	Canadian National Collection of Insects, Ottawa, Canada;
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA;

HMNH	Hungarian Museum of Natural History, Budapest, Hungary;
MEFS	Museo Entomologico Filippo Silvestri, Portici, Italy;
MZH	Finnish Museum of Natural History, Helsinki, Finland;
MZLU	Biological Museum Lund University, Lund, Sweden;
NHMD	Natural History Museum Denmark, Copenhagen, Denmark;
NHMO	Zoological Museum, University of Oslo, Oslo, Norway;
NHMUK	Natural History Museum, London, UK;
NHMW	Naturhistorisches Museum Wien, Vienna, Austria;
NIAS	National Institute of Agricultural Sciences, Jeonju, South Korea;
NMINH	National Museum of Ireland, Dublin, Ireland;
OOLL	Oberösterreichische Landesmuseum Linz, Austria;
RMNH	Naturalis Biodiversity Center, Leiden, Netherlands;
UMSP	University of Minnesota, St. Paul, Minnesota, USA;
USNM	United States National Museum, Washington, DC, USA;
ZMUN	Natural History Museum, University of Oslo, Norway.

Table 2. *Synopeas* species in the *rhanis* species group.

Species	Type repository	Type locality	Images
S. basipubens Buhl, 2014	NHMD	Togo	
S. bialowiezaensis Buhl, 2005	MZH	Poland	
S. bouceki Buhl, 2007	NHMUK	India	
S. convexum Thomson, 1859	MZLU	Sweden	https://www.flickr.com/search/?tags=MZLUTYPE02851
S. cynipsiphilum (Ashmead, 1887)	USNM	USA	https://zenodo.org/record/7662443#.Y_Up1HbMJaQ
S. decurvatum (Nees von Esenbeck, 1834)	type lost	Germany	
S. dentiscutum (Szabo, 1981)	HMNH	Hungary	https://doi.org/10.5281/zenodo.7585486
S. epigeios Buhl, 2006	NHMD	Denmark	
S. flavicorne (Ashmead, 1893)	USNM	USA	https://zenodo.org/record/7662438#.Y_Uoy3bMJaQ
S. gibberosum Buhl, 1997	ZMUN	Norway	https://zenodo.org/record/7591619#.Y9mCmnbMJaQ
S. hyllus (Walker, 1835)	NMINH	Ireland	https://zenodo.org/record/7591590#.Y9l_AHbMJaQ
S. kimi Choi & Buhl, 2006	NIAS	South Korea	
S. maximum Awad & Talamas, 2023	FSCA	USA	https://zenodo.org/deposit/7662387
S. oleae Buhl & Viggiani, 2008	MEFS, paratypes in NHMD	Italy	
S. politiventre Buhl, 2015	NHMD	Chile	
S. prospectum Förster, 1861	NHMW	Switzerland	https://zenodo.org/record/7591572#.Y9l9cnbMJaQ
S. protuberatus Buhl, 2009	RMNH	Vietnam	
S. rhanis (Walker, 1835)	NMINH	England	https://zenodo.org/record/7442827#.Y9l-M3bMJaQ
S. sheldrakei Buhl, 2014	MZLU	Sri Lanka	
S. subtilis Buhl, 2004	HMNH	Mongolia	
S. talhouki Vlug, 1976	Vlug collection, paratypes in USNM, HMNH, NHMW	Lebanon	https://zenodo.org/record/7662450#.Y_UxlnbMJaQ
S. thailandicum Buhl, 2007	OOLL	Thailand	
S. triangulatum Buhl, 2014	NHMD	Australia	
S. tuberosum Sundholm, 1970	MZLU	South Africa	
S. veenakumariae Buhl, 2014	MZLU	Sri Lanka	
S. vietnamianus Buhl, 2009	RMNH	Vietnam	

Results

Emergence cages

We collected 2221 adults of *R. maxima*. Other cecidomyiids collected from the cages included two individuals of *Lestodiplosis* spp. Two taxa of parasitoids were collected from the cages, including 16 individuals of *S. maximum* and 4 individuals of *Aphanogmus* sp. (Ceraphronidae).

DNA Barcoding

We performed DNA barcoding on each of the 16 *Synopeas* adults recovered from emergence cages (Table 1). COI sequences from these specimens had greater than 98% sequence similarity to each other but no close matches on GenBank. The most similar was a specimen identified as Platygastrinae sp., (GenBank ID MG501619.1, 97% query cover, 89.6% nucleotide identity), collected in Banff National Park, Alberta, Canada. Unfortunately, there are no photographic records of this specimen and a morphological comparison was not possible. We also verified the identity of randomly selected gall midges that emerged from the cages. The specimens were morphologically identified as *R. maxima*, had identical nucleotide sequences to each other, and a 97.67% sequence similarity to a *R. maxima* specimen from Nebraska, USA (accession number LC437340.1).

Systematics of *Synopeas*

The generic concept of *Synopeas* is rather straightforward, and it can be separated from other platygastrines by the fusion of T1–T2 and S1–S2 (Jackson 1969; Awad et al. 2021). However, taxonomic structure within the genus is essentially non-existent. Given that *Synopeas* includes over 350 species, this presents a significant challenge for species identification (Awad et al. 2021). This situation is exacerbated by the spread of numerous species by human activities, requiring revision of the world fauna to be certain that a species was not previously described. Our ability to ascertain if *S. maximum* is adventive is presently limited to the use of DNA barcode libraries, and comparison to type specimens that are in the morphological vicinity of *S. maximum*. So far, neither of these approaches have provided a match. Our efforts are not exhaustive, nor is it currently feasible to examine type material for all described species of *Synopeas*. Fortunately, *S. maximum* has a distinctive characteristic shared by a minority of species: a deep scuto-scutellar sulcus (i.e., deep divide between the mesoscutum and mesoscutellum) (Fig. 6C, D). This eliminates the need for comparison to the vast majority of described *Synopeas*. Within the Nearctic region, primary type images provided by Talamas et al. (2017) yielded only two species, *S. cynipsiphilum* (Ashmead) and *S. flavicorne* (Ashmead), with the mesosomal structure found in *S. maximum*. Given that the soybean gall midge is an emerging pest, we also considered it possible that *S. maximum* represents an adventive population, derived from a distribution outside of the United States. Our literature search and examination of type specimens found other species with the deeply divided mesosoma, but not a species-level match. Because the mesosomal divide creates such a distinctive "hunchbacked" appearance, we consider that it has high value as a diagnostic character and use it to define the *rhanis*-group of *Synopeas*, named for *S. rhanis* (Walker, 1835), which was the earliest described species with this character. The *rhanis*-group includes 26 species (Table 2) that we consider to be worth comparing to *S. maximum*. We selected five species from this group for closer examination and comparison, based on morphological similarity and occurrence in cold temperate climates. However, all species of the *rhanis*-group were considered and compared to the new species using type images or published descriptions.

***Synopeas cynipsiphilum* (Ashmead)**

Fig. 1

Leptacis cynipsiphila Ashmead, 1887: 129 (original description); Fouts 1924: 117, 128 (description, lectotype designation, keyed).
Leptacis cynipsiphilus Ashmead, 1893: 271, 274 (description, spelling error, keyed).
Leptacis cynipiphila Ashmead: Kieffer 1926: 637, 646 (description, spelling error, keyed).
Synopeas cynipsiphilum (Ashmead): Masner 1967: 303 (generic transfer); Masner and Muesebeck 1968: 99 (type information); Vlug 1995: 77 (cataloged, type information).

***Synopeas flavicorne* (Ashmead)**

Leptacis flavicornis Ashmead, 1893: 275 (original description); Fouts 1924: 117, 128 (description, type designation, keyed).
Amblyaspis flavicornis (Ashmead): Brues 1916: 532, 533 (generic transfer, description, keyed).
Synopeas flavicorne (Ashmead): Masner and Muesebeck 1968: 99 (generic transfer, type information, emendation).

***Synopeas gibberosum* Buhl**

Fig. 2

Synopeas gibberosus Buhl, 1997: 439 (original description); Buhl 1999: 39 (keyed); Buhl and Choi 2006: 133 (keyed).
Synopeas gibberosum Buhl: Buhl and Notton 2009: 1696 (cataloged, distribution, emendation); Buhl and O'Connor 2010: 4 (distribution).

Figure 1A–E. *Synopeas cynipsiphilum*, female (FSCA 00097487) **A** head, anterior view **B** head and mesosoma, dorsal view **C** head and mesosoma, ventrolateral view **D** head and mesosoma, lateral view **E** mesosoma and metasoma, dorsal view.

Synopeas prospectum Förster
Fig. 3

Synopeas prospectus Förster, 1861: 41 (original description); Dalla Torre 1885: 78 (reprint of Förster (1861)); Kieffer 1926: 668, 680 (description, keyed); Vlug 1973: 179 (lectotype designation); Vlug 1995: 81 (cataloged, type information); Buhl 1997: 27 (description).

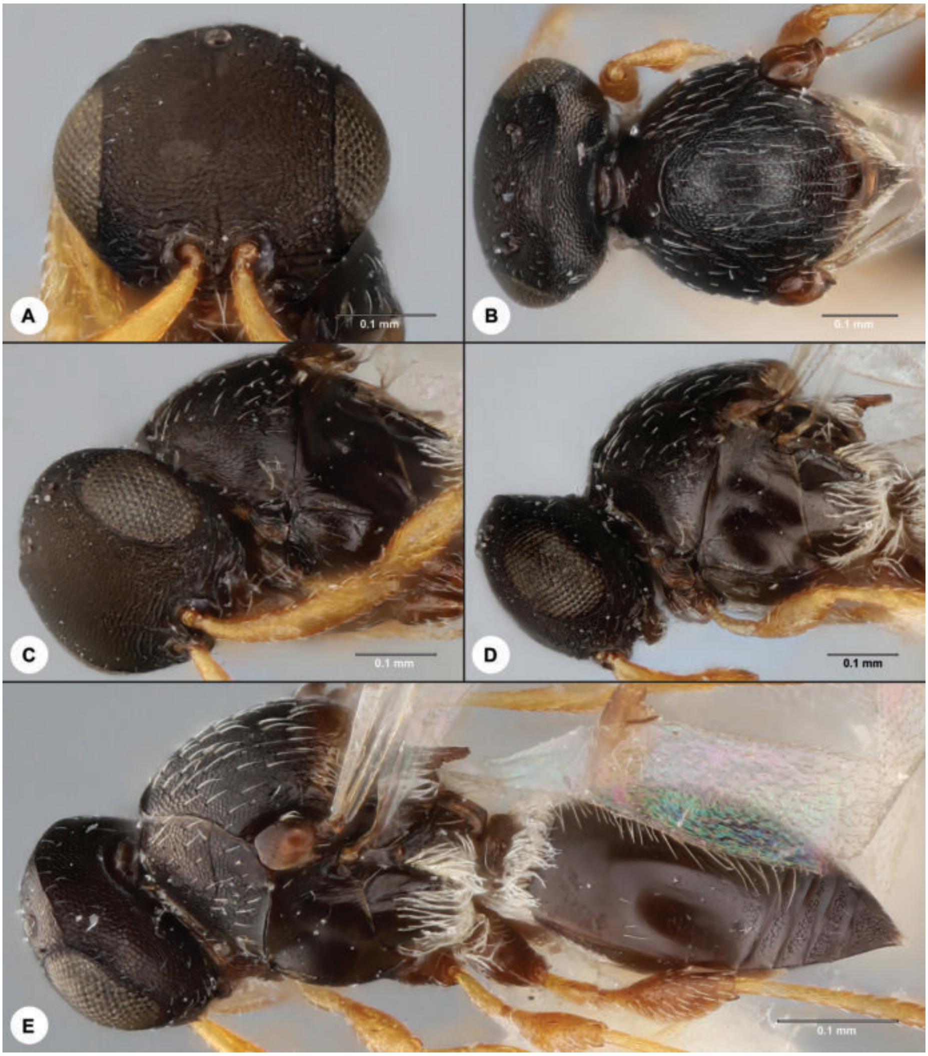

Figure 2A–E. *Synopeas gibberosum*, holotype female (NHMO 0001) **A** head, anterior view **B** head and mesosoma, dorsal view **C** head and mesosoma, ventrolateral view **D** head and mesosoma, lateral view **E** habitus, dorsolateral view.

Synopeas Prospectus Förster: Kieffer 1914: 419 (description).
Synopeas (*Synopeas*) *prospectus* Förster: Kieffer 1916: 554, 555 (description, subgeneric assignment, keyed).

Synopeas rhanis (Walker)
Fig. 4

Platygaster Rhanis Walker, 1836: 225 (original description).

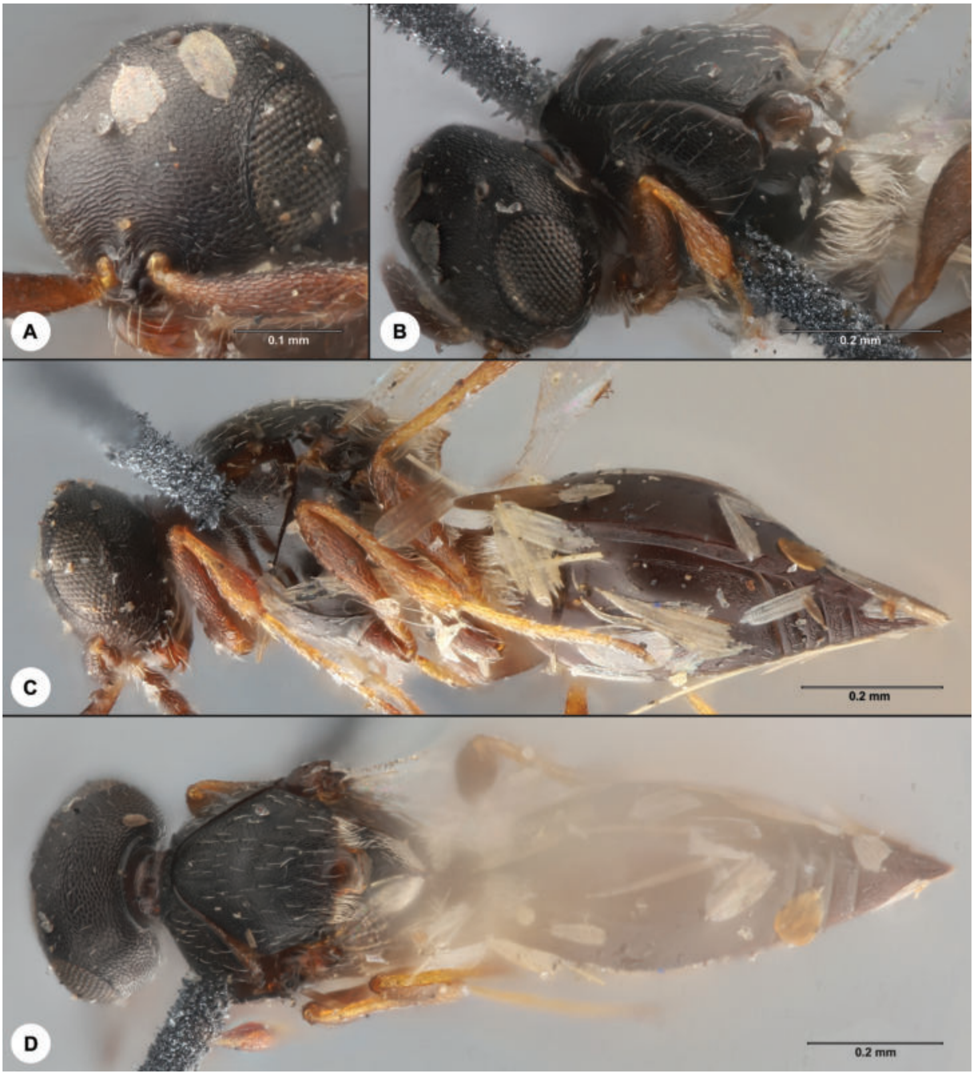

Figure 3A–D. *Synopeas prospectum*, lectotype female (NHMW-HYM #0005306) **A** head, anterolateral view **B** head and mesosoma, dorsolateral view **C** habitus, lateral view **D** habitus, dorsal view.

Platygaster Acco Walker, 1836: 229 (original description. Synonymized by Vlug (1985)); Vlug 1985: 209 (junior synonym of Synopeas rhanis (Walker)).

Synopeas Acco (Walker): Marshall 1873: 19 (generic transfer); Kieffer 1914: 427 (description).

Synopeas Rhanis (Walker): Marshall 1873: 19 (generic transfer); Kieffer 1914: 341 (description of adult and immature stages).

Synopeas rhanis (Walker): Kieffer 1906: 134 (description); Kieffer 1926: 668, 676 (description, keyed); Masner 1965: 142 (type information); Vlug and Graham 1984: 130 (lectotype designation); Vlug 1985: 209 (description of type, keyed); Vlug

1995: 81 (cataloged, type information); Buhl 1999: 39 (keyed); MacGown and Evans 2003: 6 (description); O'Connor, Nash, Notton and Fergusson 2004: 24 (catalog of Irish species); Buhl and Notton 2009: 1698 (cataloged, distribution); Buhl and O'Connor 2010: 14 (distribution).

Synopeas acco (Walker): Kieffer 1926: 669, 683 (description, keyed); Vlug and Graham 1984: 129 (lectotype designation); Vlug 1985: 209 (description of type, keyed); Vlug 1995: 75 (type information); O'Connor, Nash, Notton and Fergusson 2004: 24 (type information, catalog of Irish species).

Synopeas ?rhanis (Walker): Buhl and Choi 2006: 133, 135 (keyed, distribution in Korea).

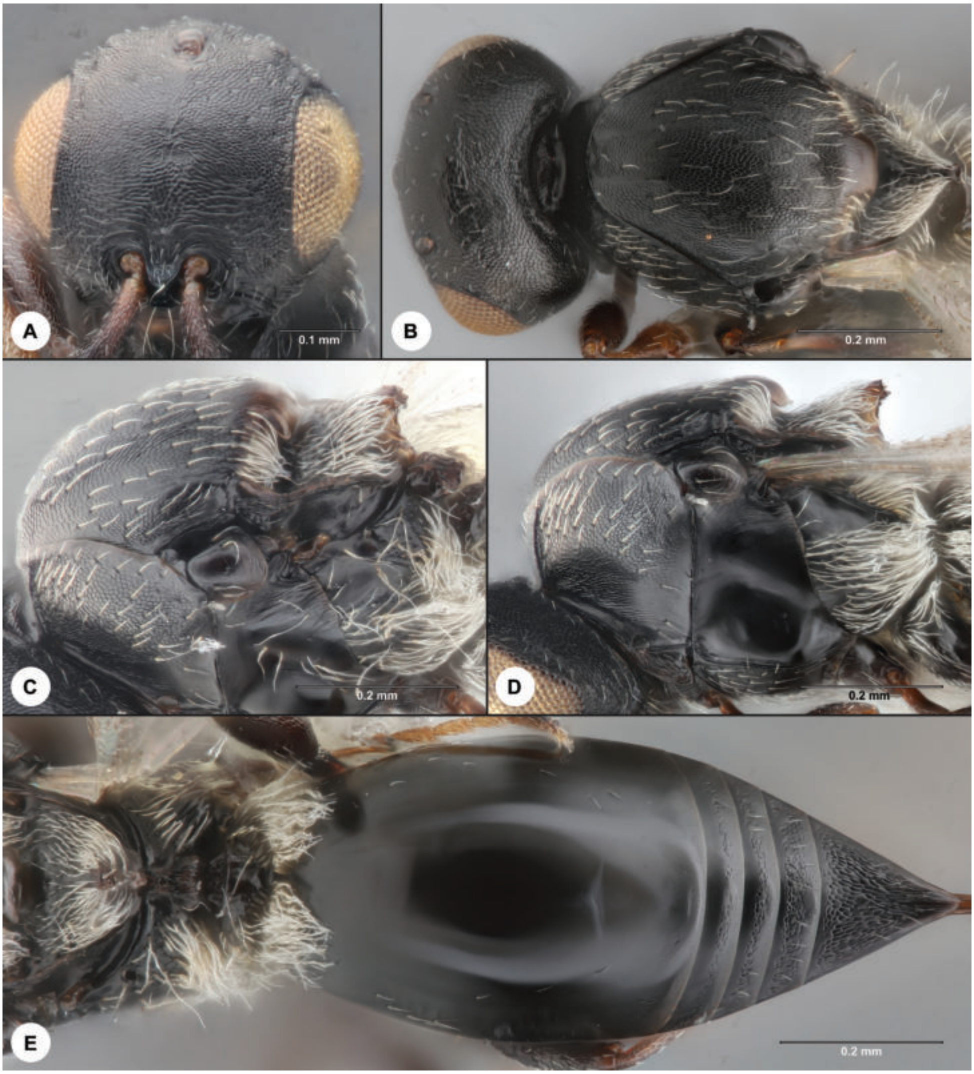

Figure 4A–E. *Synopeas rhanis*, female (FSCA 00034191) **A** head, anterior view **B** head and mesosoma, dorsal view **C** mesosoma, dorsolateral view **D** mesosoma, lateral view **E** mesosoma and metasoma, dorsal view.

Synopeas maximum Awad & Talamas, sp. nov.

https://zoobank.org/74487E47-EB76-4899-8A22-F91906954842
Figs 5, 6

Description. Females. ***Body length*:** 1.4–1.7 mm. ***Body color*:** black. ***Color of legs*:** coxae dark brown, otherwise yellow to dark brown. ***Color of mesoscutellar spine*:** concolorous with mesoscutellar disc.

Head. Shape of head in anterior view: ovoid. Central keel: absent; present only between toruli. Sculpture on frons: reticulate microsculpture. Epitorular sculpture: reticulate microsculpture; minute rugulae. Number of clypeal setae: 4. Length of median pair of clypeal setae: longer than lateral pair. Arrangement of clypeal setae: evenly spaced. Shape of mandible: bidentate. Distance between lateral ocellus and compound eye (OOL): approximately 1 ocellar diameter. OOL: LOL: 1:2. Lateral ocellar depression: present posterolaterally. Hyperoccipital carina: present between lateral ocelli. Hyperoccipital carina strength: fine, laterally weakened. Distance between lateral ocellus and hyperoccipital carina: approximately 1 ocellar diameter. Female antenna with 3 clavomeres, claval formula 1-1-1.

Mesosoma. Epomial carina: present, complete, or nearly so. Microsculpture of lateral pronotum: present anterodorsally, absent posteroventrally. Lateral pronotal sculpture coverage: more than ¾. Setation of lateral pronotum: anteroventrally glabrous, otherwise uniformly sparse (Figs 5, 6D). Mesoscutellar spine: short and pointed. Mesoscutellar spine in lateral view: pointing posteriorly; slightly upcurved at tip. Posterior margin of propodeal carina in lateral view: rounded. Mesosomal dorsum in lateral view: slightly convex. Scuto-scutellar sulcus: deep, causing mesoscutum to be elevated relative to mesoscutellum. Notauli: unmarked or faintly indicated. Parapsidal line: very faint. Setation of mesoscutum: sparse (Fig. 6B). Mesoscutal lamella: broad and rounded. Setation of mesoscutellum: anteromedially absent, posterolaterally dense.

Metasoma. Microsculpture of S2: absent; faint narrow bands in lateral portion of posterior margin. Shape of S2: medioventrally expanded. Sculpture of T2: absent. Length of T2: approximately as long as mesosoma. Sculpture of S3 to S5: reticulate. Sculpture of S6: entirely reticulate. Sculpture of T6: entirely reticulate. Shape of T6: triangular, longer than wide.

Wing. Length of setae on disc of fore wing: shorter than distance between setal bases. Density of setae on disc of fore wing: moderately dense. Arrangement of setae on disc of fore wing: uniformly setose distally, proximally glabrous with linea setosa. Fore wing marginal setae: uniformly very short.

Males. ***Body length*:** 1.1 to 1.3 mm. Identical to females except for metasoma and antenna.

Antenna. Setation: A1 and A2 with few scattered setae, A3 to A10 with long, uniformly dense setae. A2 in lateral view: slightly longer than wide, distally widened forming a "teardrop" shape. A3: round, about half the size of A2 or A4. A4: roughly cylindrical, about twice as long as wide. A5 in lateral view: about half as long as A4, proximally widened. A6 to A9: roughly ovoid, wider in lateral view than in anterior view, A6 slightly smaller than following antennomeres. A10: about twice as long as wide.

Figure 5. *Synopeas maximum* Awad & Talamas, sp. nov., holotype, female (FSCA 00095883), lateral habitus.

Metasoma. Microsculpture of S2: narrow band at posterior margin. Sculpture of T2: absent; narrow transverse band of microsculpture at posterior margin. Length of T2: approximately as long as mesosoma, or shorter.

Material examined. ***Holotype*:** USA • ♀; Minnesota, Luverne; 43.605889°N, 96.275111°W; 30.VI–30.VII.2021; Gloria Melotto leg.; *Resseliella maxima* on soybean; FSCA 00095883 (FSCA).

***Paratypes*:** USA • 1♀1♂; same collection data as for preceding; VI–VII.2021; FSCA 00095881 to 00095882 (CNCI) • 3♀3♂; same collection data as for preceding; VI–VIII.2021; FSCA 00060750 to 00060754 (FSCA) • 1♀3♂; same collection data as for preceding; VI–VII.2021; FSCA 00095876 to 00095878, 00095885 (UMSP) • 1♀2♂; same collection data as for preceding; VIII–XII.2021; FSCA 00060755 to 00060757 (UMSP) • 1♀1♂; same collection data as for preceding; VI–VII.2021; FSCA 00095879 to 00095880 (USNM).

Etymology. The species epithet refers to the ecological association with soybean gall midge, *Resseliella maxima* Gagné, and soybean, *Glycine max* (L.) Merr.

Diagnosis. *Synopeas maximum* can be separated from other species in the *rhanis* group by the following combination of characters: scuto-scutellar sulcus deep, causing mesoscutum to be elevated relative to mesoscutellum; hyperoccipital carina present

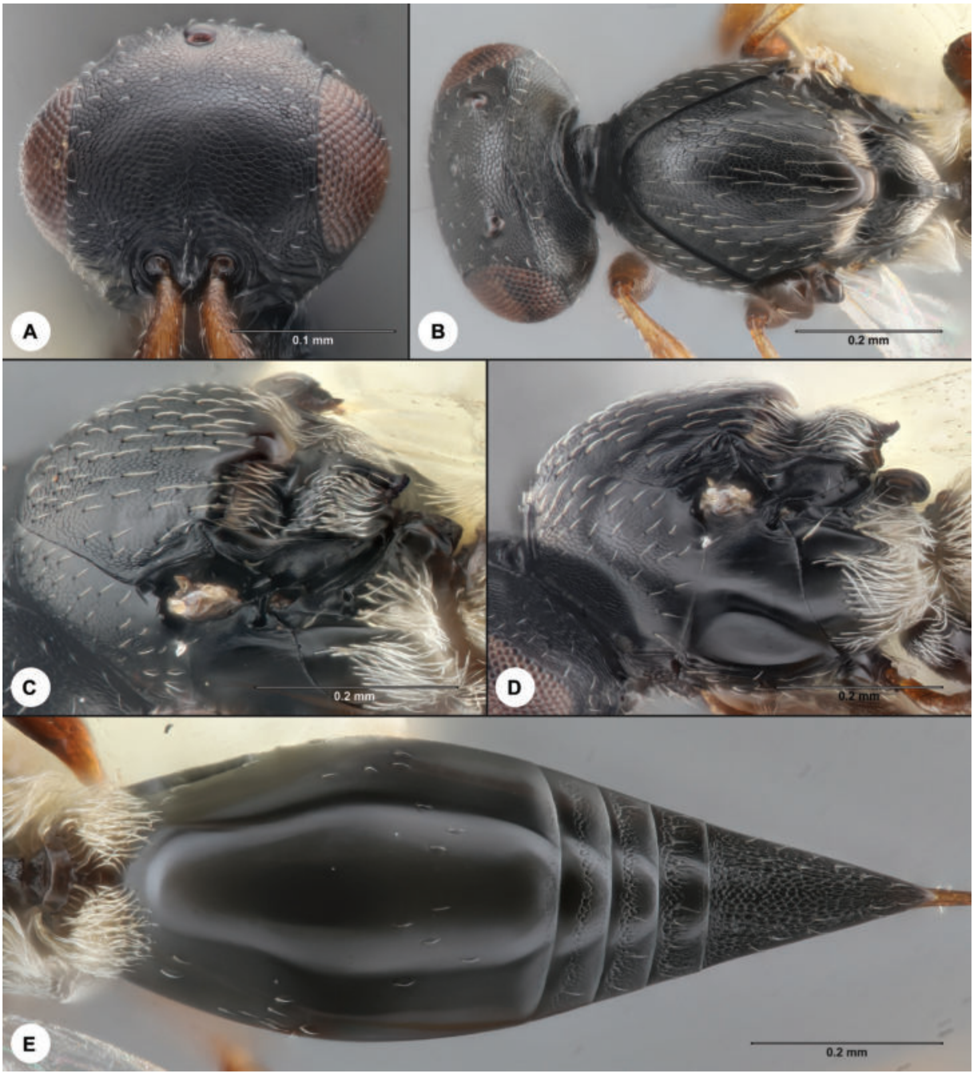

Figure 6A–E. *Synopeas maximum*, female **A** head, anterior view (FSCA 00095883) **B** head and mesosoma (FSCA 00095881) **C** mesosoma, dorsolateral view (FSCA 00095883) **D** mesosoma, lateral view (FSCA 00095883) **E** metasoma, dorsal view (FSCA 00095881).

between lateral ocelli, laterally weakened; mesoscutellar spine short, pointing posteriorly, sometimes with a slight upturn at the tip, but always originating from below the dorsal apex of the mesoscutellum (separating it from *S. gibberosum*, *S. prospectum*, and *S. rhanis*); female S2 expanded ventromedially, with microsculpture absent or very faint; female S6 and T6 entirely sculptured, triangular, about 2 times as long as wide. The latter character is very useful for separating *S. maximum* from *S. cynipsiphilum* and *S. flavicorne*, in which female T6 is wider than long.

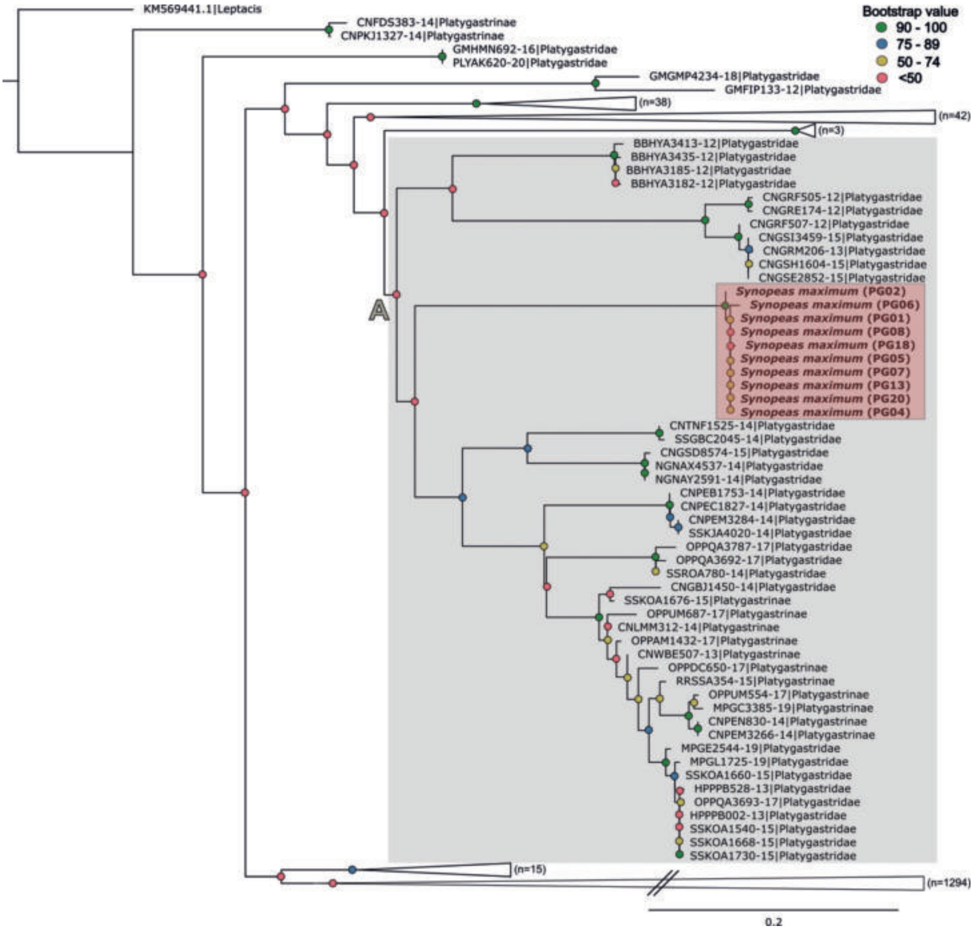

Figure 7. Simplified phylogenetic tree of the genus *Synopeas*. Maximum likelihood analyses were used to reconstruct a *Synopeas* phylogeny. This reduced version focuses on *S. maximum* (red box) and its closest relatives in clade A (gray box). Node circles are color coded to indicate bootstrap support. Specimens are named with sequence ID and taxon originated from BOLD. The full tree can be found in Suppl. material 3.

Phylogenetic reconstruction

The tree in Fig. 7 is a simplified version of the full consensus tree (Suppl. materials 3, 4) that comprises all the COI sequences derived from putative *Synopeas* sp. available in BOLD (excluding duplicates) wherein clades not relevant to species-level treatment of *S. maximum* were collapsed. While the backbone largely has lower bootstrap support (<50%), many species or putative species groups are strongly supported. ASAP analysis for species delimitation defined a total of 279 putative *Synopeas* species with 0.024 threshold distance (Suppl. material 5). Additionally, all *S. maximum* sequences were clustered into a single putative species by ASAP (Suppl. material 2).

We used the phylogenetic reconstruction (Fig. 7) to infer *S. maximum* relationships and origin. Specimens in clade A are all from Canada (n=37) and the northern

United States (n=7), suggesting that *S. maximum* is also native to North America. However, not all specimens in clade A belong to the *rhanis* group, and some representatives of the *rhanis* group are outside of clade A. Our analysis does not support the monophyly of the *rhanis* group, although the deep scuto-scutellar sulcus is still useful for identification.

Discussion

The goal of the emergence cages was to obtain *R. maxima* and potential parasitoids of cecidomyiid agricultural pests. In addition to *R. maxima*, the only other cecidiomyiids collected were two individuals identified as *Lestodiplosis* spp., which are known to be predaceous (Gagné and Jaschhof 2017). Although we detected emergence of two hymenopteran parasitoid species (i.e., 4 individuals of *Aphanogmus* sp. and 16 individuals of *S. maximum*) in our emergence cages, we focused our investigations only on *S. maximum* for several reasons. Species from the genus *Aphanogmus* are primarily hyperparasitoids (Polaszek and Dessart 1996; Jaramillo and Vega 2009; Hofsvang et al. 2014; Pérez-Rodríguez et al. 2019) or parasitoids of predaceous cecidomyiids (Gilkeson et al. 1993; Matsuo et al. 2016), while *Synopeas* is a genus that is known to parasitize only cecidomyiids (Awad et al. 2021). However, the role of *Aphanogmus* sp. in this system needs further investigation.

Platygastrinae are important natural enemies of cecidomyiids (Austin 1984; Kim et al. 2011; Johnson et al. 2013; Chavalle et al. 2015). The recent emergence and spread of *R. maxima* and several other cecidomyiids, such as *Contarinia nasturtii* Kieffer (Philips et al. 2017), *Contarinia brassicola* Rondani (Mori et al. 2019) and *Chilophaga virgati* Gagné (Calles Torrez et al. 2014), poses a threat to agriculture in the northern U.S. and Canada. To improve management for these and other cecidomyiids that may emerge as pests in the future, further work on the ecological relationships and taxonomy of *Synopeas* and other Platygastrinae is required.

Here, morphological assessments grouped *S. maximum* with the *rhanis*-group (i.e., “hunchbacked” appearance) which facilitates its identification. Although the *rhanis*-group did not form a monophyletic clade in molecular analyses, this feature appears to be useful for diagnostics. Additionally, we discovered that *S. maximum* clustered with other putative *Synopeas* species collected from Canada and the United States, suggesting that *S. maximum* may be native to North America.

Different methods for assessing parasitism of midges have been described, including rearing of field-collected hosts in the laboratory (Abram et al. 2012b), PCR-based molecular methods (Greenstone 2006; Magagnoli et al. 2022), and host dissections (Roubos and Liburd 2013). Here, we opted to rear out putative natural enemies of *R. maxima* because host dissections would not provide us with adults for taxonomic identification, and PCR-based molecular methods were impractical since we did not want to make assumptions about putative parasitoids that might be present. Our results suggest that *S. maximum* is likely a primary parasitoid of *R. maxima* because (1) it was reared out of emergence cages with field-collected soybean stems heavily infested with *R. maxima* and (2) the genus *Synopeas* is known to exclusively parasitize Cecidomyiidae. However, additional research is needed to confirm that *S. maximum* is indeed a parasitoid of *R. maxima*. Furthermore, the potential impact of *S. maximum* as a biological control agent of *R. maxima* is still unknown and more research needs to be performed in this area.

With the known geographic range of *R. maxima* expanding (McMechan et al. 2021), sustainable methods to manage this pest, such as biological control, need to be explored. As taxonomic work is foundational to the introduction, conservation, and augmentation of natural enemies (de Moraes 1987), the description of *S. maximum* will facilitate future research on the biological control of *R. maxima*.

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Supplementary material 1

CSV file with BOLD bins for putative *Synopeas* sequences

Authors: Gloria Melotto, Jessica Awad, Elijah J. Talamas, Robert L. Koch, Amelia R. I. Lindsey

Data type: table

Link: https://doi.org/10.3897/jhr.96.102865.suppl1

Supplementary material 2

ASAP partitions

Authors: Gloria Melotto, Jessica Awad, Elijah J. Talamas, Robert L. Koch, Amelia R. I. Lindsey

Data type: PDF file

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Supplementary material 3

Full phylogenetic reconstruction of *Synopeas*

Authors: Gloria Melotto, Jessica Awad, Elijah J. Talamas, Robert L. Koch, Amelia R. I. Lindsey

Data type: PDF file

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Supplementary material 4

Newick file for full phylogenetic reconstruction of *Synopeas*

Authors: Gloria Melotto, Jessica Awad, Elijah J. Talamas, Robert L. Koch, Amelia R. I. Lindsey

Data type: text file

Link: https://doi.org/10.3897/jhr.96.102865.suppl4

Supplementary material 5

Full ASAP results

Authors: Gloria Melotto, Jessica Awad, Elijah J. Talamas, Robert L. Koch, Amelia R. I. Lindsey

Data type: PDF file

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Long-term changes in the composition and distribution of the Hungarian bumble bee fauna (Hymenoptera, Apidae, *Bombus*)

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Abstract

One of the most important pollinator taxa is *Bombus* (Hymenoptera, Apidae), the genus of bumble bees, since they are important, often specialized, pollinators of many plants. As a result of climate change, warming winters and changes in landscape structure, the distribution and frequency of *Bombus* species is constantly changing. To develop appropriate protection strategies, it is essential to monitor them and update the occurrence and threat status of the species.

The last review of the distribution of *Bombus* species in Hungary was completed 20 years ago. Here we present updated distribution maps based on published data from the last 20 years together with unpublished data collected in 2018–2021. Based on the new data, we examine changes in the last two decades. In the case of 9 species further studies should be carried out to confirm the presence of stable populations, while 3 species are recommended for protection by law in Hungary. Seven species showed increasing frequency, *B. argillaceus* and *B. haematurus*.

Keywords

bumble bee, climate change, distribution data, distribution map, pollination, threatened, UTM

Introduction

Due to the intensification of agriculture and spreading urbanization, landscape diversity is decreasing with a parallel increase of air, water and soil pollution throughout Europe (Luck et al. 2004; Gaston 2005; Firbank et al. 2008). The biodiversity of both natural and cultivated lands is becoming poorer and eurytopic, while invasive species are becoming more frequent (Stoate et al. 2002). Pollination is one of the most important ecosystem services (Williams 1994; Klein et al. 2007; Ricketts et al. 2008; Ollerton et al. 2011), but these effects and the intensive use of pesticides endanger it through decreasing the species richness and abundance of pollinators, such as bumble bees (Apidae: *Bombus* spp.) (Williams 1989; Kearns et al. 1998; Brittain et al. 2010). The bumble bees are one of the most important and specialized pollinators of both wild and cultivated flowering plants in the Northern Temperate Zone, especially where and/or when the temperature is too low for honey bees to do well (O'Toole and Raw 1991; Kearns and Inouye 1997; Steffan-Dewenter and Tscharntke 1999; Kremen et al. 2002; Knight et al. 2005; Potts et al. 2010). Bumble bees are adapted to different nectar sources with their body size, morphology, and length of tongue (Inouye 1980; Williams 1986; Corbet 1996; Osborne and Williams 1996; Kearns and Thomson 2001; Raine and Chittka 2007). They are important pollinators of legumes, including cultivated alfalfa and clover (Anasiewicz and Warakomska 1969, 1977; Ruszkowski and Bilinski 1969; Ruszkowski 1971; Warakomska and Anasiewicz 1991; Tanács et al. 2009), rape seed, fruits such as apple, raspberry, blueberry and strawberry, vegetables such as tomato, green pepper, bean and cucurbits (pumpkin, melon, cucumber), and more than a thousand wildflowers (Goulson 2003). In a wider sense, they have an important role in maintaining natural- and agro-ecosystems and agricultural production (Senapathi et al. 2021).

The intensity and success of pollination are negatively affected by the decrease in the diversity and abundance of wild bees (Williams 1982; Donath 1985; Williams 1986; Rasmont 1988; Corbet et al. 1991; Buchmann and Nabhan 1996; Westrich 1996; Allen-Wardell et al. 1998; Goulson et al. 2005, 2008; Biesmeijer et al. 2006; Winfree et al. 2008; Williams and Osborne 2009; Potts et al. 2010; Szabó et al. 2012; Kerr et al. 2015). The survival probability of bumble bee populations has decreased by ca. 17% in Europe since the beginning of the 20th century (Soroye et al. 2020). Furthermore, due to the shift and loss of their area, the species composition of the bumble bee faunas of different regions is continuously changing (Novotny et al. 2021).

The last overview of the Hungarian bumble bee fauna was published in 2003 (Sárospataki et al. 2003). In order to develop our knowledge and help to conserve and maintain the diversity of bumble bees, we summarize the published, unpublished and our newly collected distribution data and provide check-list and distribution maps of the Hungarian bumble bee fauna. The frequencies of species were calculated and compared with the values from 2003.

Materials and methods

The former distribution database of Hungarian bumble bee fauna used a 10×10 km UTM system (Sárospataki et al. 2003). We built a new database combining the earlier data and the newly collected data. This new database contains partly published data of Jenő Papp collected between 1960 and 1970, Zsolt Józan collected between 1960 and 2019, Miklós Sárospataki collected after 2000 and data of Dóra Arnóczkyné Jakab and Antal Nagy collected between 2018 and 2021. Data from the "izeltlabuak.hu" website (izeltlabuak.hu 2021, licence: CC BY 4.0) were also used after revision by the authors, as were the published data of Tanács et al. 2008, Szabó and Endes 2010, Kovács-Hajdu et al. 2014, Vaskor et al. 2015 and Tóth et al. 2017.

In the case of data collected after 2003, transect counts and direct search are used. Data collected in 2018–2021 with volatile traps designed for noctua pests were also added by Dóra Arnóczkyné Jakab and Antal Nagy. For identification of the collected materials, the keys of Móczár (1985) were used. Identification of two species pairs are problematic, so that data for *Bombus hortorum* / *B. ruderatus* (Figs 11, 12, 24) (Williams and Hernandez 2000), and *B. terrestris* / *B. lucorum* (Figs 17, 30, 31) (National Biodiversity Data Centre 2012; Bossert 2015) are presented on separate maps.

The database contains the following data by species: sampling site with GPS coordinates and/or locality name, sampling dates, and data source. In the original data set, Sárospataki et al. (2003) used three periods to describe the chronology of data collections. Here, we add a fourth period for data collected after 2000. Data collected in different periods are marked with different signs in the distribution maps: +: before 1954, ×: between 1954–1970, ○ (empty circle): between 1971–2000 and ■ (grey square): after 2000. These signs differ from the original ones in order to clearly indicate the chronology of the data.

Bombus elegans is now recognized as a junior synonym of *B. distinguendus* (Williams 2011). As there were no new data for *B. bohemicus*, *B. consobrinus*, *B. distinguendus*, *B. fragrans*, *B. cullumanus serrisquama*, *B. subterraneus*, and *B. sylvestris*, as reflected in the maps (Figs 5, 8, 9, 27, 29, 33).

The relative frequencies of the species (*RF%*) were calculated based on the formula of Sárospataki et al. (2003), which provide information about the spatial constancy of a given species:

$$RF\% = \frac{\text{number of cells occupieds by species}}{\text{total number of UTM cells containing data}} \times 100$$

This index was used for comparison of former and newly calculated values. The frequency categories of species were recalculated also using this index and the original categories of Sárospataki et al. (2003): I = rare (1–10%), II = moderately frequent (11–20%), III = frequent (21–40%), IV = common (>40%). In the case of species with relative frequency lower than 1%, Sárospataki et al (2003) used the "data deficient" category. Here, we discuss the distribution, data source and age of the available data. If the presence of a species is in doubt "validation needed" category is used. This revision

Table 1. Checklist of the Hungarian bumble bee fauna with the relative frequency (*RF%*) and frequency category of the species published by Sárospataki et al. (2003) and calculated based on the actualized database built in 2021. * = protected in Hungary. E = locally extinct, cn = confirmation needed, I = rare (1–10%), II = moderately frequent (11–20%), III = frequent (21–40%), IV = common (> 41%).

	RF%		**Frequency categories**	
	2003	**2021**	**2003**	**2021**
B. (*Megabombus*) *argillaceus** (Scopoli, 1763)	7.06	15.44	I	II
B. (*Psithyrus*) *barbutellus* (Kirby, 1802)	12.53	10.73	II	II
B. (*Psithyrus*) *bohemicus* (Seidl, 1838)	4.33	3.58	I	I-cn
B. (*Psithyrus*) *campestris* (Panzer, 1801)	4.78	6.21	I	I
B. (*Bombias*) *confusus** (Schenck, 1861)	12.98	10.92	II	II-cn
B. (*Megabombus*) *consobrinus* (Dahlbom 1832)	0.23	0.19		cn
B. (*Bombus*) *cryptarum* (Fabricius, 1775)	-	0.19		cn
B. (*Subterraneobombus*) *distinguendus* (Morawitz 1869)	1.59	1.32		E
B. (*Subterraneobombus*) *fragrans** (Pallas, 1771)	3.64	3.01	I	I-cn
B. (*Pyrobombus*) *haematurus* (Kriechbaumer, 1870)	3.87	10.92	I	II
B. (*Megabombus*) *hortorum* (Linnaeus, 1761)	37.13	42.94	III	IV
B. (*Thoracobombus*) *humilis** (Illiger, 1806)	36.90	35.59	III	III
B. (*Pyrobombus*) *hypnorum* (Linnaeus, 1758)	6.38	9.42	I	I
B. (*Thoracobombus*) *laesus** (Morawitz, 1875)	8.66	6.21	I	I-cn
B. (*Melanobombus*) *lapidarius* (Linnaeus, 1758)	57.63	59.13	IV	IV
B. (*Bombus*) *lucorum* (Linnaeus, 1761)	12.53	14.69	II	II
B. (*Thoracobombus*) *muscorum** (Linnaeus, 1758)	19.59	18.46	II	II
B. (*Bombias*) *paradoxus** (*Bombus confusus paradoxus*, Dalla Torre, 1882)	3.87	3.39	I	I-cn
B. (*Thoracobombus*) *pascuorum* (Scopoli, 1763)	47.38	51.79	IV	IV
B. (*Thoracobombus*) *pomorum** (Panzer, 1805)	10.48	10.17	II	II
B. (*Pyrobombus*) *pratorum* (Linnaeus, 1761)	14.12	14.69	II	II
B. (*Thoracobombus*) *ruderarius* (Linnaeus, 1776)	37.13	39.74	III	III
B. (*Megabombus*) *ruderatus** (Fabricius, 1775)	17.54	18.08	II	II
B. (*Psithyrus*) *rupestris* (Fabricius, 1793)	17.77	14.69	II	II
B. (*Cullumanobombus*) *cullumanus serrisquama* (Kirby, 1802)	0.46	0.38		E
B. (*Kallobombus*) *soroeensis** (Fabricius, 1776)	1.37	1.69	I	I
B. (*Subterraneobombus*) *subterraneus** (Linnaeus, 1758)	9.11	7.53	I	II-cn
B. (*Thoracobombus*) *sylvarum** (Linnaeus, 1761)	40.77	42.75	III	IV
B. (*Psithyrus*) *sylvestris* (Lepeletier, 1832)	1.14	0.94	I	cn
B. (*Bombus*) *terrestris* (Linnaeus, 1758)	68.34	77.21	IV	IV
B. (*Psithyrus*) *vestalis* (Fourcroy, 1785)	12.30	12.62	II	II

was also carried out in the case of rare species. In other cases, where the species could be seen as extinct, the "revised" category is used (Table 1).

Since *RF%* considers the spatial distribution of the species based only on all occupied UTM cells, the other modified relative frequency value of species was calculated (*RF'%*) for all sampling periods. This modified value refers to both UTM-based distribution and sampling intensity as follows:

$$RF'\% = \frac{\text{number of occupied UTM cells by species from a given period}}{\text{total number of bee data from a given period}} \times 100$$

In this equation, only UTM-based distribution data could be used. Since we have numerous data without detailed locations, the fine-scale locality data cannot be calculated. Using it the bias caused by the different sampling intensity of the different periods of the study can be decreased and the changes of relative frequencies of the species can be more correctly evaluated.

In the case of the morphologically similar *Bombus hortorum* / *B. ruderatus*, and *B. terrestris* / *B. lucorum* species pairs, the calculated *RF%* and *RF'%* values were adjusted. The ratio of the two species was calculated for each sampling period based on valid data, and its minimum was chosen for both species. During the calculations of *RF%* and *RF'%* values, valid data and the ratio (equal to this minimum value) of the dubious data were taken into consideration.

Results

Composition of the fauna

The national territory of Hungary is divided into by 1052 10×10 km UTM cells, of which 531 contain 3716 bumble bee records (species/UTM cell/period). The first data were collected in 1953 (Sárospataki et al. 2003). The number of the studied UTM cells and data records have continuously increased since then. In the consecutive periods of sampling, nearly equal numbers of UTM cells were sampled (Fig. 1A), while the most data were collected in the third period, 1971–2000 (Fig. 1B). During the last, intensive period of data collection, more than 900 data records were collected, and the spatial coverage of the data set increased from 41.7% to 50.5%. From these new records, 829 were collected by the authors after 2000, with others from sources published after 2000.

The number of studied UTM cells, adjusted according to the length of the periods of data collection was nearly equal in all periods (Fig. 1A, B).

Data on 31 bumble bee species (6 of which are cuckoo bumble bees, subgenus *Psithyrus*) are presented. Two species (*B. distinguendus* and *B. cullumanus serrisquama*) have only archaic (at least 70 years old) data (Fig. 33), and we confirm Rakonczay's (1989) conclusion that they are locally extinct. Data formerly published on *B. elegans* included under *B. distinquendus*, so that our checklist comprises 29 species (Table 1). Most of the species (25/29) were already known before 1953 (Fig. 1C).

Among the listed species *B. fragrans* is strictly protected, while *B. argillaceus*, *B. confusus*, *B. humilis*, *B. laesus*, *B. muscorum*, *B. paradoxus*, *B. pomorum*, *B. ruderatus*, *B. sylvarum*, *B. soroeensis* and *B. subterraneus* are protected in Hungary (13/2001. (V. 9.) KöM decree) (Table 1).

As seen in Fig. 2, the number of records per species is very uneven, with seven having fewer than 10 records.

Changes in the relative frequencies of the species

In the last period of the studies, 835 data records of 21 species were collected from 259 UTM cells, while in the case of eight species we have no new data.

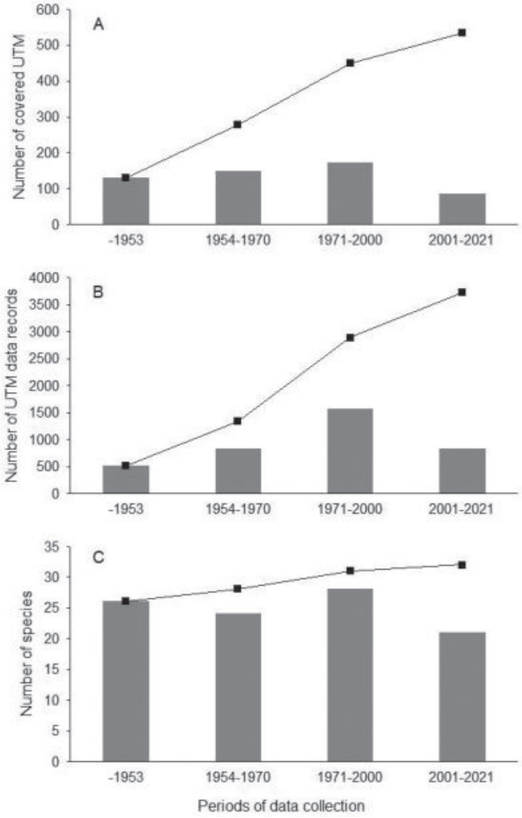

Figure 1. Number (bars) and cumulative number (line) of UTM cells with bumble bee data (**A**), number of data records (**B**) and number of species (**C**) in the consecutive periods of data collection in Hungary.

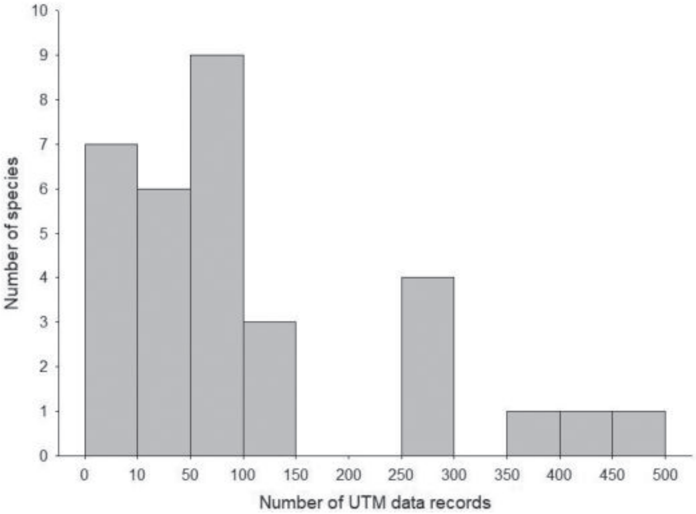

Figure 2. Distribution of data records among the bumble bee species of the Hungarian fauna.

The only valid Hungarian data on *B. consobrinus* were collected from the Gál-rét, in the Börzsöny Mountains (UTM cell: CU51) after 1970, the exact date unknown (Fig. 8). It has not been recorded in Hungary recently. *B. cryptarum*, belonging to the *B. lucorum* complex, also has only one record, thus its presence is dubious in Hungary (Fig. 17). *B. sylvestris* has only five records, collected in the 1971–2000 period, thus its relative frequency decreased to under 1% in the fauna (Fig. 29). The area of the rare *B. fragrans* had continuously decreased and it was not sampled after 2000 (Table 2, Fig. 9). Although *B. bohemicus* formerly was known both in the Bakony and the Bükk Mountains, it has not been reported in the last two decades (Fig. 5). Although *B. subterraneus* was once widely distributed but not abundant (Fig. 27), but it also has not been recorded after 2000, along with *B. confusus*, *B. laesus* and *B. paradoxus* (Figs 7, 15, 19).

Table 2. Bumble bees present in Hungary (29 species) with their modified relative frequency (*RF'%*) calculated for consecutive periods of samplings based on the revised database and the trend of frequency changes till 2005 (based on Sárospataki et al. 2005) and between 2005 and 2021. - = decreasing frequency, + = increasing frequency, u = unchanged, R = revised, ND = no data.

Species	Modified relative frequency (*RF'%*)				Trend	
	–1953	1954–1970	1971–2000	2001–2021	–2005	2005–2021
B. argillaceus	2.38	0.73	0.90	6.64	-	+
B. barbutellus	0.79	0.85	2.95	0.24		-
B. bohemicus	0.00	1.09	1.09	0.00		ND
B. campestris	0.00	1.09	1.22	1.42		+
B. confusus	2.97	2.67	2.37	0.00	-	-
B. consobrinus	0.00	0.00	0.06	0.00	ND	ND
B. cryptarum	ND	ND	ND	0.12	ND	ND
B. fragrans	2.97	0.12	0.06	0.00	-	-
B. haematurus	0.00	0.00	1.03	5.34	+	+
B. hortorum	4.75	8.13	8.34	8.19	u	u
B. humilis	9.31	9.59	6.35	3.68	-	-
B. hypnorum	0.20	0.12	1.67	2.85	+	+
B. laesus	5.94	0.24	0.45	0.00	-	-
B. lapidarius	10.10	9.10	13.09	11.39	u	u
B. lucorum	1.98	4.37	1.35	3.32	u	+
B. muscorum	6.34	3.64	2.82	1.78	-	-
B. paradoxus	1.78	0.12	0.58	0.00	-	-
B. pascuorum	9.90	11.29	9.37	11.86	u	+
B. pomorum	4.55	1.46	1.54	0.83	-	-
B. pratorum	2.18	1.94	3.08	2.02	u	u
B. ruderarius	4.75	6.92	8.28	6.64	u	u
B. ruderatus	5.94	3.76	1.86	2.14	-	-
B. rupestris	0.40	5.70	3.40	0.12		-
B. soroeensis	0.20	0.00	0.32	0.36	+	+
B. subterraneus	1.98	0.97	1.67	0.00	u	-
B. sylvarum	8.51	10.19	6.74	7.59	-	u
B. sylvestris	0.00	0.00	0.32	0.00		ND
B. terrestris	9.90	13.11	15.92	15.30	u	u
B. vestalis	0.20	2.79	3.15	1.42		u

Relative frequencies of *B. humilis*, *B. muscorum* and *B. pomorum* have continuously decreased (Figs 13, 18, 21), while for *B. rupestris* this trend appeared between 1954–1970 (Fig. 25), and for *B. barbutellus* only after 2000 (Table 2). These changes in relative frequency do not alter rarity category in any of these cases (Table 1).

In contrast, the relative frequencies of 15 species have increased since the last review (Sárospataki 2003): *B. argillaceus*, *B. campestris*, *B. haematurus*, *B. hortorum*, *B. hypnorum*, *B. lapidarius*, *B. lucorum*, *B. pascuorum*, *B. pratorum*, *B. ruderarius*, *B. ruderatus*, *B. soroeensis*, *B. sylvarum*, *B. terrestris* and *B. vestalis* (Figs 3, 6, 10, 11, 14, 16, 17, 20, 22–24, 26, 28, 30, 32). In four species, the increased relative frequency leads to changes in the rarity category as well. The rarity category of *B. argillaceus* and *B. haematurus* is changed from I to II, and the changes in their relative frequencies were significant and rapid during the last 20 years. Rarity categories of *B. hortorum* and *B. sylvarum* changed from III to IV, showing smaller shifts in relative frequencies than in the two former species (Table 1 and 2).

Considering the long-term trends of the changes in the relative frequencies, seven of the 15 mentioned species showed stable values (*B. hortorum*, *B. lapidarius*, *B. pratorum*, *B. ruderarius*, *B. sylvarum*, *B. terrestris*, *B. vestalis*), while the frequency of *B. ruderatus* slightly decreased (Table 2).

Changes in the distribution of species

New data redraw the area of many *Bombus* species. In the case of the East-Mediterranean *B. argillaceus*, the first protected *Bombus* species in Hungary, both the northern (Tiszatelek; cell EU64) and the eastern (Túristvándi; cell FU22) occurrences in Hungary were recorded after 2000. The relative frequency of the species had decreased between the 1950s and 2000, however, it has spread since 2000 and become widely distributed in the whole country (Table 2, Fig. 3).

The intensive spread of *B. haematurus* was also detected. The first data on the species were collected in the 1980s, but till 2003 it was only known from the central and southern parts of Transdanubia in western Hungary. After that, it appeared east from the Danube and the Tisza Rivers as well (Fig. 10).

We had no data on *B. hypnorum* from Hungary after the 1990s. Before that it was known from the hilly areas of Transdanubia and northern Hungary. It newly appeared in Transdanubia in 2015 and has been collected several times since 2018 also in eastern Hungary (Fig. 14).

Discussion

The last review of the Hungarian bumble bee fauna was published in 2003 (Sárospataki et al. 2003) and the vulnerability status of the species was assessed in 2005 (Sárospataki et al. 2005). Since 2000, more than 900 data records have been collected. After that 531 of the 1052 10×10 km UTM cells covering Hungary contained 3716 bumble bee data records (species/UTM cell/date), providing the possibility to recalculate the relative frequency and threatened status of the species and redraw their known distributions.

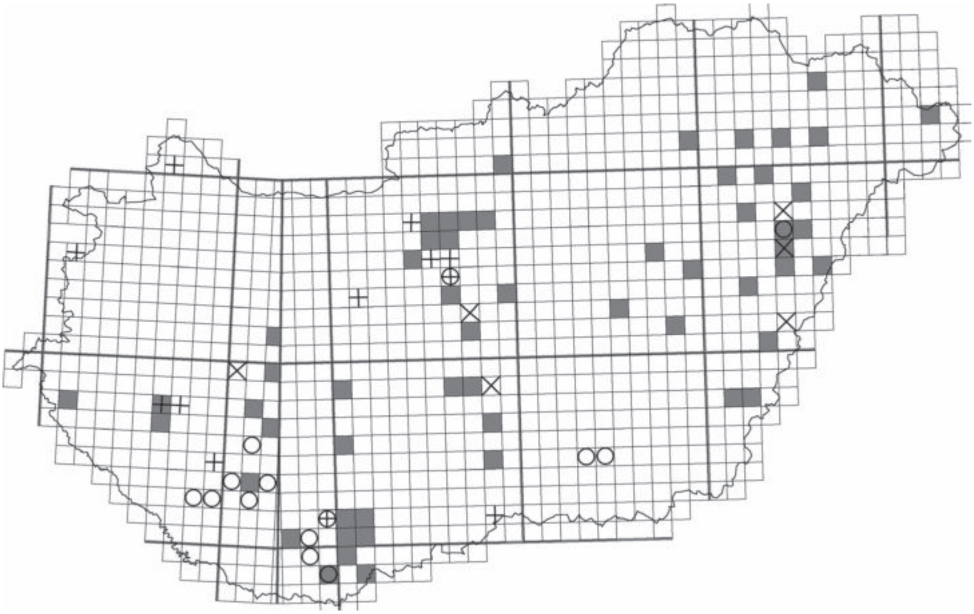

Figure 3. *Bombus argillaceus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

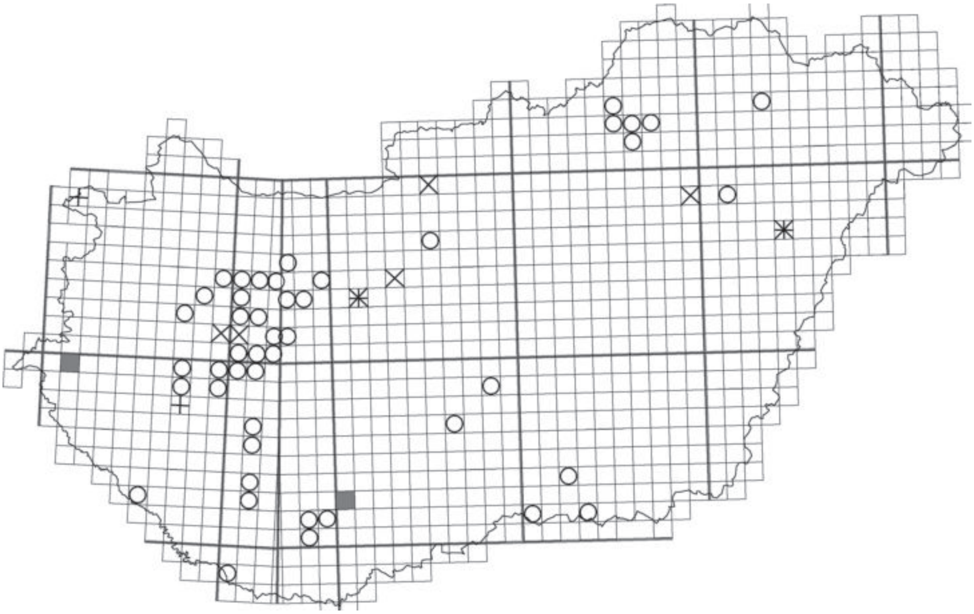

Figure 4. *Bombus barbutellus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

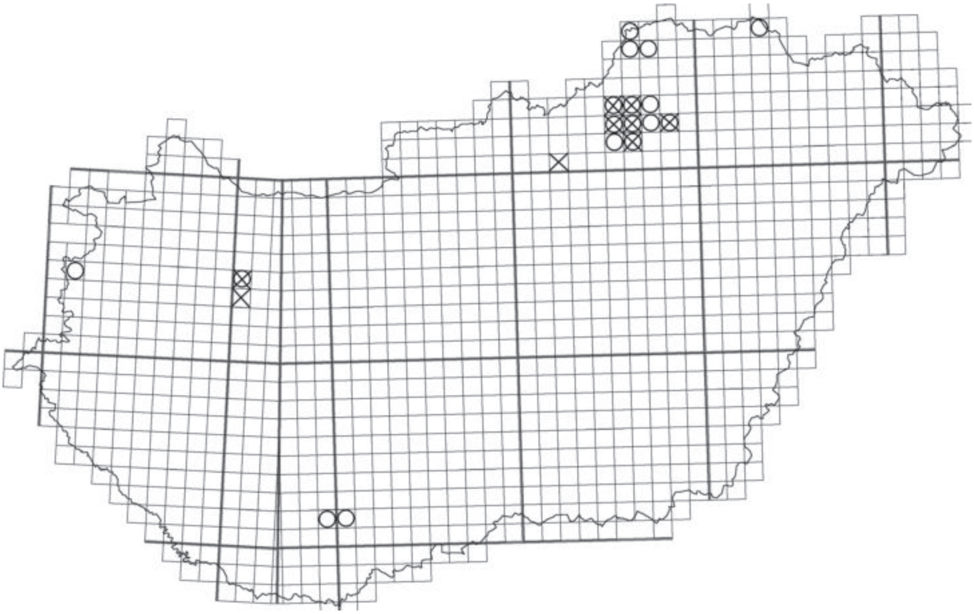

Figure 5. *Bombus bohemicus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

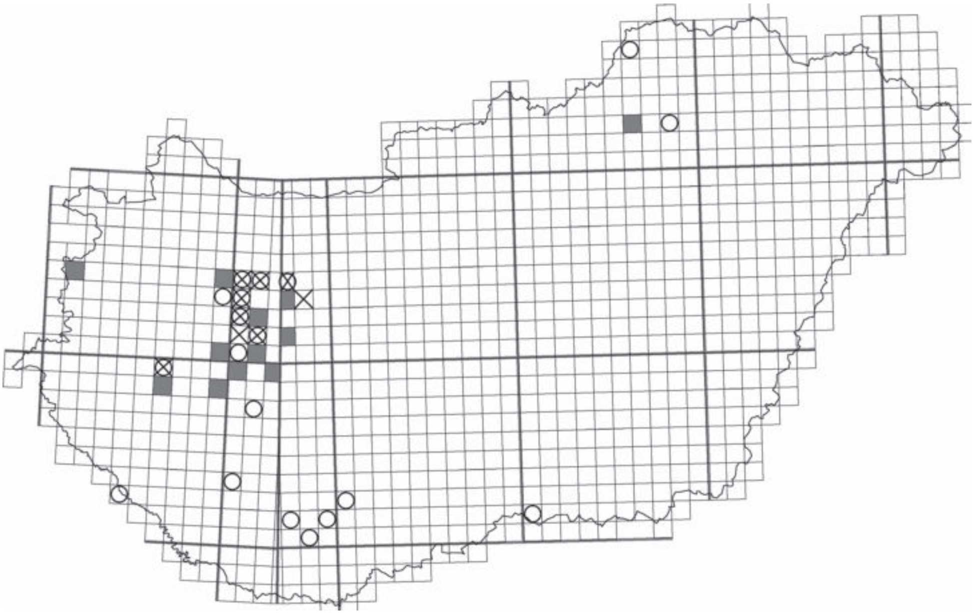

Figure 6. *Bombus campestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

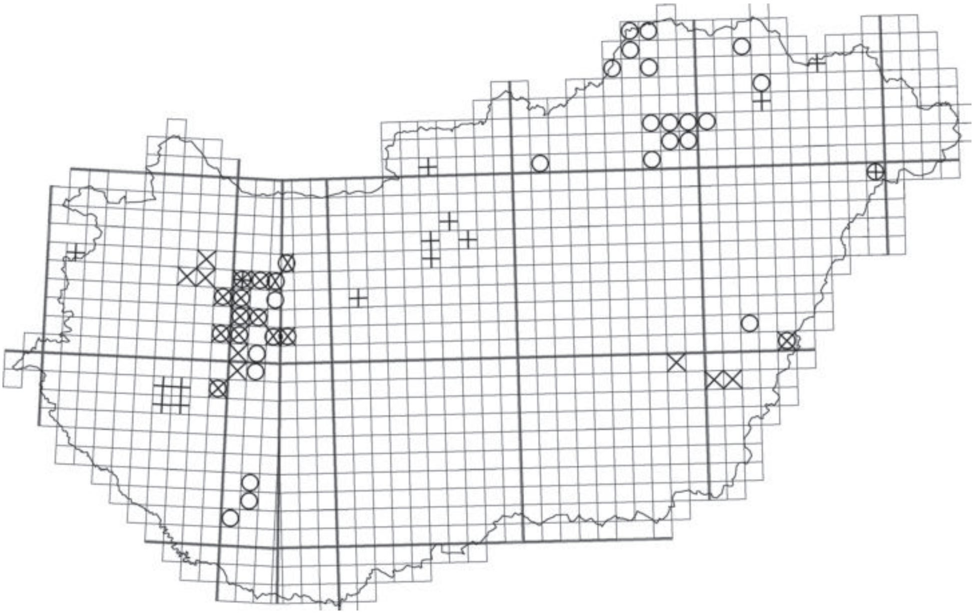

Figure 7. *Bombus confusus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

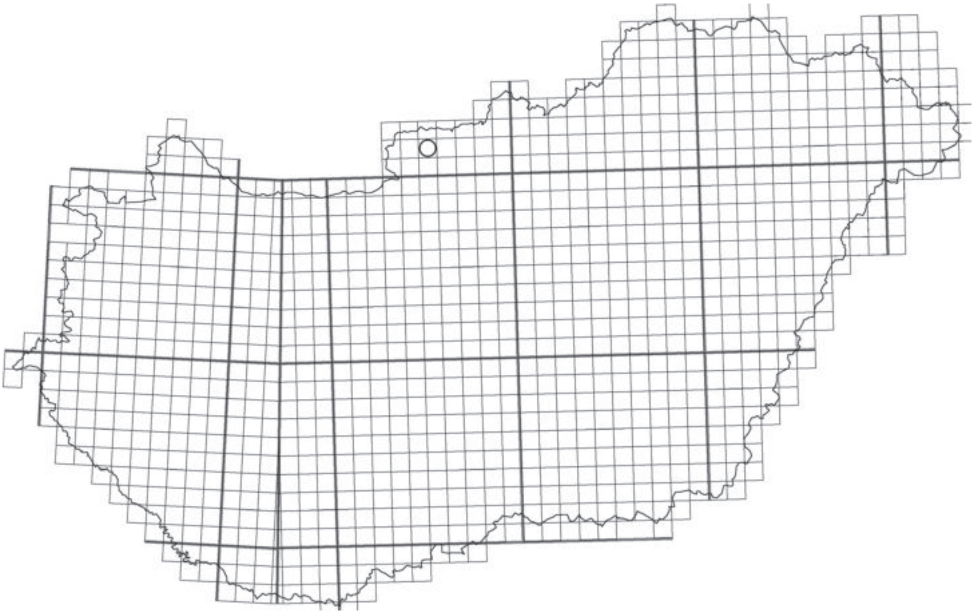

Figure 8. *Bombus consobrinus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

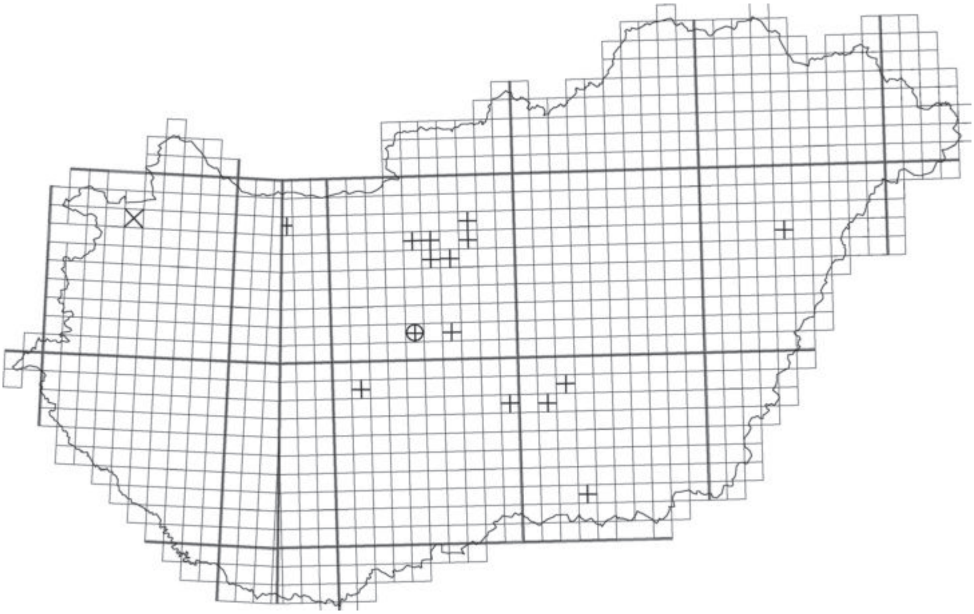

Figure 9. *Bombus fragrans* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

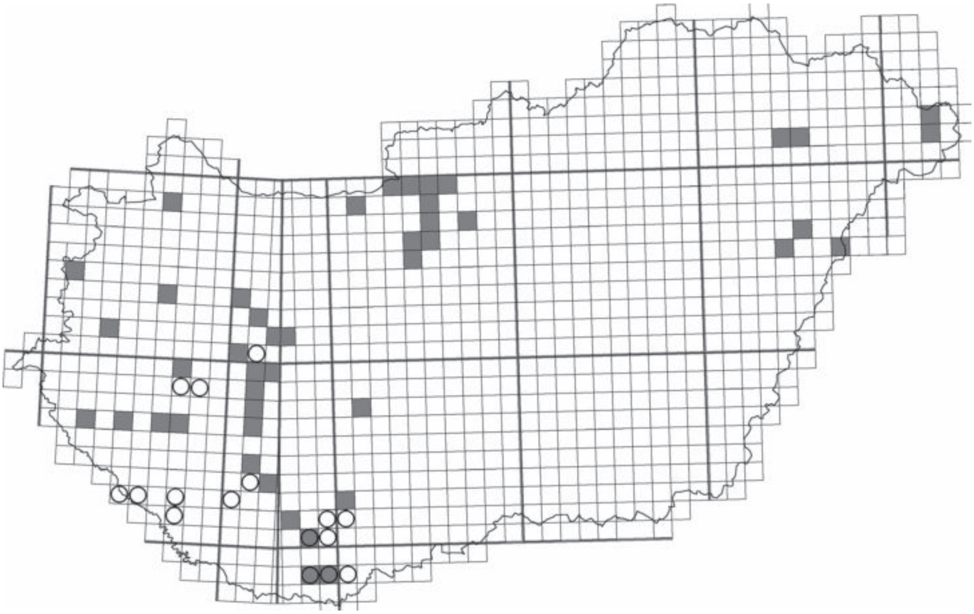

Figure 10. *Bombus haematurus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

Figure 11. *Bombus hortorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

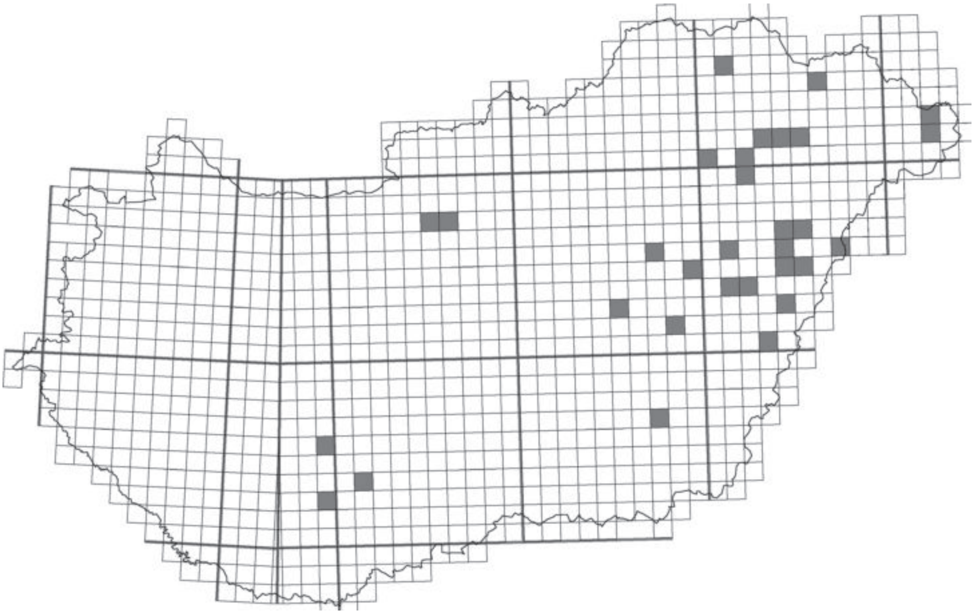

Figure 12. *Bombus hortorum/ruderatus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

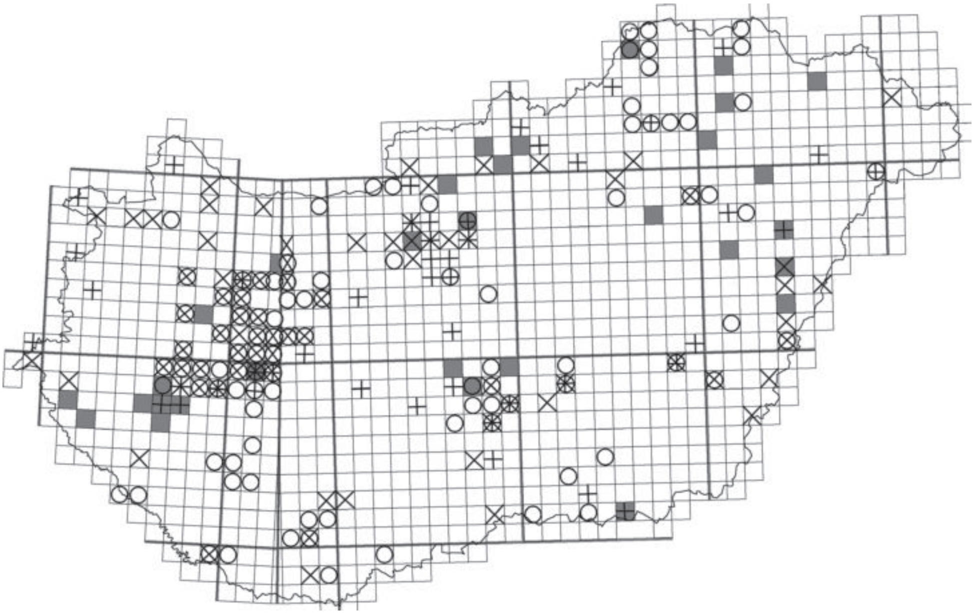

Figure 13. *Bombus humilis* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

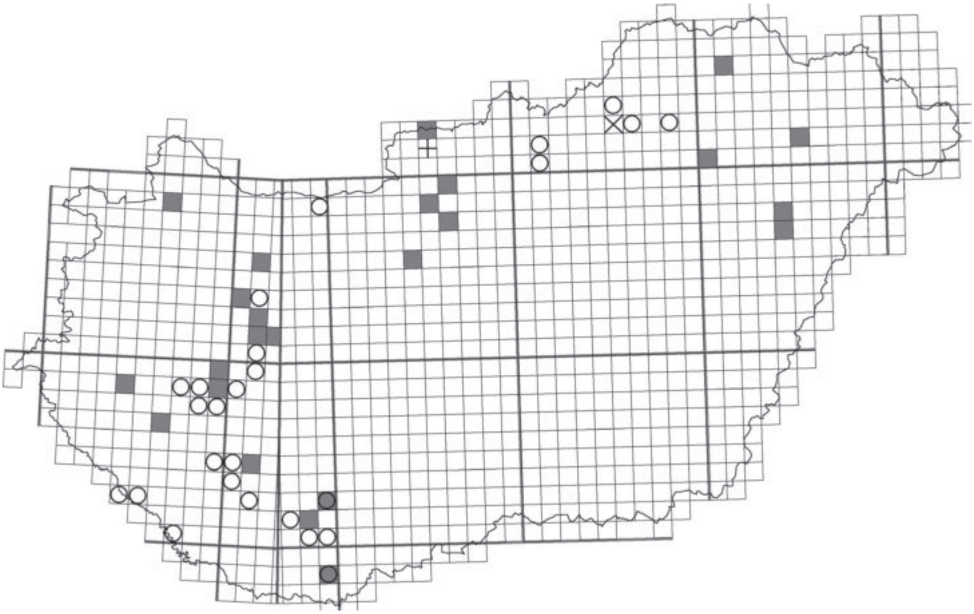

Figure 14. *Bombus hypnorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

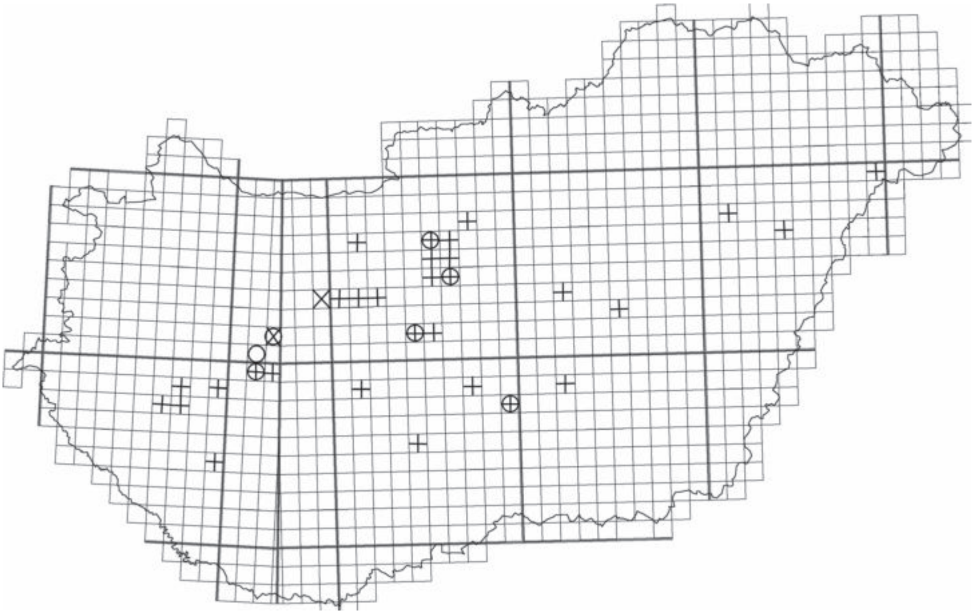

Figure 15. *Bombus laesus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

Figure 16. *Bombus lapidarius* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

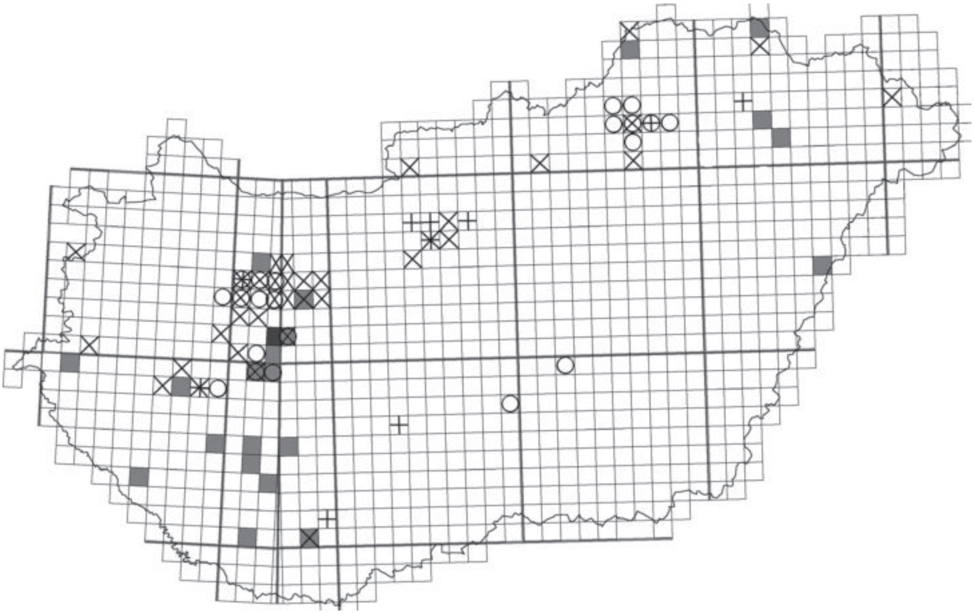

Figure 17. *Bombus lucorum* and *Bombus cryptarum*. *B. cryptarum* belongs to the *B. lucorum* species complex, with only one Hungarian data from YN21 UTM cell where *B. lucorum* have been not reported yet. Distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

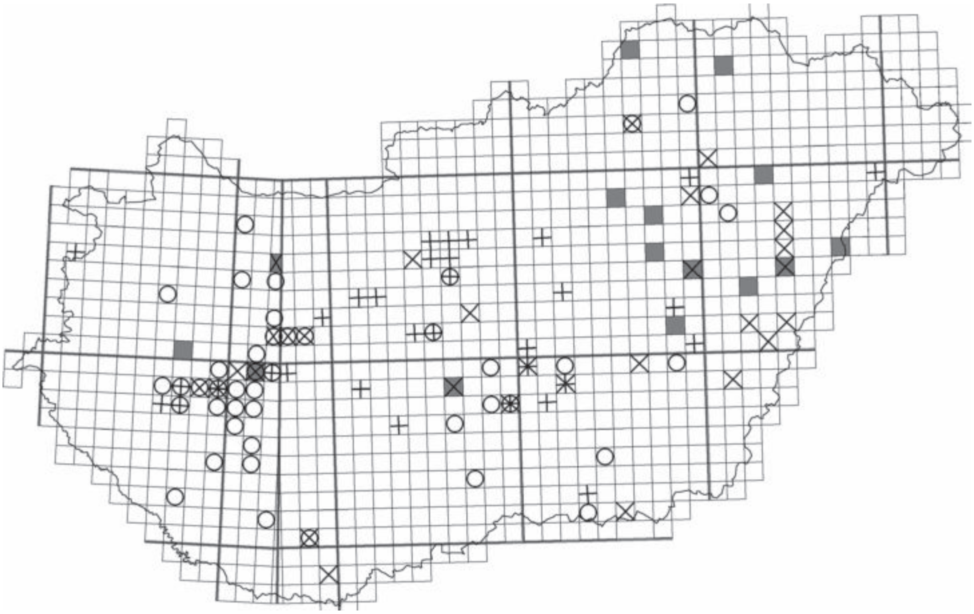

Figure 18. *Bombus muscorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

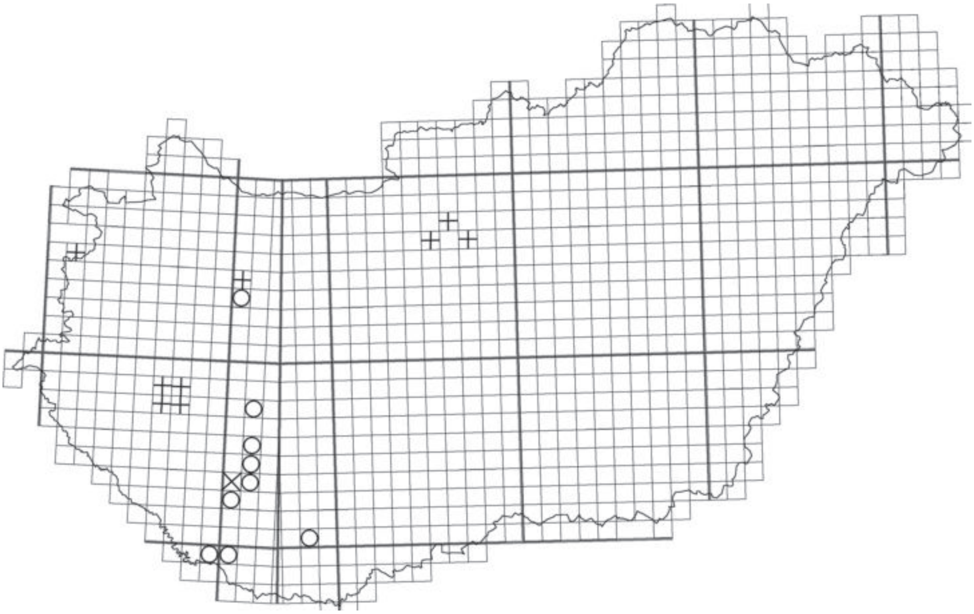

Figure 19. *Bombus paradoxus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

Figure 20. *Bombus pascuorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

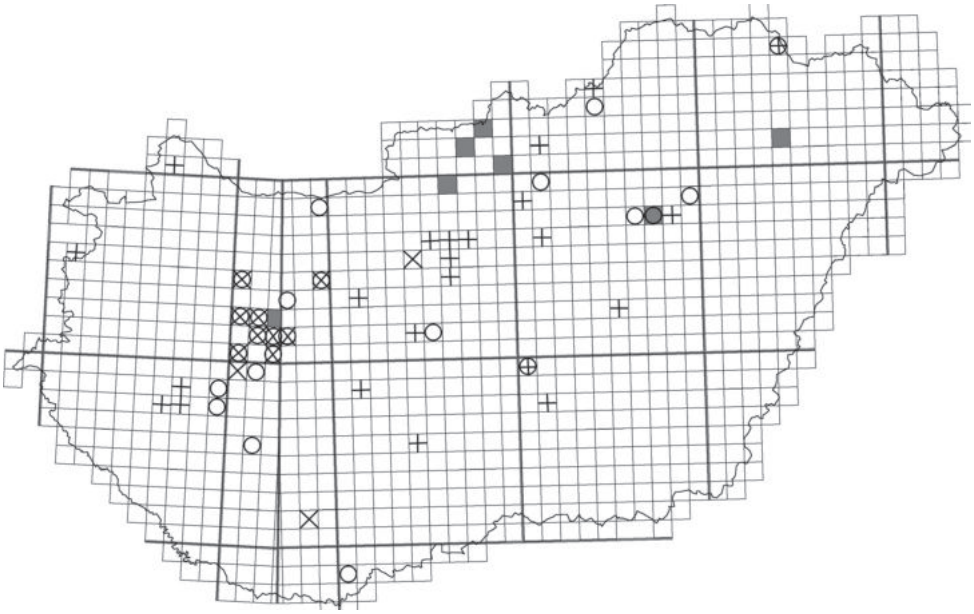

Figure 21. *Bombus pomorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

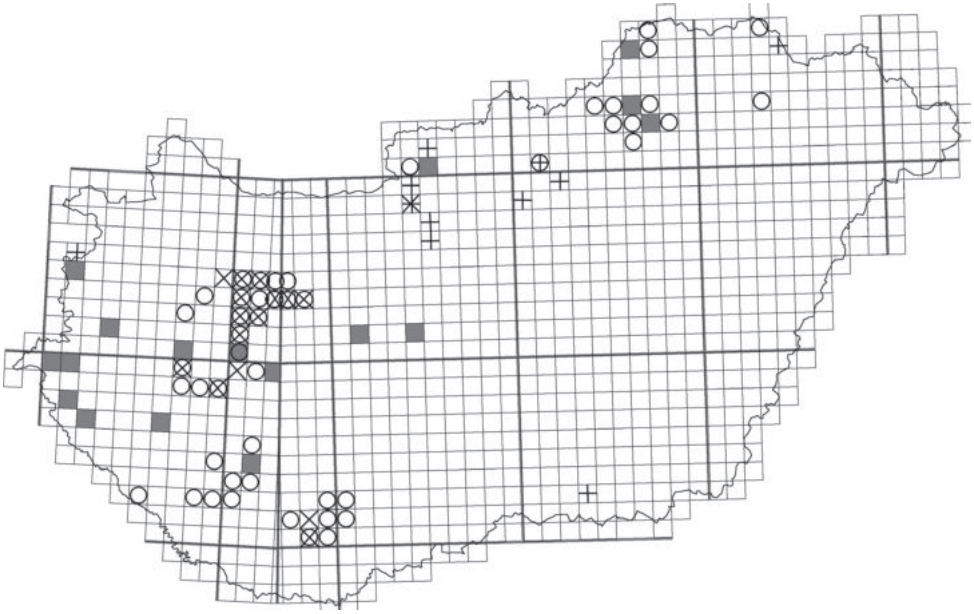

Figure 22. *Bombus pratorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

Figure 23. *Bombus ruderarius* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

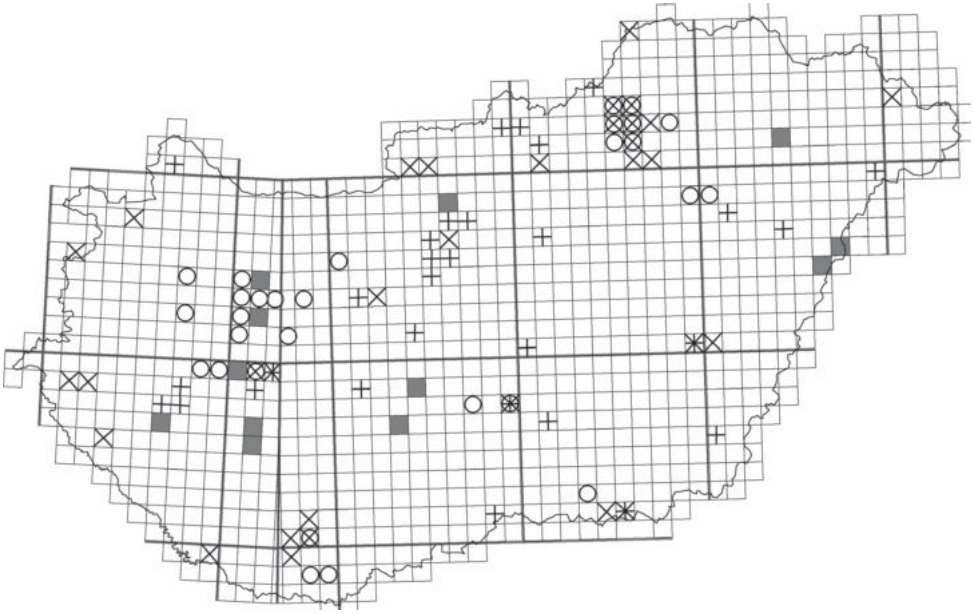

Figure 24. *Bombus ruderatus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

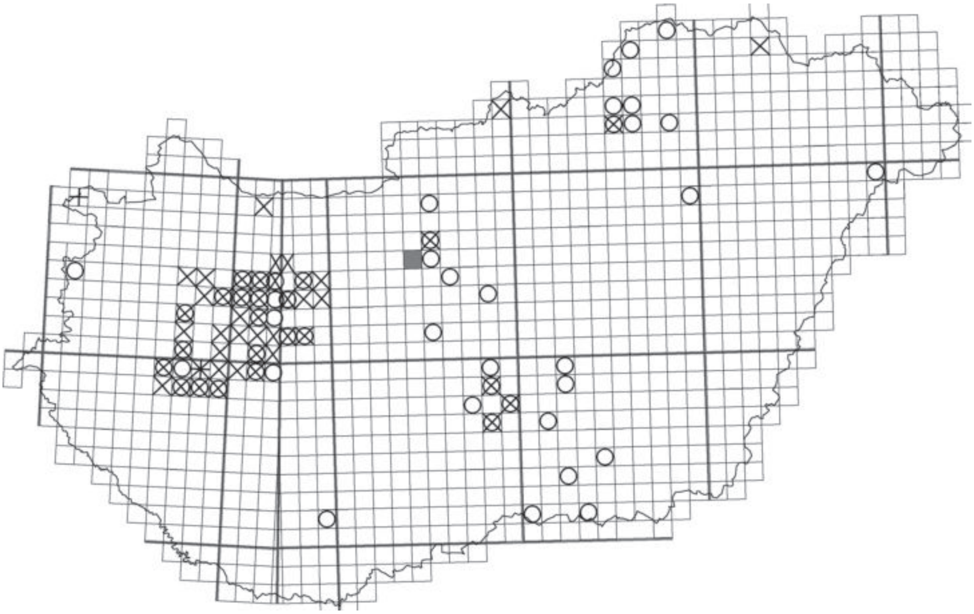

Figure 25. *Bombus rupestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

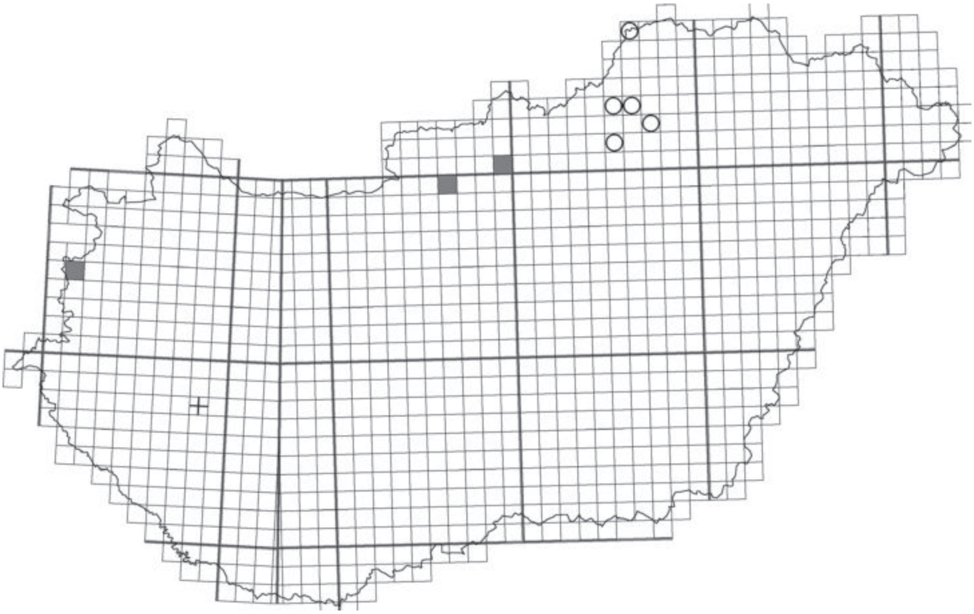

Figure 26. *Bombus soroeensis* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

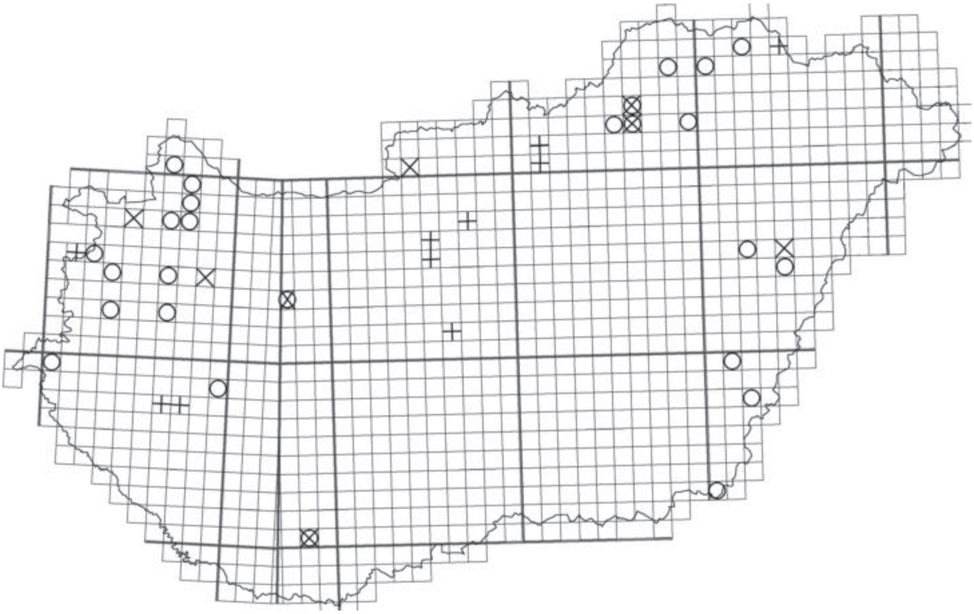

Figure 27. *Bombus subterraneus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

Figure 28. *Bombus sylvarum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

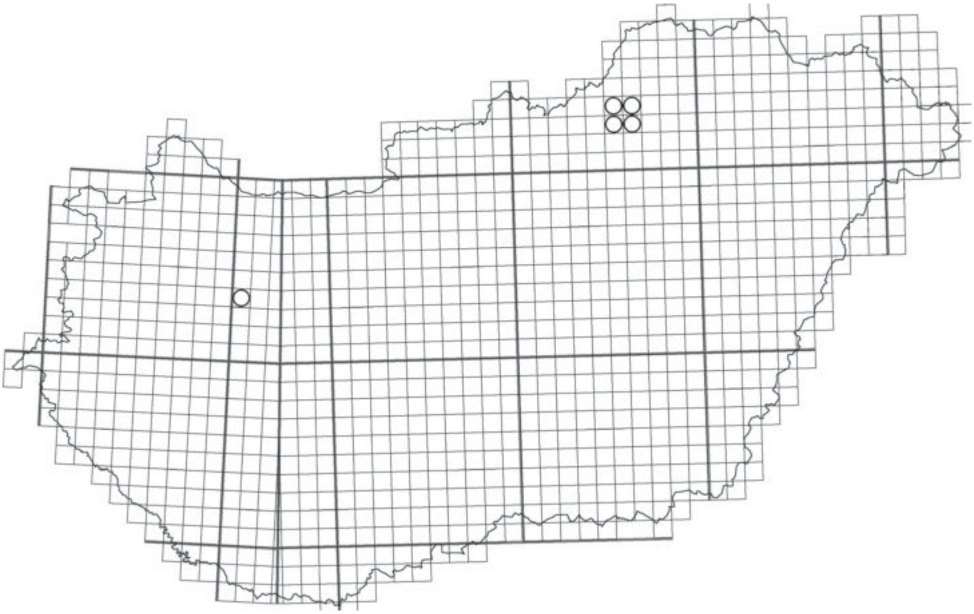

Figure 29. *Bombus sylvestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

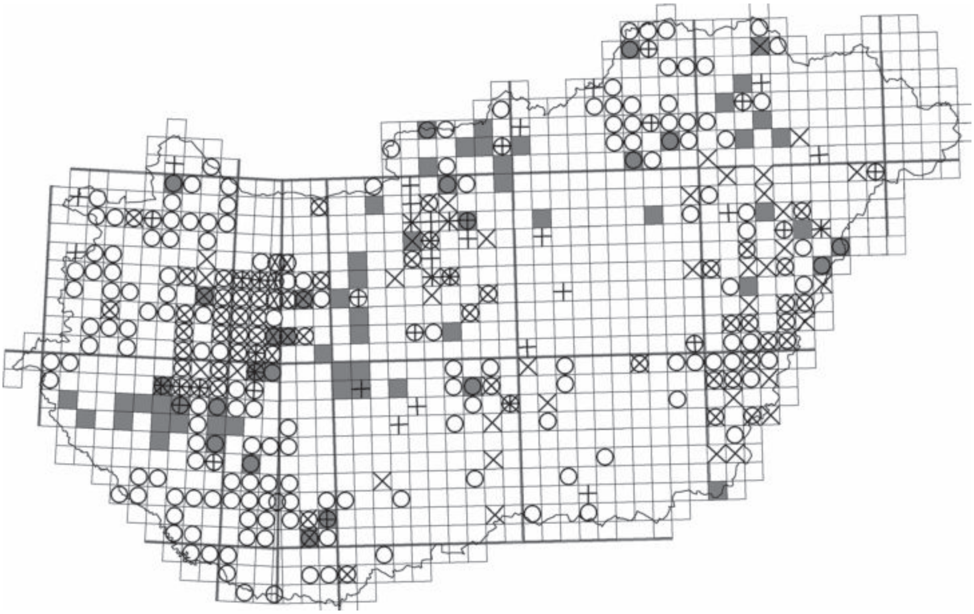

Figure 30. *Bombus terrestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

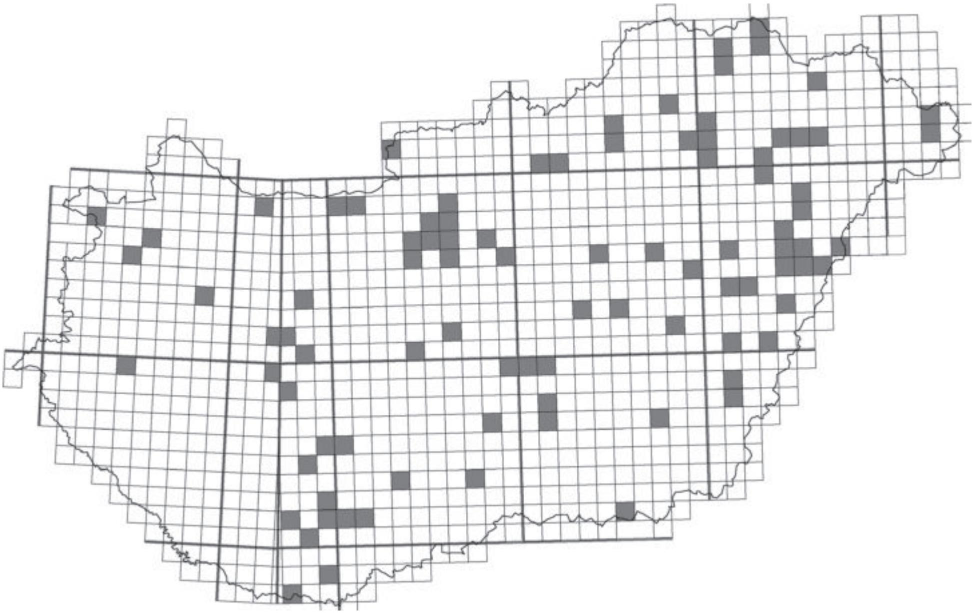

Figure 31. *Bombus terrestris/lucorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

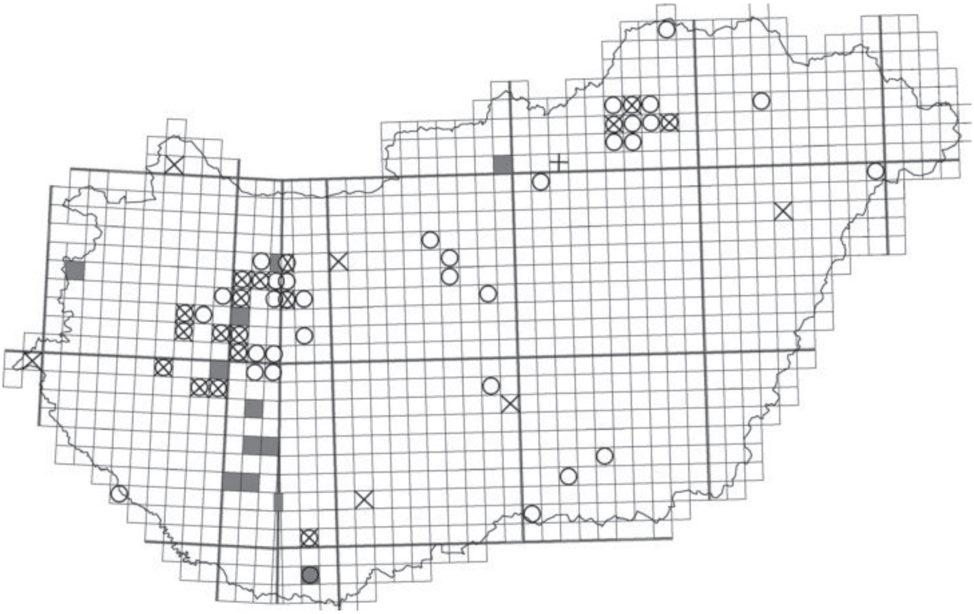

Figure 32. *Bombus vestalis* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

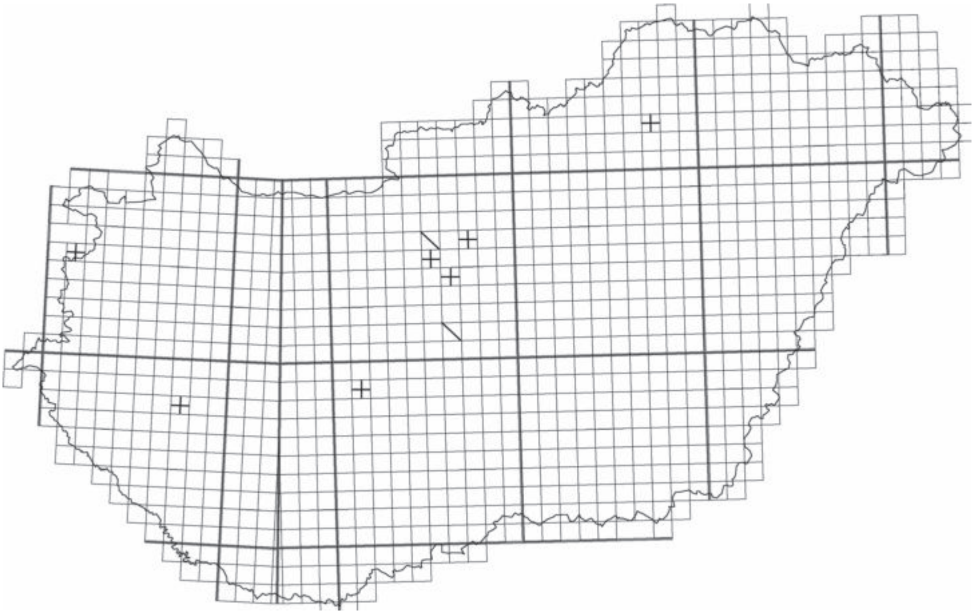

Figure 33. Local extinct species: *Bombus distinguendus* (+), *Bombus cullumanus serrisquama* (\), distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

Confirming the result of Rakonczay (1989), of the 31 species previously recorded in Hungary, *B. cullumanus serrisquama* and *B. distinguendus* can be considered extinct in Hungary, due to the lack of recent records.

Most species have only a few and in many cases even only archaic records, that accounted for the reevaluation of their status and need of further targeted investigations. The occurrence of 9 species (*B. bohemicus*, *B. confusus*, *B. consobrinus*, *B. cryptarum*, *B. fragrans*, *B. laesus*, *B. paradoxus* (synonym *B. confusus paradoxus*), *B. subterraneus*, *B. sylvestris*) in Hungary needs verification. On the other hand, distribution of other seven species have become well known with more than 250 UTM data records that allow us to draw a more realistic picture on their distribution, vulnerability status and their role in ecosystem services.

The relative frequencies of the species were recalculated and decreasing of the relative frequency of 11 species were detected and four of them has no data from the last two decades.

Seven species showed constant distribution, while seven others had increasing relative frequencies. In the case of five species, the trend of relative frequency changed during the latest period of studies: the trend of *B. sylvarum* changed from decreasing to stable, while the trend of *B. pascuorum* and *B. lucorum* changed from stable to increasing, and the trend of *B. argillaceus* changed from decreasing to increasing.

Although members of subgenus *Psithyrus* were not studied previously (Sárospataki et al. 2005), relative frequency trends of their four representatives could also be revealed based on our data: the relative frequency of *B. campestris* was increasing through all the studied periods, while the trend of *B. barbutellus* and *B. rupestris* changed from increasing to decreasing, and the trend of *B. vestalis* changed from increasing to stable. Due to their rarity and decreasing relative frequencies, their protected status can be recommended. The area of the species formerly classified as *Psithyrus* are within the area of their host species. The relative frequencies of *B. lapidarius* and *B. terrestris*, which are the hosts of *B. rupestris* and *B. vestalis* were not changed during the studied periods. Contrarily, among the hosts of *B. barbutellus*, the frequency of *B. hortorum* was stable, while frequency of *B. argillaceus* increased and *B. ruderatus* showed an opposite trend.

The previously observed increasing relative frequency of *B. hypnorum* and *B. soroeensis* remain increasing also after 2000. The intensive increase of relative frequencies of *B. haematurus* and *B. argillaceus* showed continuous spread of these species in Hungary during the last two decades. It can be explained rather with natural expansion, than artificial spreading of managed colonies, since their use is not common in Hungary, however the greening programs and promotion of sustainable agricultural methods methods can also help their spread. Although the expansion of the area of *B. haematurus* to northwest in Central Europe was already known (Biella et al. 2020), their spread to the northeast is first published here. Considering the direction of its spread it will be worth to study its appearance northeast of Hungary, e.g. in Ukraine and East Slovakia and later in Belarus.

Twenty years ago, *Bombus argillaceus* was a rare species with a decreasing distribution and was classified as critically endangered according to the IUCN (Sárospataki et al. 2005; Kosior et al. 2007). In the last 20 years, its relative frequency has increased significantly, and now it is a moderately frequent species in Hungary. As with *Bombus haematurus*, it will be worthwhile studying the northern limits of its range.

Conclusion

Climate change, warming winters and changes in landscape structure can significantly affect the distribution of bumble bee species in Hungary (Biella et al. 2020; Novotny et al. 2021). Beyond the effects of the climate change, the distribution of bumble bees is strongly affected by their heat-stress resistance. Since, the Mediterranean and temperate zone widely distributed eurytopic species are less sensitive to heat stress and warming, than the rare stenotopic species adapted to cold climate, thus further expansion of their area can be expected in the near future (Rasmont et al. 2015; Martinet et al. 2020). This ongoing process was clearly showed by our results on the intensive expansion of *B. argillaceus* and *B. haematurus*, which can resist to heat stress, and the high relative frequency of the widely distributed *B. terrestris*. Findings of Rasmont et al. (2015) were also confirmed by the decreasing relative frequency of eight species (*B. barbutellus*, *B. confusus*, *B. humilis*, *B. muscorum*, *B pomorum*, *B. ruderatus*, *B. rupestris*, *B. subterraneus*) of the Hungarian fauna, that also proved the significant and even dramatic effect of climate change on *Bombus* assemblages.

Regular monitoring of *Bombus* assemblages is recommended. The actualized distribution maps provide basis for both gap analysis and prioritization. The investigation of previously unexplored areas (white patches) and UTM cells containing only archaic data, as well as confirmation of the data of species with dubious data should be prioritized.

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In a paper about a new species of *Apanteles* (Microgastrinae) (Liu & Chen, 2023), we regret the omission of one author, Jun-hua Chen, in the second place of the author list who did a great job in the construction of the Hymenoptera Collection of Zhejiang University, Hangzhou, CHINA (ZJUH) for this study, as well as the mistakes in institution order and corresponding author. We provide the correct information below.

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MONOGRAPH

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The genus *Andrena* Fabricius, 1775 in the Iberian Peninsula (Hymenoptera, Andrenidae)

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Abstract

The Iberian Peninsula is a global hotspot for bee diversity due to its large number of different habitats, particularly Mediterranean scrubland, mountains, and hot and cold steppe. In line with its status as a hotspot of bee diversity, the peninsula hosts a very large *Andrena* fauna, which despite progress in recent years remains incompletely studied, particularly with reference to genetic investigation. Here the Iberian *Andrena* fauna is comprehensively revised, resulting in a total of 228 recorded species. Numerous taxonomic changes are necessary following inspection of museum specimens, type material, and genetic investigation. The following subgenera are described: *Pruinosandrena* **subgen. nov.**, containing six taxa previously placed in the subgenus *Campylogaster* Dours, 1873, and *Blandandrena* **subgen. nov.**, *Bryandrena* **subgen. nov.**, *Limbandrena* **subgen. nov.**, and *Ovandrena* **subgen. nov.**, containing one, one, one, and four taxa previously placed in the subgenus *Poliandrena* Warncke, 1968. *Andrena* (*Limbandrena*) *toelgiana* Friese, 1921 **syn. nov.** is synonymised with *A.* (*Limbandrena*) *limbata* Eversmann, 1852. The current lectotype of *A.* (*Micrandrena*) *obsoleta* Pérez, 1895 was incorrectly designated by Warncke; the taxon differs from *A. obsoleta* sensu Warncke, belonging instead to a taxon within the *A. mariana* Warncke, 1968 complex. A new lectotype is designated for *A. obsoleta* **sp. resurr.** from Algeria, and *A. mariana solda* Warncke, 1974 **syn. nov.** is synonymised with it; *A.* (*Micrandrena*) *alma* Warncke, 1975 **stat. nov.**, *A.* (*Micrandrena*) *mica* Warncke, 1974 **stat. nov.**, and *A.* (*Micrandrena*) *tenostra* Warncke, 1975 **stat. nov.** are raised to species status. *Andrena* (*Truncandrena*) *abunda* Warncke, 1974 **stat. nov.**, *A.* (*Micrandrena*) *lecana* Warncke, 1975 **stat. nov.**, *A.* (*Pruinosandrena*) *parata* Warncke, 1967 **stat. nov.**, *A.* (*Micrandrena*) *pauxilla* Stöckhert, 1935 **sp. resurr.**, *A.* (*Pruinosandrena*) *succinea* Dours, 1872 **sp. resurr.**, and *A.* (*Notandrena*) *varuga* Warncke, 1975 **stat. nov.** are also returned or elevated to species status. A lectotype is designated for *A.* (*Euandrena*) *lavandulae* Pérez, 1902 **sp. resurr.** which is returned to species status, and *A.* (*Euandrena*) *impressa*

Warncke, 1967 **syn. nov.** is synonymised with it. *Andrena* (*Truncandrena*) *nigropilosa* Warncke, 1967 **stat. nov.** is elevated to species status, and *A.* (*Truncandrena*) *truncatilabris espanola* Warncke, 1967 **syn. nov.** is synonymised with it as a junior subjective synonym. A lectotype is designated for *A.* (*Melandrena*) *vachali* Pérez, 1895; *A.* (*Melandrena*) *creberrima* Pérez, 1895 **syn. nov.** and *A.* (*Melandrena*) *vachali* **syn. nov.** are synonymised with *A.* (*Melandrena*) *discors* Erichson, 1841, and *Andrena* (*Melandrena*) *hispania* Warncke, 1967 **syn. nov.** is synonymised with *A.* (*Melandrena*) *morio* Brullé, 1832. *Andrena* (*Pruinosandrena*) *mayeti* Pérez, 1895 **syn. nov.** is newly synonymised with *A.* (*Pruinosandrena*) *caroli* Pérez, 1895 and *A.* (incertae sedis) *setosa* Pérez, 1903 **syn. nov.** is newly synonymised with *A.* (incertae sedis) *ranunculorum* Morawitz, 1877. *Andrena* (*Simandrena*) *cilissaeformis* Pérez, 1895 **sp. resurr.** is returned to species status, and is the correct name for *A.* (*Simandrena*) *breviscopa* auctorum. *Andrena* (incertae sedis) *breviscopa* Pérez, 1895 is returned to synonymy with *A.* (incertae sedis) *numida* Lepeletier, 1841, and *A.* (incertae sedis) *inconspicua* Morawitz, 1871 is newly synonymised **syn. nov.** with *A. numida*. *Andrena* (*Euandrena*) *isolata* **sp. nov.** and *A.* (*Micrandrena*) *ortizi* **sp. nov.** are described from the Sierra Nevada (Granada), *A.* (*Truncandrena*) *ghisbaini* **sp. nov.** is described from Málaga province, and *A.* (*Avandrena*) *juliae* **sp. nov.** is described from Cádiz province. The males of *A.* (*Micrandrena*) *alma* and *A.* (*?Euandrena*) *ramosa* Wood, 2022 are described. Additional lectotypes are designated for *A.* (*Plastandrena*) *asperrima* Pérez, 1895, *A.* (*Plastandrena*) *atricapilla* Pérez, 1895, *A.* (*Aenandrena*) *hystrix* Schmiedeknecht, 1883, *A.* (*Pruinosandrena*) *lanuginosa* Spinola, 1843, *A.* (*Notandrena*) *ranunculi* Schmiedeknecht, 1883, and *A.* (*Euandrena*) *symphyti* Schmiedeknecht, 1883. Neotypes are designated for *A.* (*Chlorandrena*) *boyerella* Dours, 1872, *A.* (*Notandrena*) *griseobalteata* Dours, 1872, *A.* (*Taeniandrena*) *poupillieri* Dours, 1872, *A.* (*Pruinosandrena*) *succinea* Dours, 1872, and *A.* (incertae sedis) *numida* Lepeletier, 1841. Type photographs and diagnostic characters are presented in each case, as well as new dietary information for understudied species. Finally, an identification key is presented in order to facilitate future research on this hyper-diverse genus in one of their global diversity hotspots, and current and future research perspectives for Iberian *Andrena* are discussed.

Keywords
Cryptic species, DNA barcoding, Iberian endemic species, solitary bees, taxonomy

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Introduction

The Iberian Peninsula is one of the best places to find and study wild bees globally, with more than 1,000 species present due to its dry and warm climate, abundance of open seasonal habitats, status as a glacial refugium, and rich diversity of flowering plants (Lhomme et al. 2020; Ortiz-Sánchez 2020; Orr et al. 2021). Within this large fauna, the most speciose element consists of bees from the genus *Andrena* which are abundant throughout the peninsula and which are a ubiquitous component of the spring pollinator community. This pattern is typical for the Holarctic, as *Andrena* are the second largest genus of bees globally with around 1,650 species following recent revisions (Ascher and Pickering 2020; Pisanty et al. 2022a; Wood and Monfared 2022) and are almost always the most speciose genus in regional faunas across this region. Considering that bees emerged in the early to mid-Cretaceous period 110–140 million years ago (Danforth et al. 2013; Branstetter et al. 2017; Murray et al. 2018), as a major bee genus *Andrena* is relatively young, arising around 25 million years ago (Pisanty et al. 2022b). Given the size of the genus, *Andrena* has speciated extremely quickly (Bossert et al. 2022), leading to enormous species richness and often extreme taxonomic difficulty in delineating and recognising species. Given the abundance and ubiquity of this genus in the Iberian fauna, it is desirable to have suitable taxonomic resources to enable study of this rich fauna. However, nothing resembling an accessible revision is currently available.

Despite the great number of species present in Iberia, very few authors have worked on this fauna in any detail, certainly compared to that of north-western Africa (e.g. Erichson 1841; Lepeletier 1841; Dours 1872, 1873; Pérez 1895, 1902, 1903; Morice 1899; Schmiedeknecht 1900; Saunders 1908; Benoist 1961). Somewhat incredibly, before 2020, only six papers were published that described currently valid *Andrena* species with a *locus typicus* in Iberia: Erichson (1835, three species), Dours (1873, one species), Pérez (1895, six species), Pérez (1902, one species), Warncke (1967, 10 species), and Warncke (1975a, 15 species), although some other works described what are now synonymous names (e.g. Spinola 1843; Pérez 1903; Friese 1922). The fauna was therefore quite unstudied before the revisionary work of Warncke (1967, 1975a, 1976), and following these publications almost no additional taxonomic work was carried out on the Iberian fauna until very recently. This attention has come in the form of revisionary taxonomic work and faunal work that has provided new distributional records, demonstrated the presence of doubtful species in Iberia, and recorded new species for the Iberian *Andrena* fauna (Baldock et al. 2018; Álvarez Fidalgo et al. 2020, 2021a, 2021b, 2022a, 2022b; Wood et al. 2020a, 2021, 2022; Álvarez Fidalgo and Aguado Martín 2022; Wood 2022; Wood and Ortiz-Sánchez 2022).

As a result of these collective efforts, our understanding of Iberian *Andrena* is as great as it has ever been. However, commencing ecological or taxonomic work on this fauna remains highly challenging due to the lack of accessible identification resources. Valuable information is available in original descriptions, group revisions (e.g. Schwenninger 2015), and treatments on other regional faunas (e.g. Schmid-Egger and Scheuchl 1997; Amiet et al. 2010), as well as in the global revisionary catalogue of Gusenleitner and Schwarz (2002). However, digging through this mountain of information is time consuming and sometimes dispiriting and confusing, in part due to persistent problems with species concepts and taxonomic nomenclature. It is therefore the objective of this present paper to resolve most of the outstanding taxonomic problems with the Iberian *Andrena* fauna and to present a new synthesis of this information in the form of a comprehensive identification key. Due to the strong faunal links between North Africa and Iberia, it is necessary to revise parts of the North African *Andrena* fauna in parallel; a subsequent paper dealing with taxonomic revisions exclusive to the North African *Andrena* fauna will follow shortly. Therefore, several taxonomic changes will be made here that affect the North African fauna, although this is not the principal objective of the current work. Finally, novel ecological data are provided concerning the pollen foraging niche of unstudied Iberian or West Mediterranean *Andrena* species.

Methodology

Species concepts

It is important to briefly discuss species concepts in the context of this work. Because *Andrena* taxonomy in the West Palaearctic region was dominated by Klaus Warncke in the second half of the 20th Century, it is his classification system that has largely been followed by subsequent workers (e.g. Gusenleitner and Schwarz 2002). Warncke recognised species solely based on their morphology, and used subspecies to delineate geographical variation. Subsequent workers have treated many of these subspecies as valid species based on morphological, genetic, and ecological data (e.g. Gusenleitner and Schwarz 2002; Schmid-Egger 2005; Schwenninger 2015; Praz et al. 2019; Kratochwil 2021; Wood et al. 2021; McLaughlin et al. 2022; Pisanty et al. 2022a).

To date, there has not been a deep discussion of species concepts in *Andrena* compared to better studied bee groups such as bumble bees (*Bombus*, e.g. Williams et al. 2020; Rasmont et al. 2021). Use of a purely biological species concept in *Andrena* is premature in almost all cases as we have extremely limited understanding of their mating systems and pre- and post-zygotic reproductive barriers, with this only being estimated *post hoc* by quantifying realised gene flow (e.g. McLaughlin et al. 2022). Given that the study of *Andrena* taxonomy using genetics is still in its infancy, it is best to consider *Andrena* species to be evolutionarily independent lineages (de Queiroz 2007), and that through the application of integrative taxonomy (including genetic, morphological, and ecological data), one can arrive at a robust species concept (Schlick-Steiner et al. 2010).

As such, the present work builds on the morphological species concepts developed by previous workers and integrates genetic and ecological lines of evidence in order to ensure evidence-based species delineation. In this context, subspecies are used pragmatically, following the position of Mayr (1963, see Rasmont et al. 2021) and drawing from the taxonomic heritage of Warncke's West Palaearctic revisions. Where sufficient data are available, these subspecies are validated as species in their own right or synonymised. Where such data are not available or the results are ambiguous, subspecies are retained in order to indicate future avenues of taxonomic study.

Genetic sampling and analysis

Andrena specimens were sampled in Iberia and Morocco, predominantly during May–July 2021 in Spain and March–July 2022 in Morocco, but also using specimens collected in previous years. For genetic barcoding, a single midleg was removed from pinned specimens and sent to the Canadian Center for DNA barcoding (CCDB) in Guelph, Canada, for DNA extraction and sequencing (Ivanova et al. 2006). Specimens were sequenced following standardised high-throughput protocols. Both Lep1 and BeeCox1F1 primers were used (Hebert et al. 2004; Bleidorn and Henze 2021) to target the COI-5 region. All sequences are published on the Barcode of Life Database (BOLD) website under the public dataset "DS-ANDWMED".

Phylogenetic trees were supplemented with additional published sequences (e.g. Schmidt et al. 2015) that were downloaded from Genbank and the Barcode of Life Data System. Trees were also significantly enriched with sequences produced by the Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO, Portugal) as part of a collaboration to barcode the Portuguese bee fauna that will be published in the near future, and sequences will be available on BOLD. Sequences beginning with the code 'IBIHM' were generated by CIBIO. Sequences were aligned using MAFFT (Katoh and Standley 2013). Aligned sequences were analysed in Seaview (Gouy et al. 2010) using a maximum likelihood analysis which was run with 1000 bootstraps. Intra- and interspecific distances were calculated using MEGA-X (Kumar et al. 2018). Outgroups were chosen based on the subgeneric analysis of Pisanty et al. (2022b) in order to ensure that the selected outgroup species is part of a subgenus or species group more basal to those selected for focused study.

Taxonomic decisions were informed by analysis of the COI gene. However, decisions were not taken exclusively on the basis of these analyses, as there are a number of inherent limitations when using this fragment to inform taxonomy. The COI fragment itself only represents a single locus of mitochondrial DNA which is inherited matrilineally, can introgress across species boundaries, can transfer to the nuclear genome, cannot detect hybridisation, and can produce topologies that do not represent species trees (e.g. Toews and Brelsford 2012). Species delineation based solely on differences in mitochondrial DNA is therefore discouraged, with integrative taxonomic preferred (Padial et al. 2010; Gallego-García et al. 2023). More broadly, more powerful genetic techniques are now available such as Ultra Conserved Elements that allow the generation of sequences from thousands of loci. These have been applied to bee taxonomy at the species-level, and whilst they often produce results concordant with COI analysis (e.g. de Oliveira Andrade et al. 2022; McLaughlin et al. 2022), they can also clearly resolve problems for which COI analysis produces ambiguous or inconclusive results (e.g. Gueuning et al. 2020). However, to date, UCEs have predominantly been employed to resolve specific questions, and not to sample across a fauna in order to have the broadest possible taxonomic coverage, as was the objective in this study. Given these limitations, combined with the conceptual points discussed above, analysis of the COI fragment is used as an additional line of evidence to support taxonomic decision making, and is never used as the sole metric.

More broadly, COI analysis is most useful when dealing with species-specific alpha taxonomic decisions. Due to the rate at which this fragment accumulates mutations, whilst closely related species are grouped together, more distantly related species often show no clear structuring and the true evolutionary relationships are not captured. For this, more conserved genes must be sampled, such as by using UCEs. In this work, several new *Andrena* subgenera are described and illustrative phylogenetic trees are presented based on analysis of the COI fragment; the description of these subgenera is based on the work of Pisanty et al. (2022b) who identified undescribed clades of *Andrena*. These clades were not discovered here through analysis of the COI fragment, and these illustrative phylogenetic trees should not be considered strong support for their existence.

Finally, there are several cases presented here where morphological and genetic data produce ambiguous results concerning the status of certain taxa. Several of these taxa are widespread, and are usually described from outside of the Iberian Peninsula (e.g. see problems with paraphyly of *A. hedikae* Jäger, 1934). In these cases, no taxonomic action is taken, as it is preferable to have topotypic genetic samples and to consider these taxa across their entire nominal range. Where multiple valid species are potentially present, these species are referred to using the phrase ‘aggregate’ to reflect this situation. In contrast, when species are described from Iberia or have ranges that are restricted to the peninsula or to the West Mediterranean region, taxonomic decisions can be and are made with a greater degree of confidence which reflects the stronger and more complete evidence base available here.

Checklist and identification

For updating the Iberian *Andrena* species total, the checklist of Ortiz-Sánchez (2020) for mainland Spain and Portugal is used as a baseline. As this list is mostly correct, it is not considered necessary to produce a full annotated list for the Iberia *Andrena* fauna here; instead, a detailed justification will be given for the changes which have been made since 2020 or which are newly made here. A full checklist is provided in Suppl. material 1.

Identification key and geographic scope

For the identification keys, the female key is partly based on an unpublished key to Iberian *Andrena* written by Klaus Warncke (in German) that was kindly shared with me by Erwin Scheuchl (Ergolding, Germany). This key contained around 170 species, so considerable modifications were needed to account for the substantially larger faunal total recorded here, as well as accounting for newly described species and other taxonomic changes. The male key is novel, but both the female and male keys have been strongly inspired by the keys of Schmid-Egger and Scheuchl (1997) and Amiet et al. (2010). Additional characters have also been integrated from published works such as Schönitzer et al. (1995), Schwenninger (2009, 2013, 2015), and Praz et al. (2019, 2022). It is not always easy to remember the precise source of specific characters used here that have been accumulated and integrated over several years of study, as many are scattered throughout the literature in original descriptions, some derive from my own observations, and many are taken from the important diagnostic characters that are embedded throughout Gusenleitner and Schwarz (2002), but which can be somewhat obscure and hidden in individual species accounts. It is my hope that this key can bring this information together as a novel synthesis, becoming a more easily digestible resource.

The geographic scope of the key is limited to the Iberian Peninsula. It cannot be used in North Africa due to the many different or endemic faunal elements found there; for example, it only covers 114 of the 201 (56.7%) *Andrena* species known from Morocco (Wood in prep.). In a European context, the key can be used in the Balearic Islands, though only a fraction of the species covered in this work occur there. It can be generally used in southern France up to (but not including) the Maritime Alps, but some taxa are missing, such as endemic species (e.g. *Andrena* (*Taeniandrena*) *vocifera* Warncke, 1975) or widespread European species that do not cross the Pyrenees into Iberia (e.g. *Andrena* (*Micrandrena*) *pusilla* Pérez, 1903). However, the existing keys of Schmid-Egger and Scheuchl (1997) and Amiet et al. (2010) can be used in conjunction with this Iberian key to cover the vast majority of the *Andrena* fauna of southern France. The Iberian key should not be used in an Italian context as the Italian fauna is already sufficiently distinct to render the key of limited use, either in northern Italy due to the presence of eastern faunal elements (e.g. *Andrena* (*Aenandrena*) *bisulcata* Morawitz, 1877) or in Sicily due to the large number of non-Iberian North African elements present there, and also because many Iberian taxa are absent from the Italian fauna which has a much lower degree of endemism. Finally, this key should not be used in Corsica or Sardinia, as their island faunas require dedicated study due to the presence of endemic and North African species, as well as local forms or subspecies.

Distribution maps

No distribution maps are presented as part of this work, as they are for other revisions such as that of Ortiz-Sánchez and Pauly (2017). This is because whilst the material that I have examined, validated, and digitised is sufficient to allow a more or less complete taxonomic understanding of the Iberian fauna, it is not sufficiently geographically comprehensive, and hence distribution maps would be incomplete at the scale of the peninsula. Moreover, the distribution maps of Warncke presented by Gusenleitner and Schwarz (2002) are sufficiently correct to be informative to students of the Iberian fauna, with the assumption that the updated taxonomy presented here and by other workers after 1993 is integrated. Important distributional information is given in the text where relevant, and also in the identification key, as many taxa (particularly Euro-Siberian taxa) are geographically limited and the place of capture can strongly inform their identification (e.g. species restricted in an Iberian context to the Pyrenees, to central or southern Spain, etc).

Dietary niches of Iberian *Andrena* species

Pollen was removed from female *Andrena* specimens in order to quantify the pollen foraging niche of understudied species. Specimens were selected from Iberia and other Mediterranean countries when the species' range extends beyond the peninsula. Pollen was removed, processed, and identified following the methodology of Wood and Roberts (2018). Dietary classification (polylecty, mesolecty, oligolecty, narrow oligolecty) follows Müller and Kuhlmann (2008).

Morphological terminology

Morphological terminology follows Michener (2007). Specimens were measured from the centre of the clypeus at the front of the head to the apical tip of the metasoma to the nearest 0.5 mm. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 5X infinity corrected objective lens. Photographs were stacked using Helicon Focus B (HeliconSoft, Ukraine) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was made in Photoshop Elements (Adobe Systems, USA) in order to improve lighting to highlight specific characters.

The following abbreviations are used in the species descriptions: **A** = antennal segments, **S** = metasomal sterna, and **T** = metasomal terga. Subgeneric concepts follow Pisanty et al. (2022b) with the necessary modifications detailed below. In diagnoses, the defining characters of a species are given, with those of the indicated comparison species given in parentheses.

Collections studied

AMC	Personal collection of Andreas Müller, Wädenswil, Switzerland;
CMHC	Carlos M. Herrera collection, Estación Biológica de Doñana, Seville, Spain;
FJOS	Personal collection of Francisco Javier Ortiz-Sánchez, El Ejido, Spain;
FLOW	FLOWer lab collection, University of Coimbra, Coimbra, Portugal;
EBDC	EBD-CSIC collection, Estación Biológica de Doñana, Seville, Spain;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
MRSN	Museo Regionale di Scienze Naturali di Torino, Turin, Italy;
MSC	Personal collection of Maximillian Schwarz, Ansfelden, Austria;
MZUR	Zoological Museum of Sapienza University of Rome, Rome, Italy;
NHMUK	Natural History Museum, London, United Kingdom;
OÖLM	Oberösterreiches Landesmusum, Linz, Austria;
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands;
SMFD	Naturmuseum Senckenberg, Frankfurt am Main, Germany;
TJWC	Personal collection of Thomas J. Wood, Mons, Belgium;
UMONS	Laboratory of Zoology collection, University of Mons, Mons, Belgium;
ZISP	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia;
ZMHB	Museum für Naturkunde, Berlin, Germany.

Results

Genetic results and taxonomic changes

Genetic study of Iberian *Andrena* resulted in a number of important necessary changes to species concepts, as well as further supporting recent decisions. These results are presented here by subgenus; not all Iberian *Andrena* subgenera are treated here, as no taxonomic problems were detected for the majority of species.

Subgenus *Aciandrena* Warncke, 1968

In Iberia, this is a species-poor subgenus, consisting solely of *A. fulica* Warncke, 1974 and *A. vacella* Warncke, 1975. Warncke described *A. astrella* Warncke, 1975 from Iberia, and used it in combination with *A. fulica* as a subspecies. The two taxa were synonymised by Wood et al. (2020b) as one of the distinguishing characters was that North African populations had males with the clypeus entirely black, and Iberian populations had males with the clypeus yellow-marked, but males with both colour forms can be found in both geographical regions. There are no clear structural differences in the tergal punctation or the structure of the male genital capsule. Genetically (Fig. 1), Iberian and Moroccan populations differ by an average genetic distance of 1.61% (range 1.31–2.09%). Although Iberian material (including specimens WPATW318-21 and WPATW354-21 which are black-faced males from the Sierra Nevada) forms a clade with bootstrap support of 100, the overall low genetic distance is not considered to be sufficient to justify species status. The synonymy of Wood et al. (2020b) is therefore maintained. The broad *A. fulica* clade as a whole is well-defined with bootstrap support of 98.

Subgenus *Aenandrena* Warncke, 1968

This subgenus was found to be paraphyletic by Pisanty et al. (2022b), and the same result is found here with a COI-based analysis (Fig. 1). *Andrena hystrix* Schmiedeknecht, 1883 falls away from *A. aeneiventris* Morawitz, 1872 and *A. hedikae* Jäger, 1934. For convenience, these taxa are retained in the same subgenus, but future work will be needed to resolve this issue and probably to describe a new subgenus for the species around *A. hystrix* (currently three Palaearctic species from Morocco to Central Asia). Type material for *A. hystrix* was recently rediscovered, and a lectotype for this species is designated below.

In the true *Aenandrena*, four species are currently recognised, of which two are widely distributed, *A.* (*Aenandrena*) *aeneiventris* Morawitz, 1872 that was described from Italy and *A.* (*Aenandrena*) *hedikae* Jäger, 1934 that was described from the western Balkans. Both of the widespread species are nominally distributed from Iberia and Morocco to Central Asia in dry and warm parts of the Palaearctic (Gusenleitner and Schwarz 2002). Barcode analysis (Fig. 1) showed that *A. aeneiventris* specimens from Austria, Hungary, Israel, and Portugal formed a clade with bootstrap support of 99,

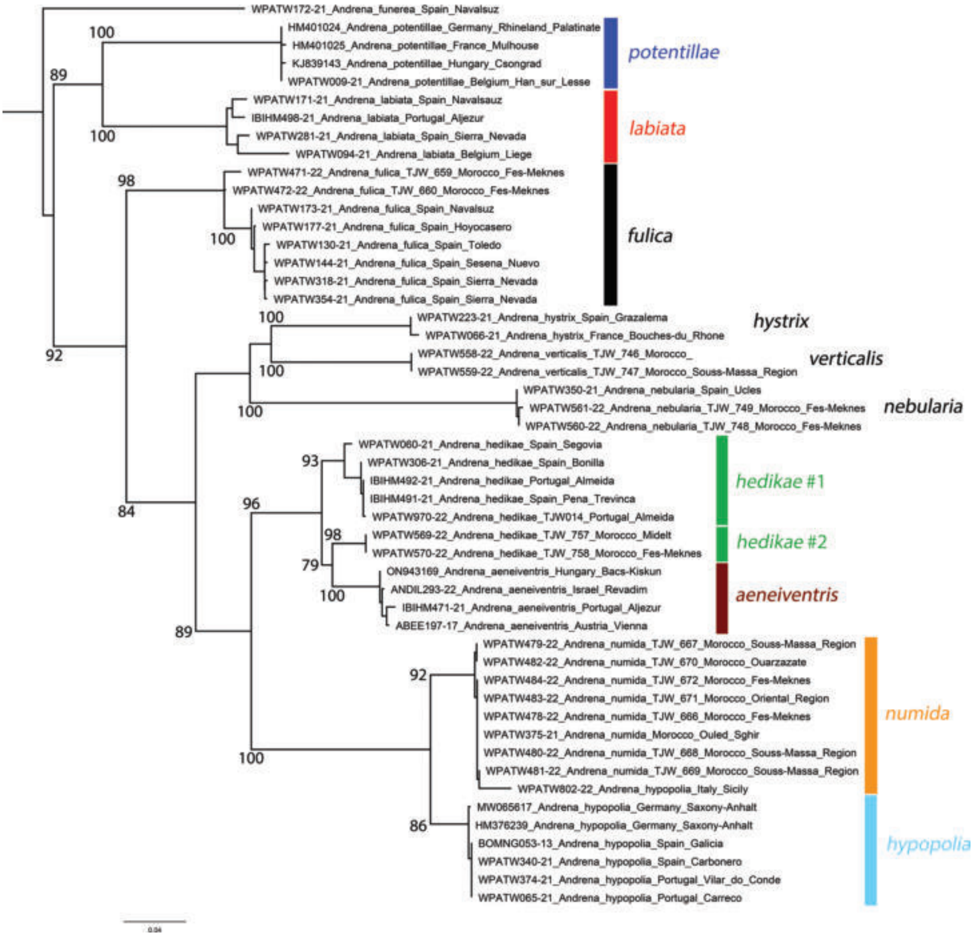

Figure 1. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Aciandrena* Warncke, 1968, *Aenandrena* Warncke, 1968 sensu lato, *Graecandrena* Warncke, 1968, *Poecilandrena* Hedicke, 1933, and the *numida*-group based on the mitochondrial COI gene. *Andrena* (incertae sedis) *relata* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

and with low average intraspecific genetic distance of 0.78% (range 0.30–1.06%). In contrast, *A. hedikae* formed two clades. Five specimens from Portugal and Spain formed a clade with bootstrap support of 93 with low differentiation of 0.82% (range 0.16–2.01%). Two specimens from northern Morocco had identical sequences and formed a clade with bootstrap support of 98. These two clades were separated by an average genetic distance of 4.55% (range 4.34–4.72%), and both were well-separated from *A. aeneiventris*, by an average genetic distance of 5.86% (range 4.98–6.67%) for Iberian specimens and 5.20% (range 4.86–5.75%) for Moroccan specimens. These genetic distances are substantial, but no taxonomic action is taken here, as sequences from south-eastern Europe are needed to i) further understand barcode variation in

A. hedikae and ii) identify which of these two clades matches populations from the *locus typicus*. Moreover, there are no apparent morphological differences between Iberian and Moroccan '*hedikae*'. Further study is required.

Subgenus *Chlorandrena* Pérez, 1890

This subgenus is clearly supported genetically (Pisanty et al. 2022b) and morphologically by the presence of a row of teeth on the posterior face of the female femur combined with strong 'crater punctures' on the terga. Barcodes generally supported all species concepts (Fig. 2), but there are some issues that must be discussed.

Andrena (*Chlorandrena*) *livens* Pérez, 1895 was described from north-eastern Spain. Warncke described *A. livens algeria* Warncke, 1967 from Tunisia on the basis of slight

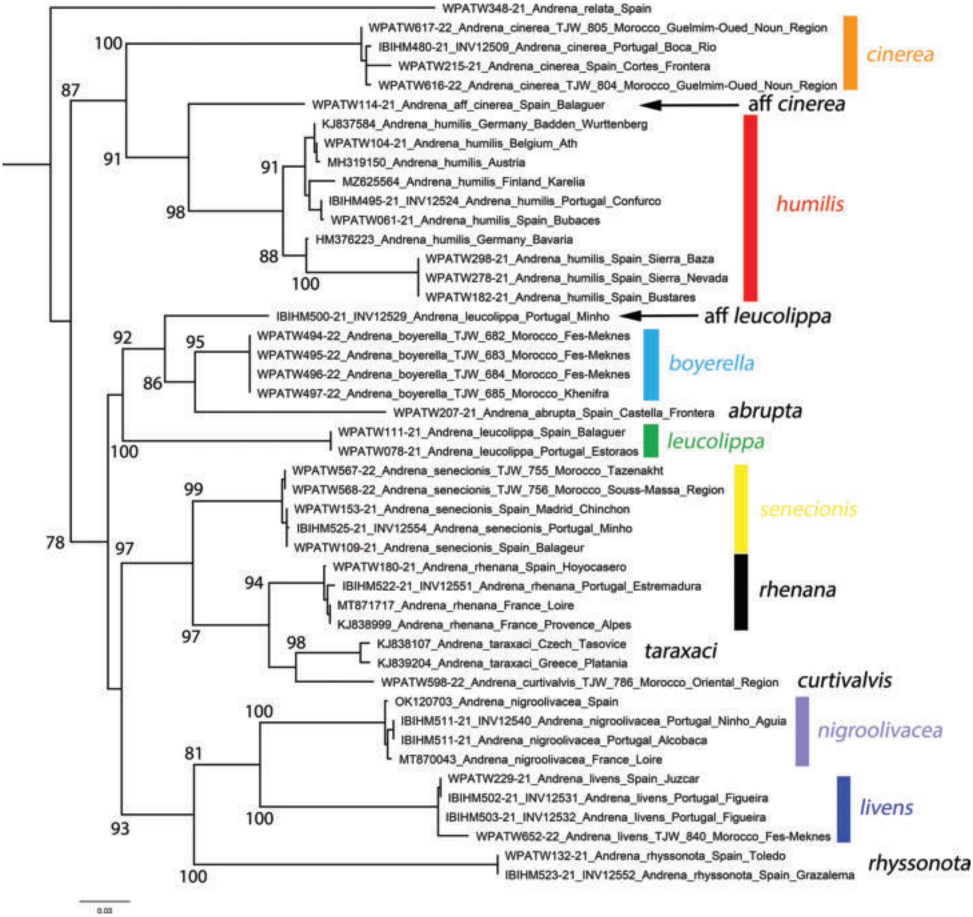

Figure 2. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Chlorandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (*Nobandrena*) *funerea* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

differences in the genital capsule and sternum eight. He also described *A. livens gruenwaldti* Warncke, 1967 from Sicily. Based on the sequences here, a Moroccan specimen conforming to *A. livens algeria* shows relatively low differentiation from Portuguese and Spanish specimens, being separated by an average genetic distance of 2.37% (range 2.16–2.47%). Additional samples are required to investigate the status of these subspecies, and also to sample *A.* (*Chlorandrena*) *agnata* Warncke, 1967 which is a poorly understood species in an Iberian context; I have seen no Iberian specimens, and it is included on the list on the basis of the single female paratype from Madrid, collected 6.vi.1946 by Dusmet (Warncke 1967). *Andrena agnata* is much closer morphologically to *A. livens* than the nearest neighbour in the current tree, *A.* (*Chlorandrena*) *nigroolivacea* Dours, 1873; no taxonomic action is taken until such sequences are available, and a broad *A. livens* concept is maintained for now.

The status of *A.* (*Chlorandrena*) *boyerella* Dours, 1872 and *A.* (*Chlorandrena*) *leucolippa* Pérez, 1895 and the relationship of these taxa to each other has been confused. Warncke (1967) used a subspecies concept, with *A. boyerella* s. str. present in North Africa and *A. boyerella leucolippa* present in Iberia and France, *A. leucolippa* being described from south-western France, *locus typicus* Riscle (Fig. 3). It is important to note that Pérez writes in his catalogue under entry 442 that he had males from Algeria; in any case, the designation of the lectotype by Warncke (1967) from France fixes this name unambiguously on European populations. North African and Iberian specimens differ, with *A. leucolippa* presenting denser tergal punctation, in the male sex the yellow colouration of the clypes extends onto the mandibles and the lower paraocular areas (only the clypeus is yellow-marked in *A. boyerella*), and there are slight differences in the genital capsule. Gusenleitner and Schwarz (2002) listed *A. leucolippa* as a distinct species.

However, this classification is not immediately stable due to the fact that the type series of *A. boyerella* is lost, as is the case for all of Dours' types. Dours (1872) described *A. boyerella*, and there is no doubt over the morphological identity of this taxon based on the clear description. However, Dours gives a distribution of southern France and Algeria. It is therefore the case that, if there are two different species, then Dours' type series was polytypic. Warncke (1967) and Gusenleitner and Schwarz (2002) give the *locus typicus* of *A. boyerella* as Algeria, but since there is no holotype or designated lectotype, the *locus typicus* is undefined. Genetically, sequences from four North African specimens from the Middle Atlas in Morocco were identical and formed a clade (Fig. 2) that was strongly separated from two sequences from Estorãos near Fafe in northern Portugal [WPATW078-21] and Balaguer in Catalonia in north-eastern Spain [WPATW111-21] by an average genetic distance of 13.27% (range 13.27–13.27%). The two clades are not sisters, being separated by *A.* (*Chlorandrena*) *abrupta* Warncke, 1967. The matter would appear to be clear, that two taxa are present. However, a specimen from Vieira do Minho in northern Portugal [IBIHM500-21] diverged from both these lineages, being separated from the Moroccan sequences by 8.95% and the two other Iberian sequences by 14.51%. This site is only 16 km from the Estorãos site. Morphologically, there are no obvious differences; all three Iberian specimens are males. Because *A. leucolippa* was described from south-western France, the sequence from north-eastern Spain is here

Figure 3. *Andrena* (*Chlorandrena*) *leucolippa* Pérez, 1895 female lectotype **A** label details **B** profile **C** face, frontal view **D** dorsal view.

assumed to be representative of true *A. leucolippa*. For now, the divergent Portuguese sequence is considered to be aberrant until it can be independently replicated. It is possible that this 'aberrant' sequence is a NUMT (nuclear sequences of mitochondrial origin) and represents amplification of nuclear DNA rather than mitochondrial. Since only a single sequence is available, and it is not possible to determine the nature of this sequence, no action is taken. It is not impossible that a third undescribed species is present, but without additional genetic data no further action is taken. Morphology supports the existence of only two species, and in order to fix the name *A. boyerella* on North African populations, a neotype is designated below from barcoded Moroccan material.

Andrena (*Chlorandrena*) *humilis* Imhoff, 1832 is the most widespread West Palaearctic *Chlorandrena*, and it is quite variable over its range. A broad species concept has been used as no consistent morphological differences can be found because of this variability. Sequences from Austria, Belgium, Finland, Germany, Portugal, and Spain formed a broad *A. humilis* clade (Fig. 2), though intraspecific variation was high at an average of 4.59% (range 0.00–8.33%). Specimens from Iberian mountain chains (Sistema Central, Sierra de Baza, Sierra Nevada) were the most strongly divergent, differing by 8.02–8.33% from specimens from Austria, Belgium, and Germany. However, multiple clades were found without clear geographic structuring. Therefore, a broad species concept is maintained here, and this overall *A. humilis* clade has bootstrap support of 98. In Iberia, *A. humilis* forms a species pair with *A.* (*Chlorandrena*) *cinerea* Brullé, 1832. *Andrena cinerea* specimens from Morocco, Portugal, and Spain formed a distinct clade with low intraspecific variation of 0.77% (range 0.00–1.54%). This clade was strongly separated from the broad *A. humilis* clade by an average distance of 15.05% (range 13.89–15.74%). However, a single specimen from Balaguer in north-eastern Spain which was originally identified as *A. cinerea* diverged from both the broad *A. humilis* clade by 11.70% (range 11.11–12.65%) and *A. cinerea* by 12.35% (range 12.35–12.35%). As for the potentially aberrant specimen of *A. leucolippa*, it is not clear what this sequence represents, though it is not *A.* (*Chlorandrena*) *kamarti* Schmiedeknecht, 1900 from North Africa and Sicily as it also diverges from Moroccan *A. kamarti* sequences (to be published in the upcoming North African revision). It may also be a NUMT; it is unknown if certain *Andrena* subgenera are more likely to generate NUMTs, but *Chlorandrena* may potentially represent one such case, with difficult to interpret results generated in the study of the East Mediterranean fauna (G. Pisanty, unpublished data). More study using additional genetic markers is necessary to understand why two seemingly aberrant strong divergent sequences have been generated from Iberian *Chlorandrena* specimens.

Finally, the *taraxaci*-group (see Schwenninger 2015) formed a monophyletic clade, with *A.* (*Chlorandrena*) *rhenana* Stöckhert, 1930 clearly separated from *A.* (*Chlorandrena*) *taraxaci* Giraud, 1861 which has its western range limit in Central Europe. The taxonomic concepts of Schwenninger (2015) are therefore supported and followed.

Material examined. ***Andrena leucolippa*****: France:** Riscle [43.6564°N, -0.0894°W], 1♀, MNHN (lectotype; Fig. 3).

Subgenus *Didonia* Gribodo, 1894

Andrena (*Didonia*) *mucida* Kriechbaumer, 1873 is a highly unusual species. It is bivoltine, with the first generation seemingly specialising on *Muscari* (Asparagaceae) and the second generation specialising on genera from the former Dipsacaceae (now Caprifoliaceae) such as *Scabiosa*. This specialisation is associated with a morphological change, with females of the first generation possessing tibial scopae composed of simple hairs, and females of the second generation possessing tibial scopae composed of plumose hairs. There is the possibility that these generations may actually represent distinct species, as for putatively bivoltine taxa like *A.* (*Holandrena*) *decipiens* Schenck, 1861 that was found to consist of two taxa (Mandery et al. 2008). However, barcodes from females from the first and second generations from central and southern Spain show that this is not the case, with an average intraspecific genetic distance of 0.30% (range 0.15–0.46%; Fig. 4). The spring and summer generation individuals from Guadalajara were separated by 0.15%, strongly supporting the position that *A. mucida* is a bivoltine species displaying the currently unique trait of intergenerational variation in the structure of the pollen collecting hairs.

Additionally, *A.* (*Euandrena*) *solenopalpa* Benoist, 1945 was previously placed in the subgenus *Didonia* (Warncke 1968a). Genetic evidence instead places this taxon in the subgenus *Euandrena* (Bossert et al. 2022). This placement is a better fit, as

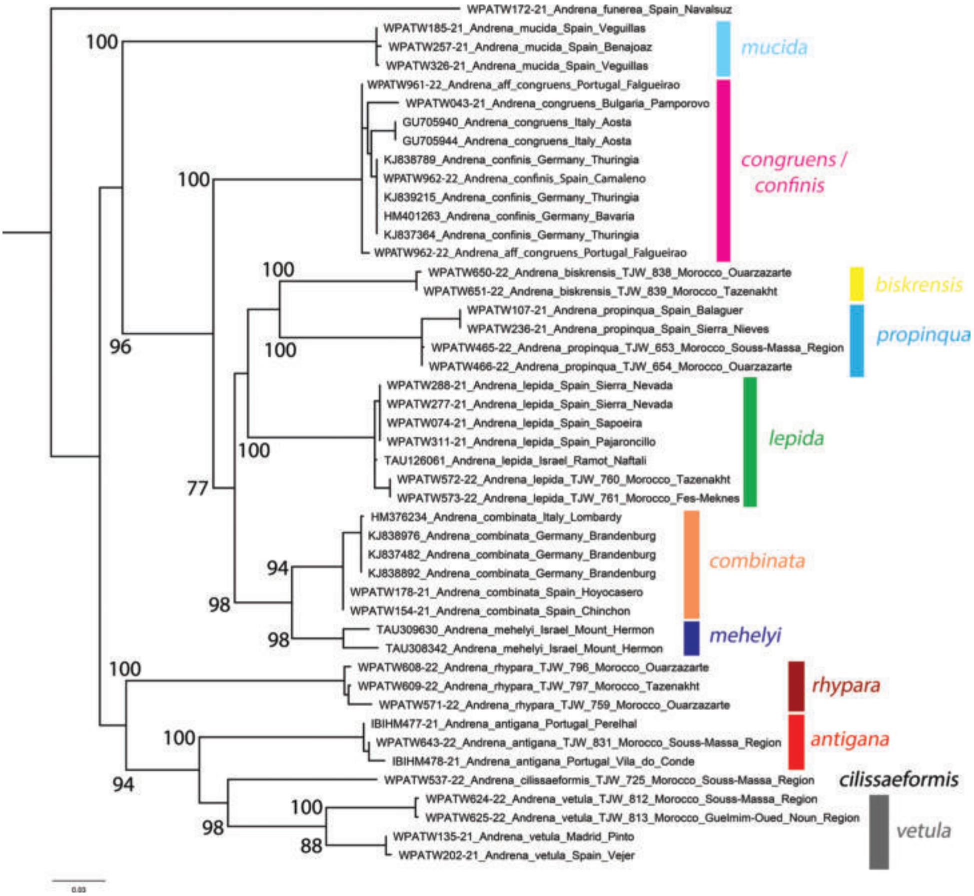

Figure 4. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Didonia* Gribodo, 1894 and *Simandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (*Nobandrena*) *funerea* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

A. solenopalpa has typical *Euandrena* foveae (narrow and narrowing further ventrally), the male A3 slightly exceeds the length of A4+5, and the process of the labrum is not so strongly thickened and elongate as in *A. mucida*; this simply represents convergence on a similar morphology. It is possible that the subgenus *Didonia* is monotypic, containing only *A. mucida*, but this requires additional study.

Material examined. ***Andrena mucida*: Spain:** Guadalajara, Veguillas, 2 km N, Barranco de la Isa, 17.v.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW185-21], on *Muscari* spp.; Málaga, Benaoján, Cueva del Hundidero, 3.vi.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW257-21], on *Scabiosa atropurpurea*; Guadalajara, Veguillas, CM-1006, 9.vii.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW326-21], on *Scabiosa atropurpurea*.

Subgenus *Euandrena* Hedicke, 1933

In comparison to the situation in the Eastern Mediterranean (Praz et al. 2019), Iberian *Euandrena* are comparatively well-resolved, with lower species diversity, fewer undescribed species, and clearer species boundaries. However, unrecognised montane species are present (Wood et al. 2021), and there are some problems related to the group of species lumped together under a broad *A. bicolor* Fabricius, 1775. This current work does not deal with the complex issue concerning the two clades of *A. bicolor* as identified by Praz et al. (2019), but instead with the status of material from southern Spain and North Africa. Material identified as *A. bicolor* s.l. from the Col du Zad in the Middle Atlas of Morocco at an altitude of 2100 m [WPATW387-22] and the southern slopes of the Sierra Nevada above Trevélez in Spain at an altitude of approximately 1800 m [WPATW368-21] fell close to *A. angustior* (Kirby, 1802) and far from *A. bicolor* s.l. (Fig. 5). The specimen from the Sierra Nevada was caught on the same *Campanula* (Campanulaceae) plant as specimen WPATW290-21 which falls into the *A. bicolor* s.l. clade. These two Spanish specimens are separated by a genetic distance of 9.80%, and clearly cannot be conspecific despite their strong morphological similarity.

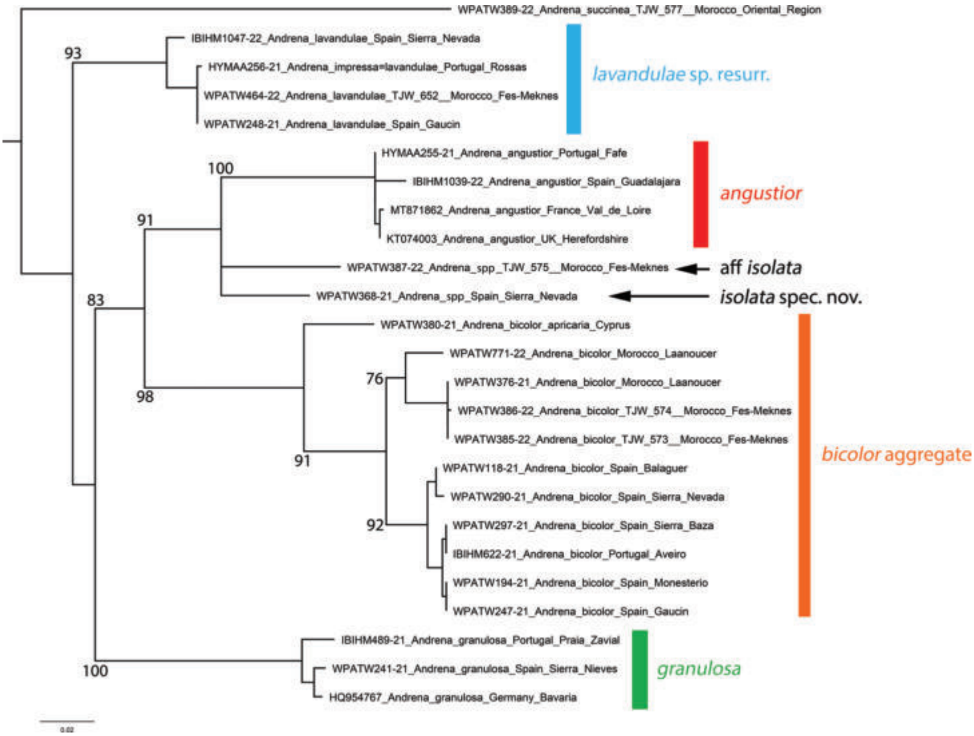

Figure 5. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Euandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena* (*Pruinosandrena*) *succinea* Dours, 1872 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

More broadly, the Sierra Nevada specimen was separated from the *A. bicolor* s.l. clade by an average genetic distance of 9.32% (range 7.95–9.80%) and the Moroccan specimen was separated from the *A. bicolor* s.l. clade by an average distance of 9.06% (range 8.50–9.80%). These two specimens were separated from each other by a distance of 4.99%. The species from the Sierra Nevada is described as new to science below, but the name to apply to the North African taxon (present also in Tunisia based on barcode data, Praz, in litt.) is complex and requires discussion. The nomenclatural and taxonomic status of *A. bicolor* s.l. will be resolved in a future revisionary work dedicated to the subgenus *Euandrena* at a West Palaearctic scale.

Andrena **(*Euandrena*)** ***bicolor*** **and associated** ***Euandrena*** **species in North Africa**

Euandrena specimens with black and orange pubescence can be found infrequently across north-western Africa. They have typically been referred to as *A. bicolor* in the literature, but two distinct taxa are present. One corresponds to *A. bicolor* s.l., but the other is clearly distinct genetically; morphologically it can be distinguished by the structure of the clypeus, with *A. bicolor* s.l. with the clypeus shiny between the punctures, whereas in the second taxon the puncture interspaces are shagreened and dull, and there is a weak longitudinal furrow, similar to what can be seen in species like *A.* (*Euandrena*) *angustior*, though more apically situated and occupying a shorter distance.

Warncke (1974) used subspecific concepts for dealing with *A. bicolor*, with two subspecies used for North African material – *A. b. oraniensis* Lepeletier, 1841 and *A. b. agraria* Warncke, 1974 (see also distribution maps in Gusenleitner and Schwarz 2002). However, the use of these names is not immediately straightforward. *Andrena oraniensis* Lepeletier, 1841 was described from Oran in northern Algeria (Lepeletier 1841) and is a confused and unclear taxon. In the MNHN collection, the type series cannot be located, and it may have been lost as many specimens have been moved between different boxes by past workers and curators. In the Pérez collection, there are long series of *Andrena* (*Melandrena*) *florentina* Magretti, 1883 that were identified by Pérez as *A. oraniensis*. Warncke (1967) noted this, but argued that this must be incorrect due to size, and instead placed the name in combination with *A. bicolor* as a subspecies found in North Africa. Warncke (1974) later authored the replacement name *A. bicolor agraria* Warncke, 1974 for *Andrena* (*Euandrena*) *nigriventris* Pérez, 1902 which was described from northern Algeria and Morocco (*locus typicus* Tangier, following lectotype designation) but which is a preoccupied name, nec. *Apis nigriventris* Gmelin, 1790 which is a synonym of *A.* (*Melandrena*) *nitida* (Müller, 1776). Warncke then used both *oraniensis* and *agraria* as subspecies, giving an overlapping distribution in Warncke (1974, e.g. both occurring at Oukaimeden in the High Atlas), but in his distribution maps (see Gusenleitner and Schwarz 2002) giving a non-overlapping distribution, with *oraniensis* more or less occurring only in Algeria and Tunisia and *agraria* occurring only in Morocco.

In the original description of *A. oraniensis*, Lepeletier (1841: 245) draws attention to the colour of the hairs on the hind legs. Specifically, he states that: "*cuisses des deux postérieures garnies des poils ferrugineux pales ; leurs jambes et leurs tarses à poils noirs en* *dessus, ferrugineux en dessous*". This bicoloured tibial scopa (dark dorsally, ferruginous ventrally) does not correspond at all to members of the *A. bicolor* s.l. group which have uniformly orange tibial scopae. It does however correspond very well to the concept of *A. florentina* which has a distinctive bicoloured scopa, one of the characters that allows it separation from its sister taxon *A. bicolorata* (Rossi, 1790). Based on the identifications made by Pérez, who probably saw the original specimen in Lepeletier's collection and Lepeletier's original description, the position is taken that *A. oraniensis* cannot be a *Euandrena* taxon displaying the colour pattern of *A. bicolor* s.l. However, without a type, it is undesirable to make *A. oraniensis* the senior synonym for *A. florentina*. *Andrena oraniensis* is therefore declared a *nomen dubium* until such time as the original syntypic series can be located.

The next oldest available name from North Africa is *A. bicolor agraria*. Pérez (1902, as *A. nigriventris*) writes: "*Abdomen très luisant, particulièrement les depressions, que précèdent les bourrelets très prononcés*". This is suggestive, as the distinct North African taxon has strongly depressed tergal margins. However, barcoded *A. bicolor* s.l. from Morocco also show this character, so it is not diagnostic in and of itself. Examination of the lectotype specimen of *A. nigriventris* (designated by Warncke 1967; Fig. 6) shows that the clypeus is apically smooth and shing between the punctures (Fig. 6C), meaning that it cannot belong to the distinct taxon, and it remains a synonym of *A. bicolor*

Figure 6. *Andrena* (*Euandrena*) *nigriventris* Pérez, 1902 (nec. Gmelin, = *Andrena bicolor agraria* Warncke, 1974) female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

s.l. One additional name is available, that of *A.* (*Euandrena*) *fervida* Pérez, 1902, a taxon described from Algeria. The lectotype is in poor condition, lacking its metasoma (Fig. 7). Diagnosis is therefore challenging, but the clypeus is shiny between the punctures and it cannot be conspecific with the distinct North African taxon. The position of Warncke (1967) that this name is synonymous with *A. bicolor* s.l. is maintained. The distinct North African taxon would therefore appear to be undescribed. No taxonomic action is taken in the current work – further genetic data will either demonstrate a closer affinity with the specimen from the Sierra Nevada, in which case this name will be available to apply to North African populations, or these sequences will confirm its distinct nature, and it can be described. In any case, a name is required for the Iberian lineage which is unambiguously undescribed.

Material examined. ***Andrena bicolor*: Algeria:** Theniet El Had [35.8727°N, 2.0007°E] (1♀, MNHN (lectotype of *A. fervida*); **Morocco:** Tanger [35.7537°N, -5.7906°W], 1♀, MNHN (lectotype of *A. nigriventris* Pérez).

Andrena (***Euandrena***) ***lavandulae*** **Pérez, 1902, sp. resurr.**

Andrena (*Euandrena*) *lavandulae* Pérez, 1902: 156 ♀♂ [France, lectotype by present designation: MNHN].

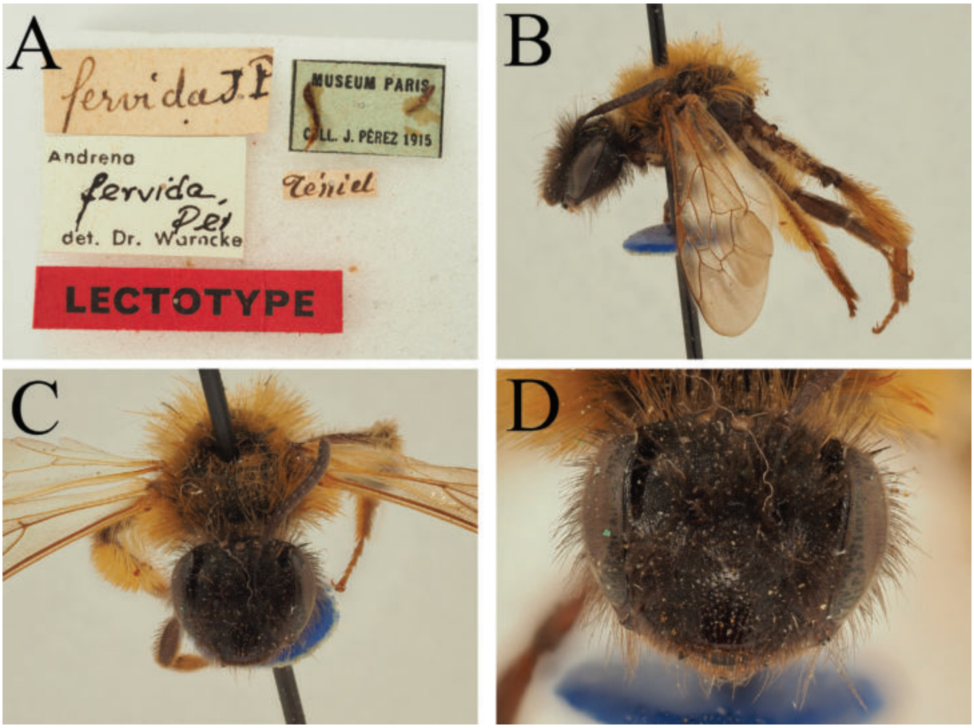

Figure 7. *Andrena* (*Euandrena*) *fervida* Pérez, 1902, female lectotype **A** label detail **B** profile **C** face, frontal view **D** face detail, frontal view.

Andrena (*Euandrena*) *angustior impressa* Warncke, 1967: 234, ♀♂ [Morocco: OÖLM, examined] syn. nov.

Remarks. Warncke (1967) synonymised *A. lavandulae* with *A. bicolor* without apparently inspecting the type. This is not explicitly clear in the text of Warncke (1967), but in this publication he typically reported lectotypes in the Paris collection when he designated them, and usually labelled paratypes as well, often taking a selection for his personal collection. There are no specimens of *A. lavandulae* in the Warncke collection, which combined with the lack of mention of a lectotype in Warncke (1967) leads me to believe that he did not inspect the type series. He then described *Andrena angustior impressa* Warncke, 1967 in the same publication, a taxon that was subsequently elevated to species status by Wood et al. (2021) based on genetic and morphological evidence.

In the MNHN collection, specimens of *A. lavandulae* are labelled as lectotype and paralectotype by Teunissen (August 1986; Fig. 8), but these designations were never published. The female specimen is therefore recognised here as a lectotype, by present designation. Examination of these specimens shows that they are clearly the same taxon as *A. impressa* and distinct from *A. bicolor*, with the weakly depressed, shagreened, and weakly shing tergal margins, the black terminal fringe and hairs flanking the pygidial plate, the intermixed light and dark hairs on the face, and in the male sex by the broadened gena (broader than the width of the compound eye). The lectotype comes from Banyuls-sur-Mer in the south-west of France, which falls within the distribution of the taxon as presented by Wood et al. (2021). Additional genetic sequences from Spain and Morocco closely match the Portuguese sequence of *A. impressa* presented by Wood et al. (2021), forming a well-supported clade (Fig. 5; bootstrap support of 93) that is distinct from both *A. angustior* and *A. bicolor*. *Andrena impressa* syn. nov. is therefore synonymised with *A. lavandulae* sp. resurr. The distribution is Morocco, Algeria, Portugal, Spain, and France (Wood et al. 2021).

Material examined. France: Banyuls [Banyuls-sur-Mer, 42.5658°N, 2.8658°E], 1♂, 1♀, MNHN (female lectotype, by present designation).

Subgenus *Graecandrena* Warncke, 1968

This subgenus is also species-poor in Iberia, containing only *A. impunctata* Pérez, 1895, *A. montarca* Warncke, 1975, *A. nebularia* Warncke, 1975, and *A. verticalis* Pérez, 1895. Two taxa are uncommonly collected in Iberia (*A. impunctata* and *A. montarca*). *Andrena nebularia* was considered to be endemic to Spain, but new collections in Morocco have demonstrated its presence in a small part of the Middle Atlas. Genetically, there is almost no differentiation, with the Moroccan specimens separated by 0.26% and 0.52% (Fig. 1).

Material examined. ***Andrena nebularia*: Morocco:** Fès-Meknès, Boulemane, 5 km SE, junction of R503 and N4, 1900 m, 19.v.2022, 2♀, leg. T.J. Wood, TJWC; Fès-Meknès, Boulemane, R503, 7 km SE of Boulemane, 1900 m, 1♂, 6♀, 22.v.2022, leg. T.J. Wood, TJWC; Fès-Meknès, Boulemane, R503, SE of Ait Karmosse, 1750 m, 22.v.2022, 1♂, leg. T.J. Wood, TJWC.

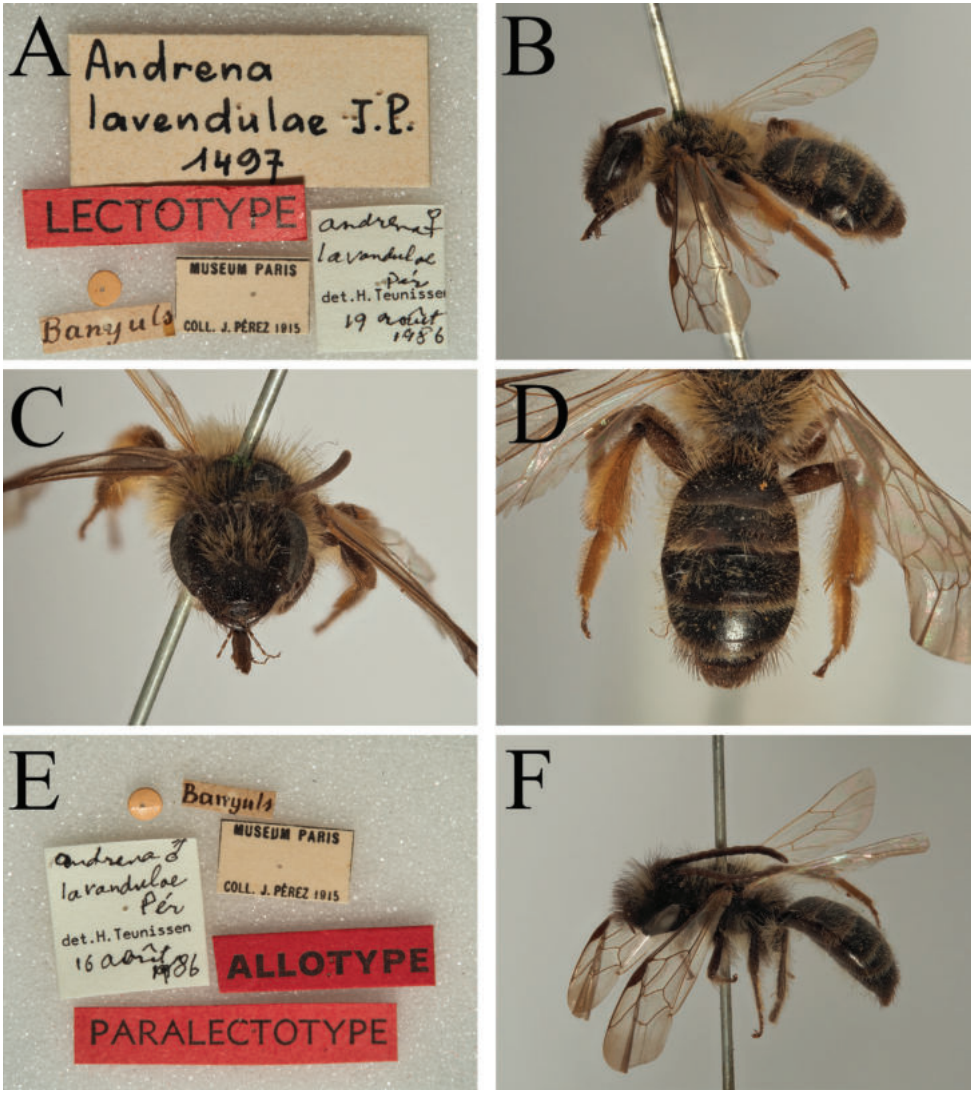

Figure 8. *Andrena* (*Euandrena*) *lavandulae* Pérez, 1902, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view; male syntype **E** label details **F** profile.

Subgenus *Melanapis* Cameron, 1902

Andrena (*Melanapis*) *fuscosa* Erichson, 1835

Andrena fuscosa was described from southern Spain by Erichson (1835). *Andrena fuscosa* has had a complicated taxonomic history, and has been described many times due to its variation in colouration and size (Gusenleitner and Schwarz 2002). Iberian genetic data are therefore of interest since the peninsula represents the *locus typicus*.

Iberian sequences were identical with each other, and closely matched sequences from Israel and India (the latter identified as *A.* (*Plastandrena*) *agilissima* Scopoli, 1770 but clearly misidentified; *Melanapis* was actually described as a genus based on material from India), being separated by an average of 1.53% (range 0.88–1.82%; Fig. 9). They were more clearly separated from Moroccan sequences, by an average of 5.43% (range 3.94–5.93%). Given the lack of morphological differences between North African and Iberian specimens, a broad interpretation of this species is taken here. Including all sequences together, average intraspecific distance is 3.14% (range 0.00–6.23%) which is considered to be acceptably small. Additional study is necessary to establish whether North African material is consistently distinct; the first nominally available name would be *A.* (*Melanapis*) *rutila* Spinola, 1838 which was described from Egypt.

Subgenus *Melandrena* Pérez, 1890

This subgenus is strongly derived within *Andrena*, but it shows substantial morphological variation that has led to the description of the subgenera *Hyperandrena* Pittioni, 1948 and *Zonandrena* Hedicke, 1933, both of which are now placed within an expanded *Melandrena*. There are several problems within this subgenus in an Iberian context.

Andrena (*Melandrena*) *morio* Brullé, 1832

Andrena (*Melandrena*) *morio* Brullé, 1832: 353, ♀♂ [Greece: MNHN, not examined].
Andrena (*Melandrena*) *hispania* Warncke, 1967: 212, ♀♂ [Spain: OÖLM, examined] syn. nov.

Remarks. *Andrena hispania* Warncke, 1967 was described from Algeciras in southern Spain. The identification characters given by Warncke are comparatively weak and rely on hair colour and the degree of infuscation of the wings, without mentioning definitive structural characters. Genetically, the three *A. hispania* sequences from Spain and Portugal mixed with *A. morio* sequences from Israel, Morocco, Portugal, Spain, Tunisia, and Turkey without forming a cluster, this group having bootstrap support of 100 (Fig. 10). Confusingly, additional sequences from Greece, Morocco, and Tunisia formed two sister groups to this clade. There is no clear geographic pattern, and so a broad *A. morio* concept is adopted, including *A. hispania* syn. nov. as a direct synonym of *A. morio*. Additional genetic data using more powerful techniques are required before an alternative taxonomic conclusion can be drawn. *Andrena morio* is known to be highly variable in its colouration, leading to a higher than average number of synonyms for an *Andrena* species (Gusenleitner and Schwarz 2002). *Andrena hispania* was classically thought of to have only a single generation in the spring, which may explain why its wings are less infuscate than *A. morio*, particularly in the summer generation of this species that can be noticeably darker than spring flying individuals.

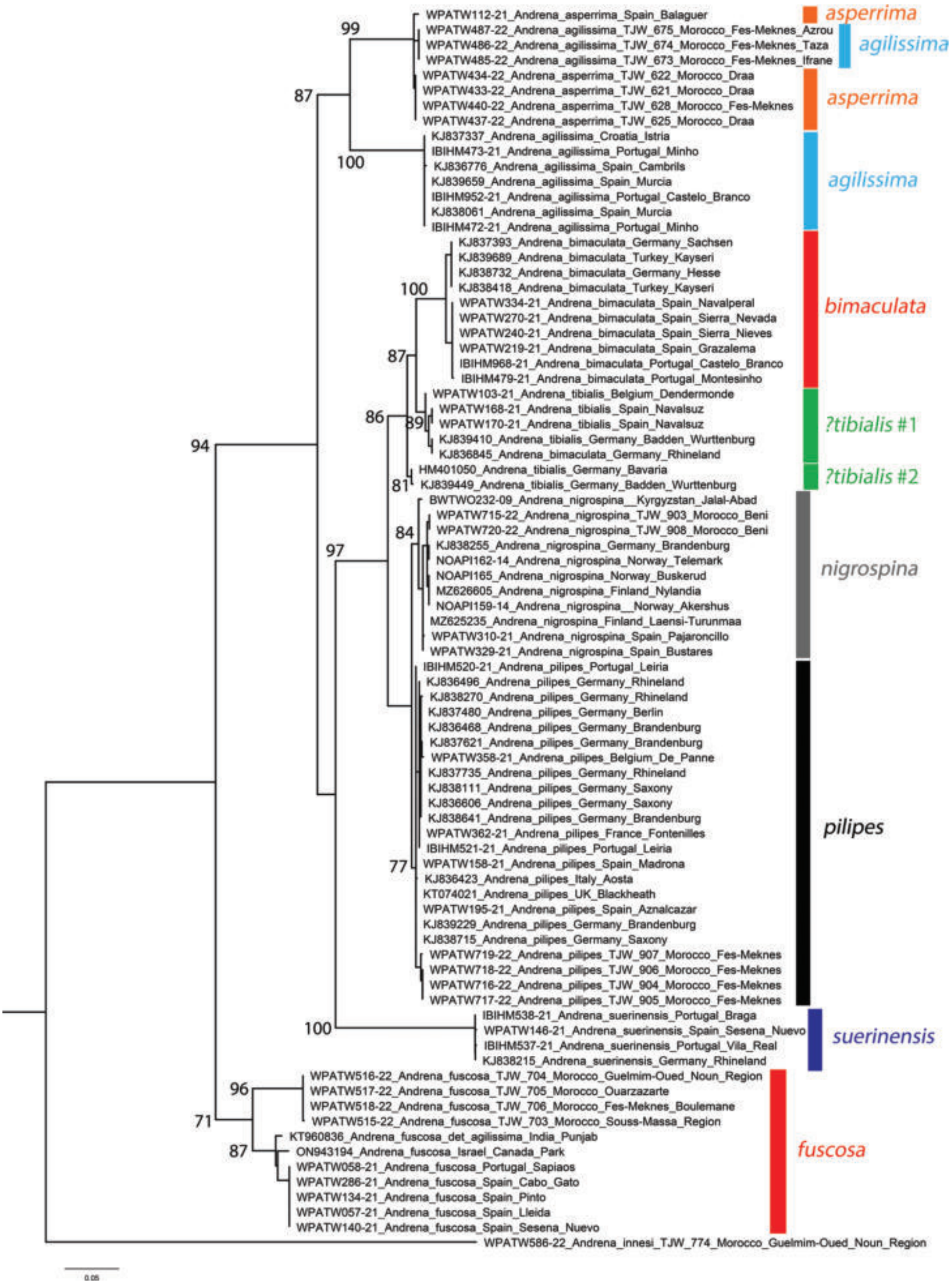

Figure 9. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Melanapis* Cameron, 1902, *Plastandrena* Hedicke, 1933, and *Suandrena* Warncke, 1968 based on the mitochondrial COI gene. *Andrena* (incertae sedis) *innesi* Gribodo, 1894 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

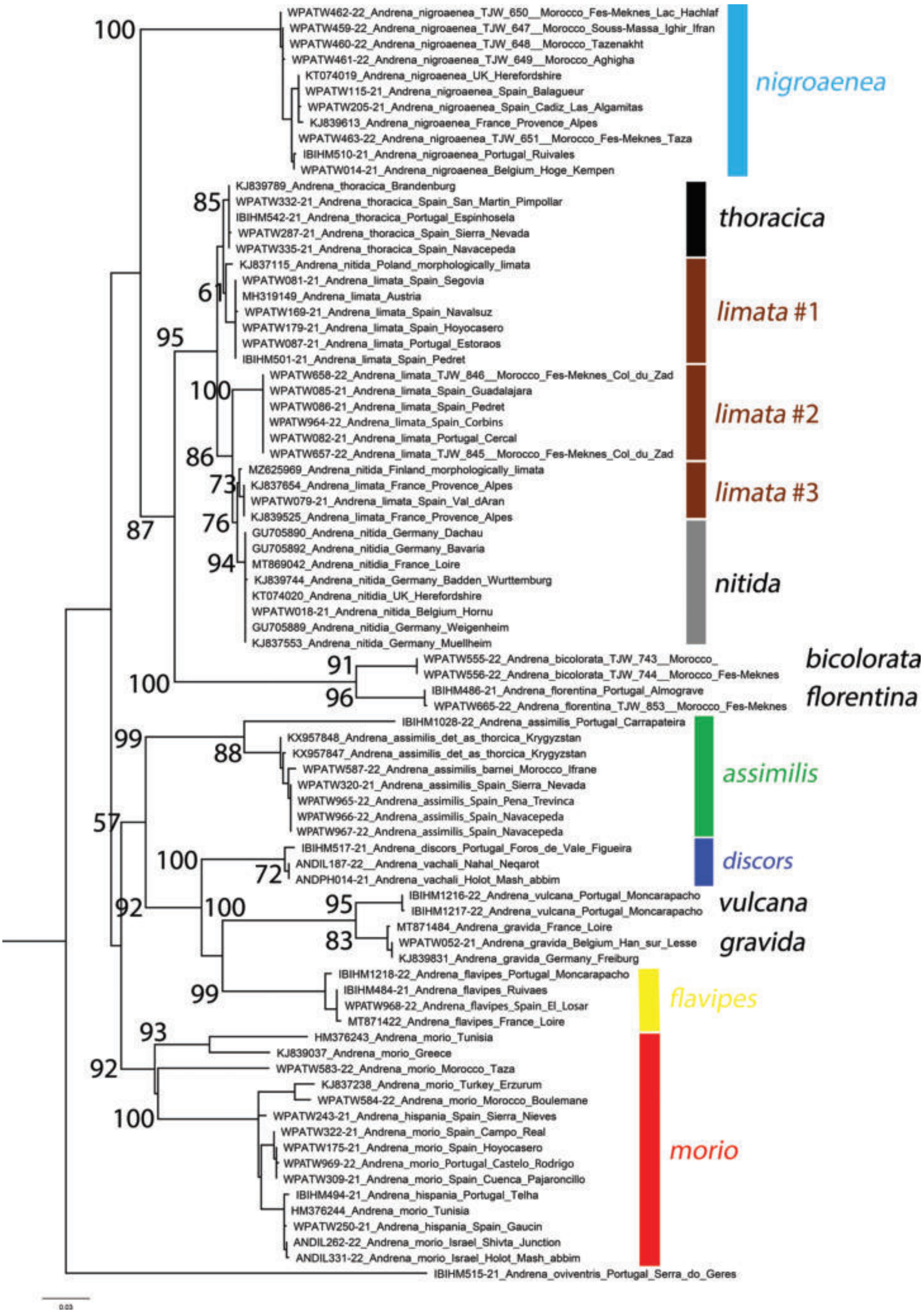

Figure 10. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Melandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

Andrena (*Melandrena*) *nitida* (Müller, 1776), *Andrena* (*Melandrena*) *thoracica* (Fabricius, 1775), and *Andrena* (*Melandrena*) *limata* Smith, 1853

Remarks. The specific differences between these taxa is unclear across southern Europe. In some northern countries, only two taxa are present (*A. nitida* and *A. thoracica*, e.g. the United Kingdom), with no introgression observed. *Andrena nitida* flies only in the spring, whereas *A. thoracica* is bivoltine, flying in both the spring and the summer. In Central Europe, *A. limata* can be found, this taxon also being bivoltine. Differentiation between the three taxa in Central Europe has often utilised hair colouration characters, as in this region the three taxa are separable with reference to the hairs on the sides of the mesosoma (light in *A. nitida* and *A. limata*, dark in *A. thoracica*) and the hairs of the face and the tibial scopal (light and dark in *A. nitida*, uniformly dark in *A. limata* and *A. thoracica*). There are additional characters such as the colour of the hind tibial spur and the density of the punctures T1, but these are less commonly referred to; both *A. nitida* and *A. limata* have dense punctures on T1 (separated by up to 1 puncture diameter), whereas they are more clearly spaced in *A. thoracica* (punctures separated by 1–2 puncture diameters). It is important to note that *A. limata* is a replacement name for *A. lucida* Lepeletier, 1841 nec. *A. lucida* Panzer, 1798 which is nominally a synonym of *A. bicolor* Fabricius, 1775 but this must be established (see section on subgenus *Euandrena*). *Andrena lucida* Lepeletier was described from 'France', without further details. I have not been able to inspect the type which should be in the MNHN collection, but which I could not locate.

The situation in southern Europe is much more challenging. In south-western Europe, *A. limata* becomes much darker, and therefore closely resembles the colour form of *A. thoracica*, with extensive black pubescence on the mesosoma laterally. This colour form was described as *A. limata mixtura* Warncke, 1967 (illustrated by Wood et al. 2020a). This form can be recognised by the dense punctures of T1, separating it from Iberia *A. thoracica*; the colour of the hind tibial spur is variable and of little consistent utility. Because of this variation, Warncke later adopted a much broader concept of *A. nitida*, with *A. nitida* s. str., *A. nitida limata*, and *A. nitida mixtura* (e.g. Warncke 1974). This position was not followed by Gusenleitner and Schwarz (2002) who followed a three distinct species interpretation (*nitida*, *limata* including *mixtura*, *thoracica*).

Analysis of barcodes does not provide clarity (Fig. 10). Whilst *A. thoracica* and *A. nitida* form reciprocally monophyletic clades, three different clades are formed for *A. limata*. There is no geographic pattern to these clades; clade #1 contains individuals from Austria, Poland (KJ837115; specimen identified as *A. nitida* but associated photograph on BOLD shows *A. limata* colour pattern), Spain, and Portugal; clade #2 contains individuals from Morocco, Spain, and Portugal; and clade #3 contains individuals from Finland (MZ625969; specimen identified as *A. nitida* but associated photograph on BOLD shows *A. limata* colour pattern), France, and Spain. Confusingly, sequences IBIHM501-21 and WPATW086-21 come from two different female specimens collected from the same field near Pedret i Marzà in north-eastern Spain. As Iberian individuals fall into three of these clades and the power of COI analysis is clearly insufficient to deal with potential hybridisation and introgression, no further action can be taken on the basis of these results. A dedicated study using more powerful genetic markers is necessary to resolve this issue. For now, I maintain the position of Gusenleitner and Schwarz (2002) in that there are three species in this group (*nitida*, *limata* including *mixtura*, and *thoracica*). It will probably be necessary for a future study to designate a neotype for *A. limata* if Lepeletier's original specimens cannot be definitively located.

***Andrena* (*Melandrena*) *discors* Erichson, 1841**

Andrena (*Melandrena*) *discors* Erichson, 1841: 192, ♀ [Algeria: ZMHB, examined].
Andrena (*Melandrena*) *creberrima* Pérez, 1895: 46, ♀♂ [Algeria: MNHN, examined] syn. nov.
Andrena (*Melandrena*) *vachali* Pérez, 1895: ♀ [Tunisia, lectotype by present designation: MNHN] syn. nov.
Andrena (*Melandrena*) *bodemeyeri* Benoist, 1969: 246, ♀ [Tunisia: MNHN, examined].

Remarks. There has been extensive confusion between *A. discors* and *A. creberrima*. Erichson (1841) described *A. discors* from Algeria; a specimen is preserved in the ZMHB collection which may be automatically the holotype, but this is ambiguous as it is unclear if Erichson described the species from multiple specimens (Fig. 11). In any case, the specimen is a syntype, and Erichson described the species only in the female sex. The specimen conforms to the classical concept of the species, having the typical features of the former members of the subgenus *Zonandrena*, i.e. a clypeus with punctures forming a pattern of weak longitudinal channels. The pubescence of the face is black (Fig. 11C), and there are numerous intermixed dark hairs on the scutum (Fig. 11D). The tibial scopae are orange (Fig. 11E), and there are weak indications of light tergal hair bands but these are degraded and scarcely visible (Fig. 11F). Warncke (1974) gave numerous localities for *A. discors* from Morocco, Algeria, and Tunisia. He listed *A.* aff *discors* from Madrid based on two specimens (Warncke 1976), but later discarded these records, giving only two points in southern Spain in his distribution maps in addition to the points from north-western Africa (Gusenleitner and Schwarz 2002). I have examined 14 female and six male specimens of *A. discors*, all from southern parts of Portugal and Spain (Algarve, Alto Alentejo, Cádiz, Huelva, Málaga, Sevilla), where it is active from late February to April.

The situation is confused due to the status of two additional taxa described by Pérez, *A.* (*Melandrena*) *creberrima* Pérez, 1895 and *A.* (*Melandrena*) *vachali* Pérez, 1895. *Andrena creberrima* was described from Algeria like *A. discors*. Warncke (1967) designated a lectotype for *A. creberrima* (Fig. 12), but did not understand the concept of this species, listing only the type locality of Bône in Warncke (1974). He later gave a distribution map of Algeria (the holotype point), Italy, and Greece (Crete). Examination of the lectotype shows that the specimen is slightly paler than the type of *A. discors*, with fewer dark intermixed hairs on the scutum (Fig. 12B), and the tergal hair bands

Figure 11. *Andrena* (*Melandrena*) *discors* Erichson, 1841, female holotype/syntype **A** label details **B** profile **C** face, frontal view **D** scutum, dorsolateral view **E** tibial scopa, profile view **F** terga, dorsal view.

in better condition and therefore slightly more pronounced (Fig. 12D). This can be contrasted with the type of *A.* (*Melandrena*) *bodemeyeri* (Fig. 13; known synonym of *A. discors*, see Warncke 1967) which is comparatively dark. This kind of variation in hair colour is typical for the subgenus *Melandrena*, and has led to the large number of synonymous names being described, for example for *A.* (*Melandrena*) *flavipes* Panzer, 1799.

Grouping *A. creberrima* under *A. discors* is straightforward. The problem comes with *A. vachali* which was classically considered to be distinct from *A. discors* and with a greater range extending from the Canary Islands to southern Israel (Gusenleitner

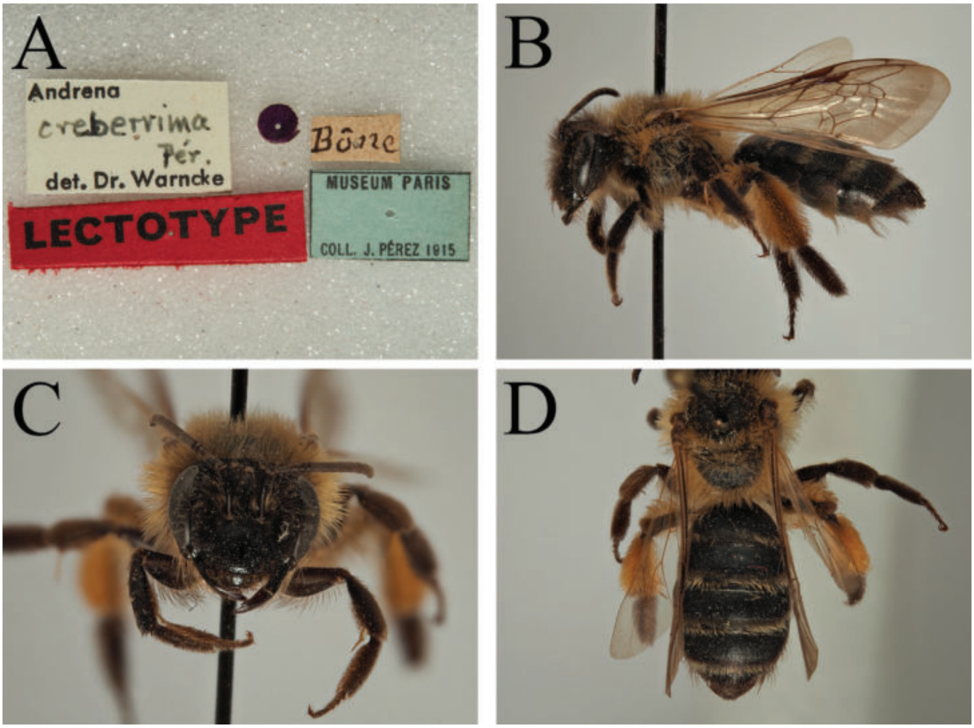

Figure 12. *Andrena* (*Melandrena*) *creberrima* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

and Schwarz 2002). Moreover, type material for *A. vachali* has not actually been designated, as Warncke (1967) could not find material in the MNHN collection. Examination of the MNHN showed several specimens of *A. vachali* in the Vachal collection from Foum Tatahouine [Tataouine, Tunisia] labelled "*Andrena vachali type Pérez*" in the handwriting of Vachal (Fig. 14). One specimen was labelled as a lectotype with a handwritten '*A. vachali*' determination label by H. Teunissen (Fig. 14A), but this designation was never published. Pérez (1895) did not mention the collection locality, and Warncke (1967) indicated that the species was described from Algeria. However, Gusenleitner and Schwarz (2002) give the *locus typicus* as Tunisia. Examination of the catalogue of Pérez did not reveal an entry for *A. vachali*, as is often the case, either because Pérez did not write one, or because the information is hidden under a name that differs from the published name (see below for the case of *A.* (*Plastandrena*) *asperrima* Pérez, 1895). It is therefore very difficult to know the type locality with certainty. However, on the basis that the MNHN specimens are labelled as 'type' by Vachal, they were present in his collection, and the species was named after Vachal, the position is taken that these represent genuine syntypes. The female specimen labelled as 'type' by Vachal is chosen as a lectotype, by present designation. Morphologically, it corresponds to the concept of *A. vachali*, with black pubescence on the face and mesepis-

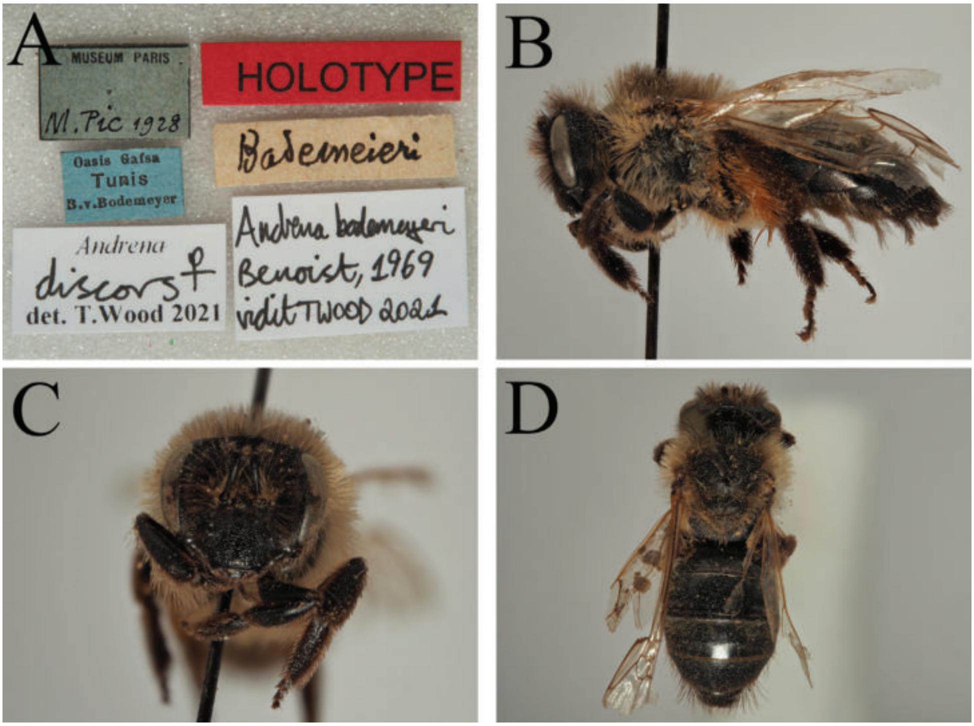

Figure 13. *Andrena* (*Melandrena*) *bodenmeyeri* Benoist, 1969, female holotype **A** label details **B** profile **C** face, frontal view **D** dorsal view.

ternum, with reddish-brown pubescence on the remaining parts of the mesosoma, and with predominantly reddish-brown tibial scopae, though this specimen shows some darker hairs dorsally (c.f. Fig. 13D); specimens of *A. vachali* can be found with entirely orange-red tibial scopae. Comparison of sequences from *A. discors* from southern Portugal and two *A. vachali* from southern Israel show a very small difference of 0.91% (range 0.91–0.91%; Fig. 10). These three specimens group together and have posterior support of 100, and are clearly separated from the three other former *Zonandrena* species that group together in this clade, namely *A. flavipes*, *A.* (*Melandrena*) *gravida* Imhoff, 1832, and *A.* (*Melandrena*) *vulcana* Dours, 1873.

Taking a step back, the differentiation between *A. creberrima*, *A. discors*, and *A. vachali* has almost always been based on colouration, with *A. discors* the darkest, *A. vachali* the lightest, and *A. creberrima* somewhat intermediate. Males are generally rarer in collections; taken together, I have examined 215 female specimens, but only 73 male specimens of this *discors-creberrima-vachali* group. However, examination of males has led me to the conclusion that there are no apparent differences in the males of *A. creberrima*, *A. discors*, and *A. vachali*, and indeed the male of only one of these nominal taxa was actually originally described. All have white hairs over the majority of the face with clear black hairs laterally along the inner margins of the compound eyes,

Figure 14. *Andrena* (*Melandrena*) *vachali* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

a genital capsule that is typical of the former *Zonandrena* with the dorsal surface of the gonocoxae with granular shagreen, with the penis valves moderately broad, and without an emargination in the outer margins of the gonostyli (Fig. 15). Indeed, the genital capsule of a syntype of *A. creberrima* (Fig. 15B), the barcoded *A. discors* from southern Portugal [IBIHM517-21] (Fig. 15C), and *A. vachali* specimens from Morocco have identical genital capsules (Fig. 15D). Moreover, numerous 'aberrant' female individuals can be found across this range with more or less pronounced tergal hair bands and variably dark or light pubescence, particularly in Crete where individuals corresponding in different ways to the concepts of *A. creberrima*, *A. discors*, and *A. vachali* can be found.

Based on this colour variation, the lack of variation in the male genital capsule, the unclear and overlapping distributions given by Warncke (*A. creberrima* and *A. vachali* both reported from Crete, *A. creberrima* and *A. discors* both reported from Algeria), and the very low genetic distance between Portuguese and Israeli specimens, both *A. creberrima* syn. nov. and *A. vachali* syn. nov. are synonymised with *A. discors*. This resolves this long-running confusion as to the correct name and identity of this taxon (Baldock et al. 2018; Wood et al. 2020a).

Distribution. Portugal, Spain (Canary Islands, mainland), Morocco, Algeria, Tunisia, Italy, Malta, Libya, Greece (Crete), Egypt, Israel, Jordan.

Figure 15. *Andrena* (*Melandrena*) *creberrima* Pérez, 1895, male syntype **A** label details **B** male genital capsule; *Andrena* (*Melandrena*) *discors* Erichson, 1841 **C** male genital capsule; *Andrena* (*Melandrena*) *vachali* Pérez, 1895 **D** male genital capsule.

Material examined (illustrative). **Algeria:** label information illegible, possibly '*Bone*' [= Annaba], 1♀, ZMHB (holotype/syntype of *A. discors*); Bône [=Annaba, 36.9092°N, 7.7264°E], 1♀, MNHN (lectotype of *A. creberrima*); Alger, Birmandreis [Bir Mourad Raïs], 24.iii.-30.iv.1910, 1♂, 1♀, leg. J. Bequaert, ZMHB; **Greece:** Krete, Anidri b. Paleochora, 200 m, 31.iii.2002, 1♀, leg. A. Müller, AMC; Krete, Palaeochora, 0–50 m, 29.iii.2002, 5♀, leg. A. Müller, AMC; Kreta, Kavalos [Kavallos], 21.v.1986, 1♀, leg. Brande, OÖLM; Crete, Dept. Heraklion, Moulia, S. of Aghia Varvara, 26.iv.1973, 1♀, leg. v. Ooststroom, RMNH; **Italy:** Lazio, Roma, Via Falcognana, 8.iv.1990, 1♀, leg. G.G.M. Schulten, RMNH; Roma, Via Falcognana, 15.iv.1993, 1♀, leg. G.G.M. Schulten, RMNH; **Israel:** Negev, 15 km S of Be'er Sheva, 31.iii.1988, 2♀, leg. R. Leys, RMNH; **Jordan:** Petra, 800 m, 28.ii.-4.iii.1986, 1♂, 2♀, leg. K.M. Guichard, NHMUK; **Malta:** Buskett [woodlands, Ħad-Dingli], 7.iii.2018, 1♀, M. Balzan Colln.; **Morocco:** Drâa-Tafilalet, Tazenakht, Anezal, 5 km NE Ait Igga, 21.iv.2022, 1♂, 4♀, leg. T.J. Wood, TJWC; Souss-Massa, R105, Tizirt, 8 km N, Ighir Ifran env., 12.iii.2022, 1♂, 1♀, leg. T.J. Wood, TJWC; **Portugal:** Foros de Vale Figueira, Montemor-o-Novo, 20.iii.2019, 1♂, leg. T.J. Wood, TJWC; Montemor-o-novo, Foros de Vale de Figuera, 24.iv.2011, 1♀, leg. A. Albernaz-Valente, TJWC; **Spain:** Canary Islands, Lanzarote, Haria, 6.ii.1979, 1♂, leg. Ellis & Simon-Thomas, RMNH; Bollullos Par del Condado (Huelva), 160 m, 28.iii.2009, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Puerto de Gáliz, P.N. Alcornocales (Cádiz), 425 m, 28.iv.2007, 1♀, leg. F.J. Ortiz-Sánchez, FJOS; Cádiz, Zahara de los Atunes, 12.iii.1977, 1♀, leg. Madey, NHMUK; **Tunisia:** Foum Tatahouine [32.9361°N, 10.4458°E], 1♀, MNHN (lectotype of *A. vachali*, by present designation); Oasis Gafsa [34.4350°N, 8.7678°E], 1928, 1♀, leg. B. v. Bodemeyer, MNHN (holotype of *A. bodemeyeri*); Fritissa, 17–19.iv.1983, 1♀, TJWC.

Subgenus *Micrandrena* Ashmead, 1899

This is by far the most species-rich subgenus in Iberia, containing 37 species. Pisanty et al. (2022b) took the decision to synonymise the subgenera *Distandrena* Warncke, 1968, *Fumandrena* Warncke, 1975, and *Proxiandrena* Schmid-Egger, 2005 with a broad concept of *Micrandrena*, as morphological differences such as the shape of the foveae, propodeal triangle, and presence or absence of striations on the clypeus are inconsistent and insufficient to allow unambiguous differentiation between the groups, as well as lacking phylogenetic support. This broad *Micrandrena* definition is followed here.

Andrena (*Micrandrena*) *obsoleta* Pérez, 1895 and *Andrena* (*Micrandrena*) *mariana* Warncke, 1968 sensu lato

The treatment of *A. obsoleta* has a long and confused history that has caused many problems. Warncke (1967) designated a female lectotype from Babor in northern Algeria (Fig. 16). However, this lectotype designation is incorrect. In the catalogue of Pérez, under entry 1506 (p. 214), Pérez writes: "*Sicile,* ♀ *- M'pellier* ♀. *– Tebessa, avril*, ♀. *– Biskra, mars*, 3♀, *rares*. *– Bône*, ♀. *– Marseille*, ♂. *- Bône*, 27/iv ♂♀ *in cop. Souci et autres* [illegible – presumably a type of flower]". Babor is not mentioned, and so Warncke's lectotype designation is rejected. Examination of specimens labelled as *obsoleta* by Pérez from the localities indicated shows that they belong to a different taxon to that of Warncke's false lectotype. Warncke's false lectotype is a female *Distandrena* (=*Micrandrena*) with a clearly striate clypeus, and T1 is polished. This conforms to the concept of *A.* (*Micrandrena*) *nitidula* Pérez, 1903, and indeed Warncke (1967) synonymised *A. nitidula* with *A. obsoleta*. Only female specimens of *A. obsoleta* from Bône [=Annaba] in northern Algeria could be found in the Pérez collection, and almost all were in very poor condition, missing their metasomas. A single female from Bône was however in good condition, and it is here designated as a new lectotype (Fig. 17). This new lectotype specimen (i.e. the true *A. obsoleta*) morphologically falls within the *A.* (*Micrandrena*) *mariana* Warncke, 1968 complex within the former *Distandrena*, as it lacks striations on the clypeus. The larger *A.* (*Micrandrena*) *merimna* Saunders, 1908 can be excluded as this species has a very long A3 that clearly exceeds the length of A4+5, whereas members of the *A. mariana* complex have A3 at most slightly exceeding A4+5, A4 and A5 are sub-quadratic and slightly shorter than wide, A6–12 are as long as wide.

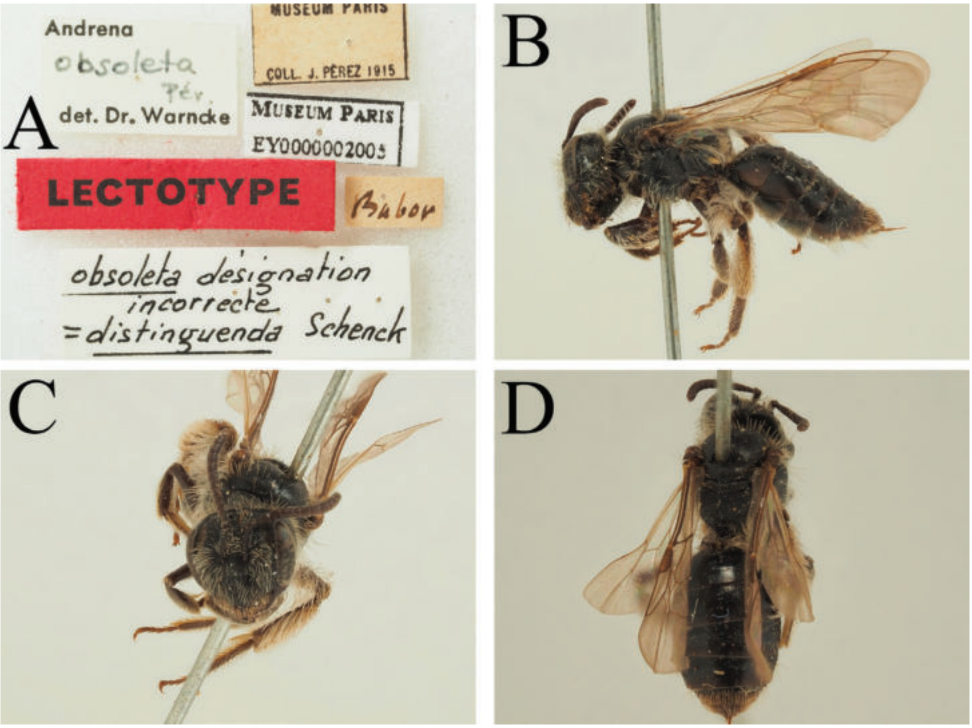

Figure 16. *Andrena* (*Micrandrena*) *obsoleta* Pérez, 1895, false female lectotype, =*Andrena* (*Micrandrena*) *nitidula* Pérez, 1903 **A** label details **B** profile **C** face, frontal view **D** dorsal view.

Warncke described *A. mariana* s. str. from the island of Fuerteventura in the Canary Islands, stating that the species could potentially be found in Morocco (Warncke 1968b). He then described five subspecies in subsequent publications (Warncke 1974, 1975a): *A. m. mica* Warncke, 1974, *A. m. leptura* Warncke, 1974, *A. m. solda* Warncke, 1974, *A. m. alma* Warncke, 1975, and *A. m. tenostra* Warncke, 1975. For North African taxa, Warncke (1974) described *A. mariana solda* from Morocco (Tangier) and Algeria (Algiers, including Husseyn-Dey [Hussein Dey] the *locus typicus*, Constantine, Bone, Blida) and Tunisia (Carthago), and noted that this species corresponds to the *Andrena* forms from Bone identified as *iota*, *kappa*, and *lambda* by Saunders (1908), though this is clearly wrong for *lambda* as the genital capsule illustrated by Saunders shows *A.* (*Micrandrena*) *djelfensis* Pérez, 1895. The *A. mariana solda* taxon differs from *A. mariana* s. str. in the female sex by the darker tergal margins, the darker antennae, and the more extensively shagreened clypeus. Warncke (1974) described *A. mariana mica* from southern Algeria (*locus typicus* Ghardaia) and Morocco, giving it a more arid distribution. It also differs from *A. mariana* s. str. in the female sex by the darker tergal margins and darker antennae, but the clypeus is more extensively shiny than in *A. mariana solda*, and the nervulus is said to be more antefurcal. *Andrena m. leptura* is a more eastern taxon, being described from Libya and Egypt, and having a broader process of the labrum than any of these species.

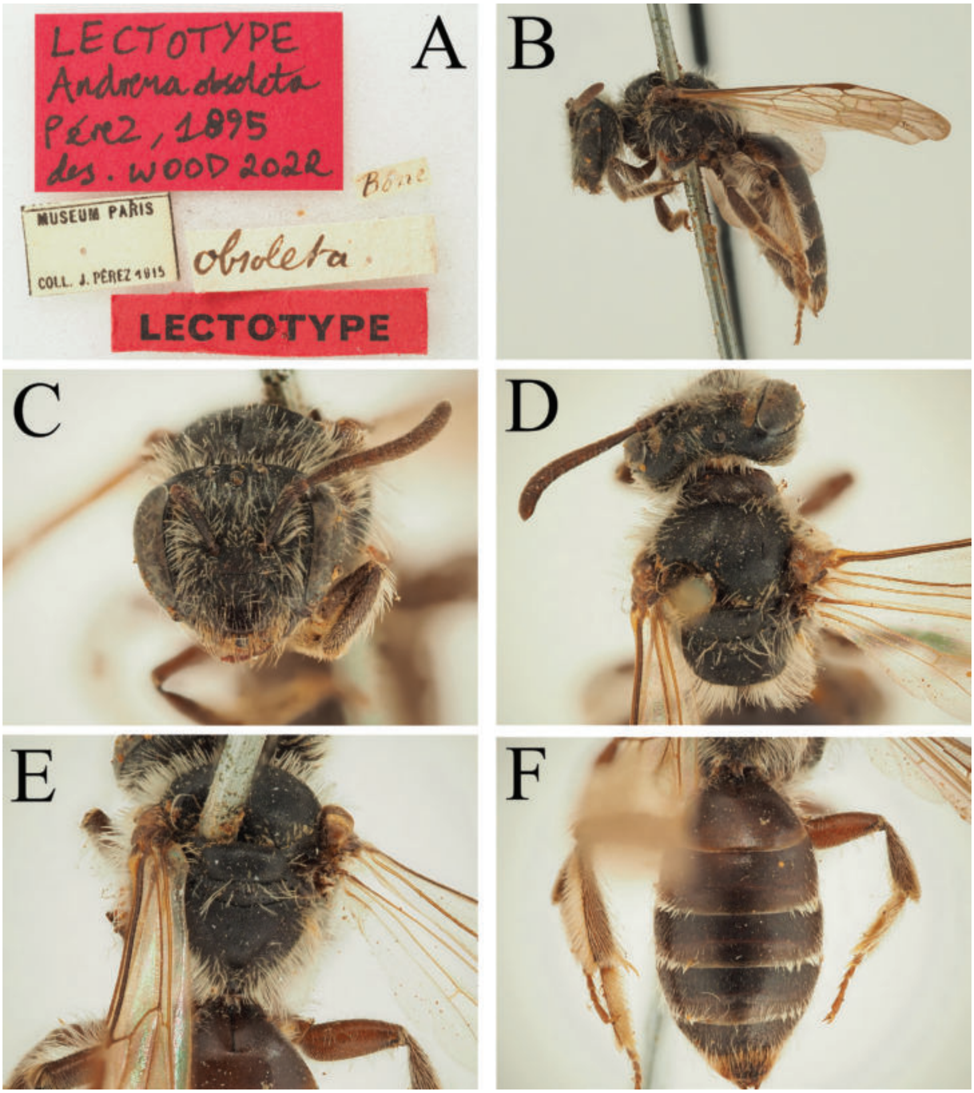

Figure 17. *Andrena* (*Micrandrena*) *obsoleta* Pérez, 1895, true female lectotype **A** label details **B** profile **C** face, frontal view **D** scutum, dorsal view **E** propodeal triangle, dorsal view **F** terga, dorsal view.

Examination of *A. mariana solda* material reveals that it is conspecific with the newly designated lectotype of *A. obsoleta* and is synonymised with it syn. nov. As identified by Warncke, the taxon has a wide distribution across Mediterranean parts of Morocco, Algeria, and Tunisia (Warncke 1974, as *A. m. solda*). Pérez's reference to specimens from France indicates that his original syntypic series would have been polytypic, or he may have changed his mind between writing this catalogue entry and his 1895 publication, or even after this point. Warncke (1974: 40) indicated that *A. m. solda* is present in Sicily which is supported by a newly examined specimen (see below), though he did not designate any Italian specimens as paratypes. As no specimens from France labelled as *obsoleta* could be found in Pérez collection, the conservative position is taken here that this species does not occur in France. The implications for Warncke's misinterpretation of *A. obsoleta* are discussed below.

As *A. mariana solda* is actually a synonym of a valid species that was described prior to *A.* (*Micrandrena*) *mariana* s. str., this has implications for the species-status of the other taxa lumped under *A. mariana* by Warncke. Genetic sequences were available for *A. mariana mica* Warncke, 1974 from southern Morocco, *A. mariana* s. str. from south-western Morocco, and *A. mariana alma* Warncke, 1975 from Portugal (*locus typicus* near Córdoba, southern Spain; Fig. 18). Contrary to the position of Warncke (1968b), examination of material from Morocco, Algeria, and Tunisia shows that *A. mariana* is actually widely distributed across this region, predominantly in southern, more arid areas. Genetically, *A. mariana* s. str. was more closely related to *A.* (*Micrandrena*) *abjecta* Pérez, 1895, separated by an average genetic distance of 5.55% (range 5.49–5.61%), and was strongly separated from *A. m. mica* by 12.73% (range 12.50–12.95%) and *A. m. alma* by 10.94% (range 10.65–11.39%). *Andrena abjecta* + *A. mariana* s. str. therefore formed a clade with bootstrap support of 99. *Andrena m. mica* and *A. m. alma* formed a clade, but were strongly separated from each other by 11.26% (range 10.97–11.41%). The conclusion therefore is that each of these taxa is distinct, and so *A. mica* stat. nov. and *A. alma* stat. nov. are raised to species status. Morphologically, all three taxa can clearly be separated by the structure of the female clypeus, the colour of the antennae, the extent of lightening on the tergal margins, the strength of the scutal punctures, and the shape of the process of the labrum.

Warncke described two further subspecies of *A. mariana*: *A. mariana leptura* from Egypt and *A. mariana tenostra* from south-eastern Spain, the latter specifically from a single female specimen from Villajoyosa in the province of Alicante, then listing additional specimens from Almería and Murcia (Warncke 1976). The status of *A. mariana leptura* will be dealt with in a future publication, as its exact species concept and its eastern and western limits are unclear, though it will be a valid species as it clearly differs from *A. mariana* s. str.; its relationship with *A. mariana* s.l. specimens from southern Israel must also be clarified (Pisanty, in litt.). In Iberia, *A. m. tenostra* is very poorly known. The distinguishing features given by Warncke (1975a) are that the process of the labrum is narrowly trapezoidal and that the clypeus is arched and somewhat flattened in the middle, in contrast to *A. alma* where the clypeus is largely flattened. Additional female specimens were found in Granada which highlight a difference not noted by Warncke, which is that the scutellum is polished and shiny, whereas it is dull in *A. alma*, and more broadly the scutal punctures are less strongly pronounced. Given that subtle differences within this group represent large genetic differentiation, *A. tenostra* stat. nov. is raised to species status.

Finally, a number of specimens were found in the very south of Spain (Málaga, Sevilla) which show a morphology very close to that of *A. mica*. However, ecologically this does not make sense as *A. mica* is not known from the more humid and Mediterranean areas north of the Atlas Mountains. Examination of these specimens shows that A3 is much longer than A4+5, whereas it is as long as A4+5 in *A. mica*. These specimens probably represent an additional undescribed species in the *A. mariana* complex, but

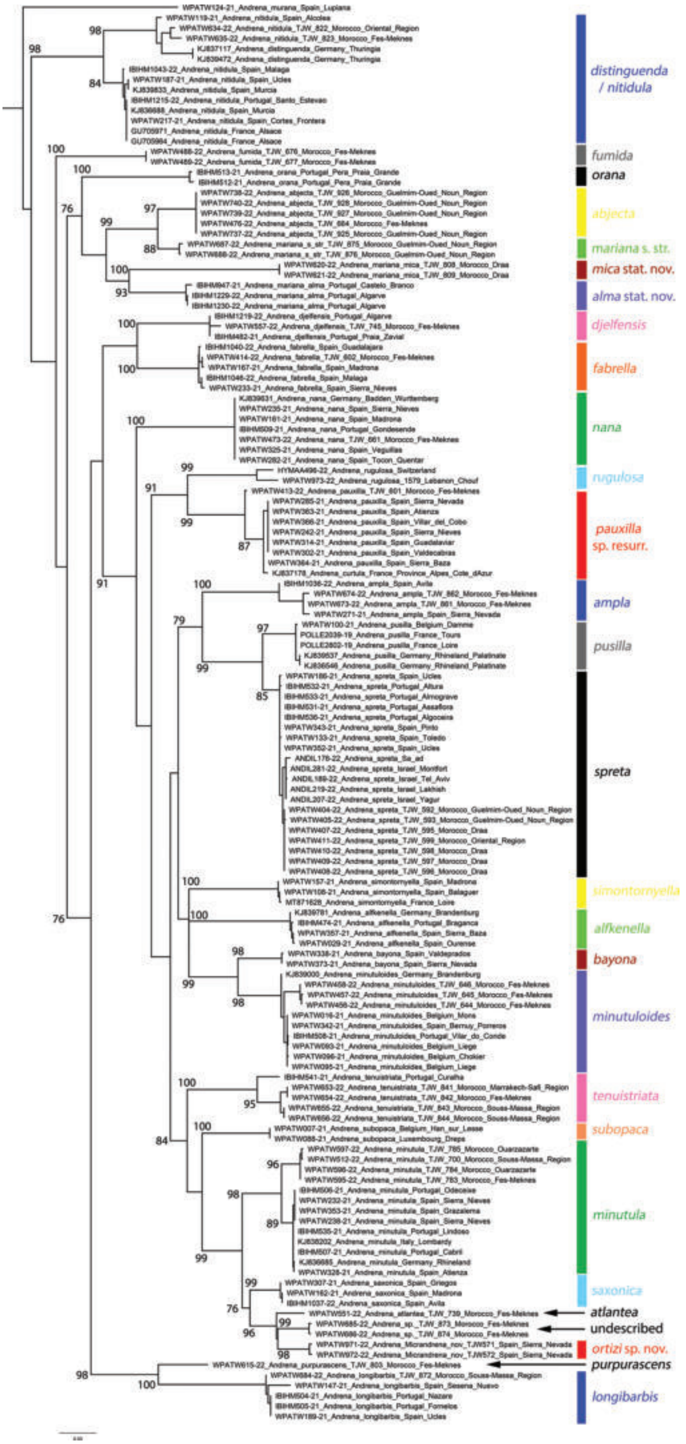

Figure 18. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Micrandrena* Ashmead, 1899 based on the mitochondrial COI gene. *Andrena* (incertae sedis) *murana* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

they are not described at this time, as it would be beneficial to have barcoded specimens to confirm this differentiation. They are therefore referred to as aff *mica* in the identification key.

It is important to note that this material does not belong to *A. abjecta*, the status of which in Iberia is unclear. Warncke (1976) did not record this species from Iberia, and only his distribution maps (Gusenleitner and Schwarz 2002) indicate the presence of this species in northern and eastern Spain. This distribution does not make sense given that all other known records of *A. abjecta* come from north-western Africa (Morocco, Algeria, Tunisia), so the species would naturally be expected to occur in southern Iberia. Dardón (2014) listed two female specimens from Huelva (22.iv.1987) and Zaragoza (9.iii.1991). The specimen from Huelva may represent the undescribed aff *mica* taxon, but it is more difficult to conclude on the specimen from Zaragoza. For now, *A. abjecta* is retained on the Iberian list, but I have not examined any specimens and I consider its presence in Iberia doubtful.

Material examined. ***Andrena alma*****:** **Portugal:** Albandeira, near Lagoa, 20.iv.2005, 1♀, leg. D.W. Baldock, TJWC; Algarve, Casaqueimada (7 km N of Silves), 20.iii.1995, 1♀, leg. T. & M. Simon Thomas, RMNH; Algarve, Monte Gordo, Retur, Praia do Cabeço, 29.iii.2022, 1♂, leg. T.J. Wood, TJWC; Algarve, Tavira, Cacela Velha, 28.iii.2022, 1♂, leg. T.J. Wood, TJWC; Castelo Branco, Fundão Vale de Prazeres, 17.iv.2021, 1♀, leg. C. Siopa, FLOW; **Spain:** El Soldado, Córdoba [38.3747°N, -5.0001°E], 1♀, leg. Seyrig, OÖLM (holotype); Almodóvar del Campo (Ciudad Real), 700 m, 24.iii.2005, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Santa Ana la Real, Sierra Aracena (Huelva), 630 m, 13.iv.2006, 2♂, leg. F.J. Ortiz-Sánchez, FJOS; El Hongo (P.N. Doñana), 30.iii.2018, 1♂, leg. F. Molina, EBDC.

Andrena mariana **s. str.:** **Algeria:** Saida, 15 km S of Sfissifa, Ben Ikhou, st. 6, 6.iv.1983, 6♀, leg. R. Leys & P. v. d. Hurk, RMNH; 23 km NE of Ras El Ma, st. 38, 26.iv.1983, 1♀, leg. R. Leys & P. v. d. Hurk, RMNH; Dayet el Kerch [Daïet el Kerch], st. 5, 5.iv.1983, 2♀, leg. R. Leys & P. v. d. Hurk, RMNH; **Morocco:** Guelmim-Oued Noun, Guelmim, Asrir, 1 km W, 20.iii.2022, 1♀, leg. T.J. Wood, TJWC; **Spain:** Fuerteventura, Valley Granadillos [28.3864°N, -14.0865°W], 17.iv.1934, 1♀, OÖLM (holotype); **Tunisia:** Ksar Hadada, 4–5.iv.1996, 46♀, leg. K. Deneš, OÖLM; M'saken, 20–21.iv.1998, 2♀, leg. K. Deneš, OÖLM; Wadi Ram, 45 km E Douz, 4.iv.2006, 1♀, leg. J. Straka, OÖLM.

Andrena mica**:** **Algeria:** Ghardaia [32.5047°N, 3.6419°E], 1♀, OÖLM (holotype); **Morocco:** 30 km E Midelt, 13.v.1995, 1♀, leg. Mi. Halada, OÖLM; Drâa-Tafilalet, Ouarzazate, P1506, Telouet, Adaha, 1700 m, 18.iv.2022, 6♀, leg. T.J. Wood, TJWC; Drâa-Tafilalet, Ouarzazate, 2 km W Agouim, 1800 m, 13.iv.2022, 3♀, leg. T.J. Wood, TJWC; Ifkern, 25 km E Boulemane, 24.v.1995, 1♀, leg. Mi. Halada, OÖLM; M'rirt (30 km N), 11.iii.1989, 1♀, leg. H. Teunissen, RMNH; **Tunisia:** Hammamet env, 15.iii.1996, 1♀, leg. K. Deneš, OÖLM; Kasserine, 13.iv.1998, 1♀, leg. K. Deneš, OÖLM; Nefta [Naftah], 20.v.1993, 1♀, leg. J. Batelka, OÖLM.

Andrena **aff** ***mica*****:** **Spain:** 40 km W Málaga, Yunquera, 800 m, 29.iv.2003, 5♀, leg. J. Halada, OÖLM/TJWC; La Corchuela (Dos Hermanas, Sevilla), 35 m, 27.iii.2009, 2♂, 2♀, leg. F.J. Ortiz-Sánchez, FJOS; Río Blanco, Aguadulce (Sevilla), 300 m, 17.v.2008, 1♀, leg. F.J. Ortiz-Sánchez, FJOS.

***Andrena nitidula*: Algeria:** Babor, 1♀, MNHN (false lectotype of *A. obsoleta*).

***Andrena obsoleta*: Algeria:** Bône [=Annaba, 36.9092°N, 7.7264°E], 1♀, MNHN (lectotype of *A. obsoleta*, by present designation); 23 km NE of Ras El Ma, st. 38, 26.iv.1983, 1♀, leg. R. Leys & P. v.d. Hurk, TJWC; 5 km N of Mecheria, Djebel Antar, st. 10, 7.iv.1983, 1♀, leg. R. Leys & P. v.d. Hurk, RMNH; **Italy:** Sicilia orient., Taormina, 200 m, Ghardino [Giardini Naxos], 25.iii.1950, 1♂, Hartig & Grisham, MZUR; **Tunisia:** Tunis, 1911, 3♀, leg. O. Schmiedeknecht, SMFD.

***Andrena tenostra*: Spain:** Villajoyosa [38.5097°N, -0.2299°E], 11.v.1936, 1♀, leg. Andréu, OÖLM (holotype); Salobreña, Granada, 8.v.1983, 3♀, leg. W. Perrandin, OÖLM/TJWC.

Andrena (*Micrandrena*) *distinguenda* Schenck, 1871 and *Andrena* (*Micrandrena*) *nitidula* Pérez, 1903

The status of these two species has been extensively argued over, and despite much attention the position remains somewhat unclear. Warncke (1967) argued that *A. distinguenda* Schenck, 1871 was an unavailable name because it was preoccupied by *A. distinguenda* Schenck, 1853. He then authored the replacement name *A. obsoleta spongiosa* Warncke, 1967, using the incorrect concept that *A. obsoleta* was the oldest available name for this group of species, as discussed above. Schönitzer et al. (1992) clarified the situation, and argued that *A. distinguenda* Schenck, 1853 was a *nomen nudum* because it appears without a description in a discussion concerning species related to *A. bicolor*. As a *nomen nudum*, the name is available and cannot preoccupy its later usage. Therefore, the name *A. distinguenda* Schenck, 1871 is both available and valid as the senior synonym; *A. obsoleta spongiosa* is consequently an unnecessary replacement name.

Andrena distinguenda was described from western Germany, and *A. nitidula* was described from south-western France (lectotype from Bordeaux [though this is not indicated on the specimen, it bears the number '675' which refers to the entry for *A. nitidula* in the catalogue of Pérez], designated by Warncke 1967, Fig. 19). As discussed above, Warncke (1967) incorrectly recognised a specimen that morphologically corresponds to *A. nitidula* as the lectotype of *A. obsoleta*, and then synonymised *A. nitidula* with *A. obsoleta*. He then treated *A. distinguenda* Schenck, 1871 as a subspecies of *A. obsoleta* in the form *A. obsoleta spongiosa*. He then later adopted a three subspecies model, *A. o. obsoleta* (North Africa), *A. o. nitidula* (Western Europe), and *A. o. spongiosa* (Central Europe) (see Schönitzer et al. 1992), finally introducing a fourth subspecies *A. o. puella* Alfken, 1938 in Sardinia and Sicily (see Gusenleitner and Schwarz 2002). Schönitzer et al. (1992) argue that both *A. distinguenda* and *A. nitidula* can be morphologically separated in north-western Italy (Bordighera). They argue that *A. nitidula* occurs in North Africa, citing Pérez (1903) and Alfken (1914). They also argue that specimens from southern Spain (Tarifa) appear to be somewhat intermedi-

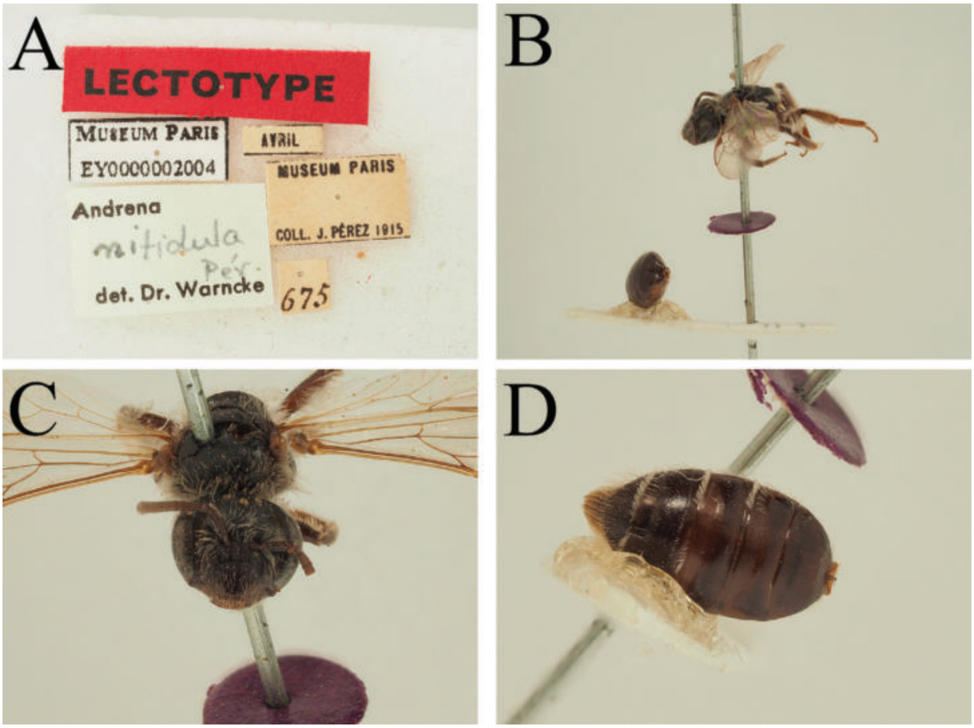

Figure 19. *Andrena* (*Micrandrena*) *nitidula* Pérez, 1903, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

ate between *A. distinguenda* and *A. nitidula*, concluding that the question as to whether there are two species or simply a very variable single species remains open.

Burger and Herrmann (2003) revised European material from this species pair using the names *A. distinguenda* and *A. nitidula*, after having examined syntypes of *A. nitidula* in the ZMHB collection. Using morphological characters, they conclude that (in a European context) *A. distinguenda* has a predominantly eastern distribution, from Central Europe to Greece, with populations also in the south of France and a few records from north-eastern Spain. In contrast, *A. nitidula* is a western species, from Iberia to the south and east of France and into south-western Germany and the north-west of Italy. They reach the same conclusion as Schönitzer et al. (1992), that where these two forms occur in sympatry (Germany, France, Italy) they can be morphologically separated. They do not conclude on the status of *A. obsoleta*, but note that *A. nitidula* occurs in North Africa, and that Warncke's treatment is unclear. This problem arises because it does not appear that any of the authors of Schönitzer et al. (1992) or Burger and Herrmann (2003) inspected the lectotype of *A. obsoleta* designated by Warncke in the MNHN. This lectotype bears a handwritten label that the lectotype designation is incorrect, and that the specimen corresponds to *A. distinguenda* Schenck (Fig. 16A). However, it is unclear who wrote this, as neither Schönitzer et al. (1992)

nor Burger and Herrmann (2003) mention this explicitly, and I do not recognise the handwriting on the label.

Barcode analysis complicates this matter further (Fig. 18). Analysis of sequences from France, Germany, Morocco, Portugal, and Spain shows the presence of two clear clades. One clade is composed of specimens identified as *A. nitidula* from France, Portugal, and Spain, including specimens from the south of Iberia (Algarve, Málaga, Murcia). This clade would appear to be the true *A. nitidula*. However, the second clade contained sequences from specimens identified as *A. distinguenda* from central Germany, but also from a specimen identified as *A. nitidula* from central Spain (Guadalajara) and two specimens identified as *A. nitidula* from northern Morocco (Fès-Meknes, Oriental). These two clades were consistently separated genetically, by an average genetic distance of 7.08% (range 5.58–8.77%). The nominally true *A. nitidula* clade showed low intraspecific variation of 0.26% (range 0.00–0.63%). However, the situation in the clade containing *A. distinguenda* sequences from Germany showed intraspecific variation of 2.84% (range 0.00–4.10%), with the 4.10% genetic distance recorded between specimens from Germany and the Middle Atlas (Bakrit, near Azrou) in Morocco.

Morphologically, both Spanish and Moroccan specimens falling into the *A. distinguenda* clade conform to the concept of *A. nitidula* using the criteria specified by Burger and Herrmann (2003). Indeed, all material I have identified from north-western Africa morphologically conforms to the concept of *A. nitidula* sensu Burger and Herrmann. Although the genetic data strongly supports the existence of two species, the conflict between the genetic and morphological results suggests that, at the moment, they cannot be consistently separated morphologically across their range. No taxonomic action is taken here, and the morphological criteria of Burger and Herrmann (2003) are followed for the purpose of the identification key. In Iberia, *A. nitidula* is considered to be present throughout, but *A. distinguenda* is limited to the extreme north-east of Spain. However, it is clear that there is a major disagreement between the morphological and genetic methods, and these two species may ultimately not be consistently separable. Further analysis using more powerful genetic techniques is necessary.

Relictual species morphologically related to *Andrena* (*Micrandrena*) *rugulosa* Stöckhert, 1935

Inspection of *Micrandrena* specimens from high altitude in the Sierra Nevada revealed the presence of a species that morphologically resembles *A.* (*Micrandrena*) *rugulosa* Stöckhert, 1935 due to its head that is only slightly shorter than wide rather than clearly shorter than wide, an unusual character in *Micrandrena*. This finding is remarkable, because although widely distributed in Central and Eastern Europe, *A. rugulosa* has a western limit in the Swiss Alps, and has not been previously recorded from France, Spain, or Portugal (Gusenleitner and Schwarz 2002). Samples collected from the Sierra Nevada at high altitude (2000–2100 m) during 2021 are strongly differentiated from *A. rugulosa*, separated by an average genetic distance of 16.01% (range 15.81–16.41%;

Fig. 18). Instead, they form a clade with bootstrap support of 96 with sequences of *A.* (*Micrandrena*) *atlantea* Wood, 2021 (High and Middle Atlas in Morocco) and a morphologically similar undescribed *Micrandrena* from high altitude (1800–1900 m) in the Moroccan Middle Atlas.

The Sierra Nevada sequences were separated from *A. atlantea* by an average genetic distance of 6.04% (range 5.71–6.38%) and from the undescribed *Micrandrena* by an average genetic distance of 6.34% (range 6.31–6.38%). These three species would therefore seem to represent an isolated *Micrandrena* lineage that is restricted to the Sierra Nevada and the High and Middle Atlas Mountains in Morocco, with consequent genetic and morphological divergence. This is the same pattern as observed in the subgenus *Euandrena*, suggesting that the Sierra Nevada hosts the remnants of a fauna that was presumably once more widespread across Iberia and North Africa. Additional sampling and genetic analysis is required to determine if this pattern holds true for other bee groups. The new *Micrandrena* species from the Sierra Nevada is described below, and the undescribed *Micrandrena* species from Morocco will be described in an upcoming publication.

***Andrena* (*Micrandrena*) *niveata* Friese, 1887 sensu lato**

Andrena niveata was described from Germany and Hungary, without further information (Friese 1887). The exact type locality is unclear, as well as the type depository, with no clearly identifiable syntypes located during searches in the SMFD and ZMHB collections, the suggested possible depositories (Gusenleitner and Schwarz 2002). Nevertheless, the concept of *A. niveata* in Central Europe is clear, and *A. niveata* is a well-defined species in this region (Schmid-Egger and Scheuchl 1997; Gusenleitner and Schwarz 2002; Amiet et al. 2010). Warncke described three subspecies; *A. n. lecana* Warncke, 1975 (Spain; *locus typicus*: Rivas-Vaciamadrid), *A. n. haloga* Warncke, 1980 (Italy; *locus typicus*: Lecce), and *A. n. bubulca* Warncke, 1975 (Turkey; *locus typicus*: Erzurum); the status of the Italian and Turkish subspecies is not addressed here. Unfortunately, all nine freshly collected *A. n. lecana* specimens from central and southern Spain (including from the *locus typicus*) sent for genetic analysis failed to produce sequences. More specific primers will be required to address this question using genetic evidence.

Warncke (1975a) described *A. n. lecana* extremely briefly, noting that in both sexes the first tergum was finely but clearly shagreened, and finely but more strongly punctured than in *A. niveata* s. str., with the following terga also more clearly and strongly punctured. He then gave a distribution of *A. n. lecana* across much of central Spain south to hilly parts of the provinces of Granada (Huéscar) and Almería (Tíjola). In contrast he gives a distribution for *A. niveata* s. str. of the whole of Iberia, though his distribution maps (Gusenleitner and Schwarz 2002) show a distribution covering eastern, central, and south-eastern Spain. There is therefore the possibility that the two subspecies exist in sympatry, suggesting that they may be distinct.

Examination of material from Spain shows that the two taxa are distinct, but morphological separation is challenging, may not be possible in all cases when old, abraded, or dirty specimens are available, and is best made with reference to the male genital capsule. Taking male specimens, the shape of the gonostyli are distinctive. In *A. niveata* s. str., the gonostyli are elongate, with the inner margins of the gonostyli only weakly produced towards the penis valves (Fig. 20A). In contrast, in *A. n. lecana*, the inner margins of the gonostyli are strongly and clearly produced towards the penis valves (Fig. 20B); the apical spatulate part of the gonostyli are also comparatively shorter, thus the gonostyli appear shorter and more compact in *A. n. lecana* and longer and more elongate in *A. niveata* s. str. The structure of the genital capsule of *A. niveata* s. str. is consistent across Spain to the province of Málaga (the most southerly *A. niveata* s. str. male examined). Furthermore, the male scutum is shagreened in *A. niveata* s. str., whereas it is extensively shiny in *A. n. lecana*, and the terga are also more strongly shagreened in *A. niveata* s. str. compared to *A. n. lecana* (Fig. 20C, D). Separation of females (recognised by their wide and poorly defined propodeal triangle, Fig. 20E, F, in combination with their depressed tergal margins) is more challenging and may not be possible in all situations. Typically, *A. niveata* s. str. has the terga shagreened, with punctures on the tergal discs partially disappearing into this shagreenation (Fig. 20G). In contrast, *A. n. lecana* has the terga shiny, almost without shagreen, with the dense punctures on the tergal discs strong and clearly visible, not disappearing due to the absence of background shagreenation (Fig. 20H). The scutum and scutellum are also more extensively shiny, whereas in *A. niveata* s. str. these areas usually show at least some shagreenation and are never polished and smooth. The problem comes that some individuals nominally assigned to *A. niveata* s. str. have partially shing terga, and without genetic sequences it is not possible to say with complete confidence if they belong to *A. niveata* s. str. or *A. n. lecana*. Moreover, all Iberian *A. niveata* s. str. have tergal shagreenation that is weaker than that of *A. niveata* s. str. populations in Central Europe.

The position is taken here that the strength of tergal shagreenation in *A. niveata* s. str. females is variable across Europe, but that *A. lecana* stat. nov. is a valid species based on the overlapping range in combination with the consistent difference in the shape of the male genital capsule. It has a distribution across steppic parts of central Spain, extending into mountainous areas in south-eastern Spain. Females displaying any level of shagreenation on the tergal discs are considered to represent Iberian populations of *A. niveata* s. str., and females with completely polished tergal discs without a trace of shagreenation represent *A. lecana* (see identification key). Future genetic investigation using more targeted primers will be necessary to confirm this position. Finally, specimens of *A. lecana* from high altitude in the Sierra Nevada show slightly different antennal ratios in the male sex, though the male genital capsule is otherwise identical; this requires further investigation.

Material examined. ***Andrena lecana*: Spain:** Ribas [Rivas-Vaciamadrid, 40.3503°N, -3.5390°E], 6.v.1908, 1♀, leg. Dusmet, OÖLM (holotype); Carboneras de Guadazaón (Cuenca), 1030 m, 16.v.2009, 1♀, leg. F.J. Ortiz-Sánchez, FJOS; Guadalajara, Alcolea del Pinar, 12.v.2021, 1♀, leg. T.J. Wood, TJWC; Guadalajara, Lupiana, 12.v.2021, 1♀, leg. T.J. Wood, TJWC; Huéscar (Granada), 1900, 1♂, leg. Escalera, OÖLM (paratype); La Cabrilla, Sierra Cazorla (Jaén), 1600 m, 1–3.vi.2022,

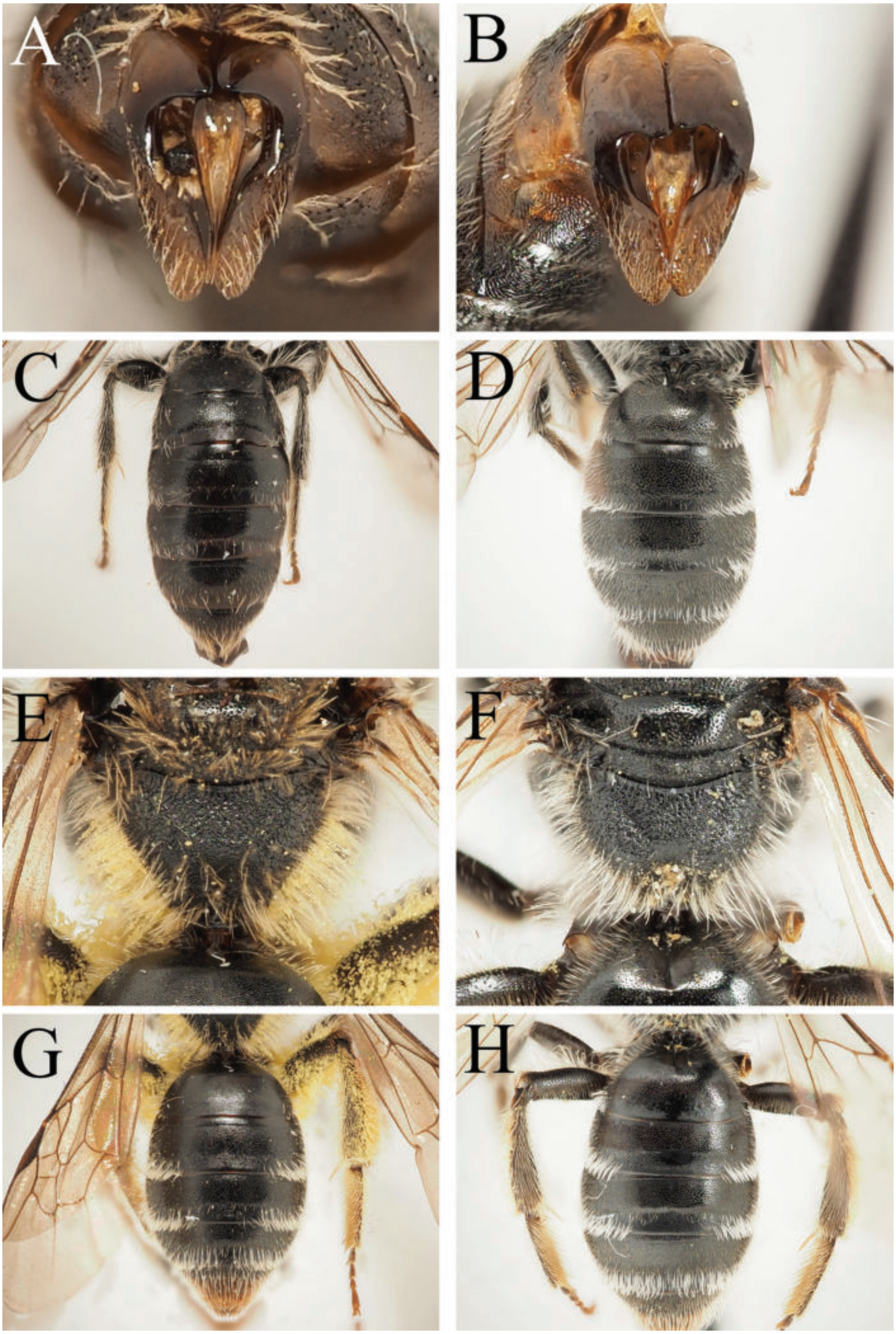

Figure 20. *Andrena* (*Micrandrena*) *niveata* Friese, 1887 **A** male genital capsule **C** male terga, dorsal view **E** female propodeal triangle **G** female terga, dorsal view; *Andrena* (*Micrandrena*) *lecana* Warncke, 1975 **B** male genital capsule **D** male terga, dorsal view **F** female propodeal triangle **H** female terga, dorsal view.

1♀, leg. C.M. Hererra, CMHC; Madrid, Rivas-Vaciamadrid, Canal de Manzanares to Camino de Uclés, 19.v.2021, 2♀, leg. T.J. Wood, TJWC; Órgiva, N, 1300 m, Sierra Nevada, 26.vi.1988, 1♀, leg. M. Schwarz, OÖLM; Pozuelo, La Fuente, 1♂, OÖLM (paratype); Segovia, Madrona, 500 m NE, Arroyo del Hocino, 15.v.2021, 2♀, leg. T.J. Wood, TJWC; Sierra Nevada, Trevélez, Refugio La Campiñuela, 2400 m, 14.vi.2021, 7♂, 2♀, leg. T.J. Wood, TJWC.

Andrena niveata **s. str.: Spain:** Cáceres, Cuacos de Yuste, 500 m, 11.v.1999, 1♀, leg. H. & J.E. Wiering, RMNH; Cádiz, Grazalema, Río Guadalete, 28.v.2021, 1♀, leg. T.J. Wood, TJWC; Cádiz, Embalse de Barbate Sw, 1♂, 3♀, 6.v.2017, leg. Barták & Kubik, OÖLM/TJWC; Granada, Sierra de Baza, Prados del Rey, 2000 m, 19.vi.2021, 11♀, leg. T.J. Wood, TJWC; Málaga, 5 km W of Alhaurín de la Torre, 4.vi.1962, 1♀, leg. Jeekel & Wiering, RMNH; Málaga, Cortes de la Frontera, path to Llano de las Labores, 26.v.2021, 3♀, leg. T.J. Wood, TJWC; Málaga, Estepona, 21.iv.1983, 1♀, leg. H. Teunissen, RMNH; Navarra, Tudela, 16.iv.1978, 1♀, leg. C. Gielis, RMNH; Gerona, Figueras, 15.iv.1971, 1♀, leg. J. Leclercq, UMONS.

Andrena* (*Micrandrena*) *spreta **Pérez, 1895,** ***Andrena* (*Micrandrena*) *curtula*** **Pérez, 1903,** ***Andrena* (*Micrandrena*) *pusilla*** **Pérez, 1903, and** ***Andrena* (*Micrandrena*) *pauxilla*** **Stöckhert, 1935**

Members of this species group are challenging to identify and have been inconsistently treated in the literature, with variable species concepts. *Andrena spreta* was described from Algeria, with Warncke (1967) designating a lectotype from Biskra (Fig. 21A; Pérez also mentions a female from Constantine in his catalogue). *Andrena curtula* was described from north-eastern Spain, with Warncke (1967) designating a lectotype from Barcelona (Fig. 21B). *Andrena pusilla* was described from the south of France (Bordeaux, Nantes) and Spain, with Warncke (1967) designating a lectotype from Nantes (Fig. 21C). Finally, *A. pauxilla* was described from the Upper Rhine valley in south-western Germany, with Stöckhert (1935) designating a female from Karlsruhe as the holotype.

Warncke (1967) recognised three species, *A. spreta*, *A. curtula*, and *A. pauxilla*, treating *A. pusilla* as a subspecies of *A. spreta*. Warncke (1974) recognised only one taxon in North Africa (*A. spreta spreta*), but Warncke (1976) surprisingly recognised only *A. spreta pauxilla* in Iberia, not mentioning *A. curtula* as a species despite its description from Iberia, only referring to its listing in Ceballos (1956) but indicating that this referred to *A.* (*Micrandrena*) *tenuistriata* Pérez, 1895. This treatment is difficult to understand. Warncke later adopted an extremely broad position (see distribution maps in Gusenleitner and Schwarz 2002), lumping all members of the group into a broad *A. spreta*. In this model, *A. spreta* s. str. was restricted to North Africa, *A. spreta curtula* was distributed across Iberia to southern France, *A. spreta pusilla* was found in northern and Central Europe, with two more subspecies in i) Italy and ii) south-eastern Europe to the Levant.

This position was not adopted by subsequent authors. Schwarz et al. (1996) accepted *A. pusilla* as a valid species, as well as *A. curtula*. However, they synonymised *A. pauxilla* with *A. curtula*. Schmid-Egger and Scheuchl (1997) did not follow this inter-

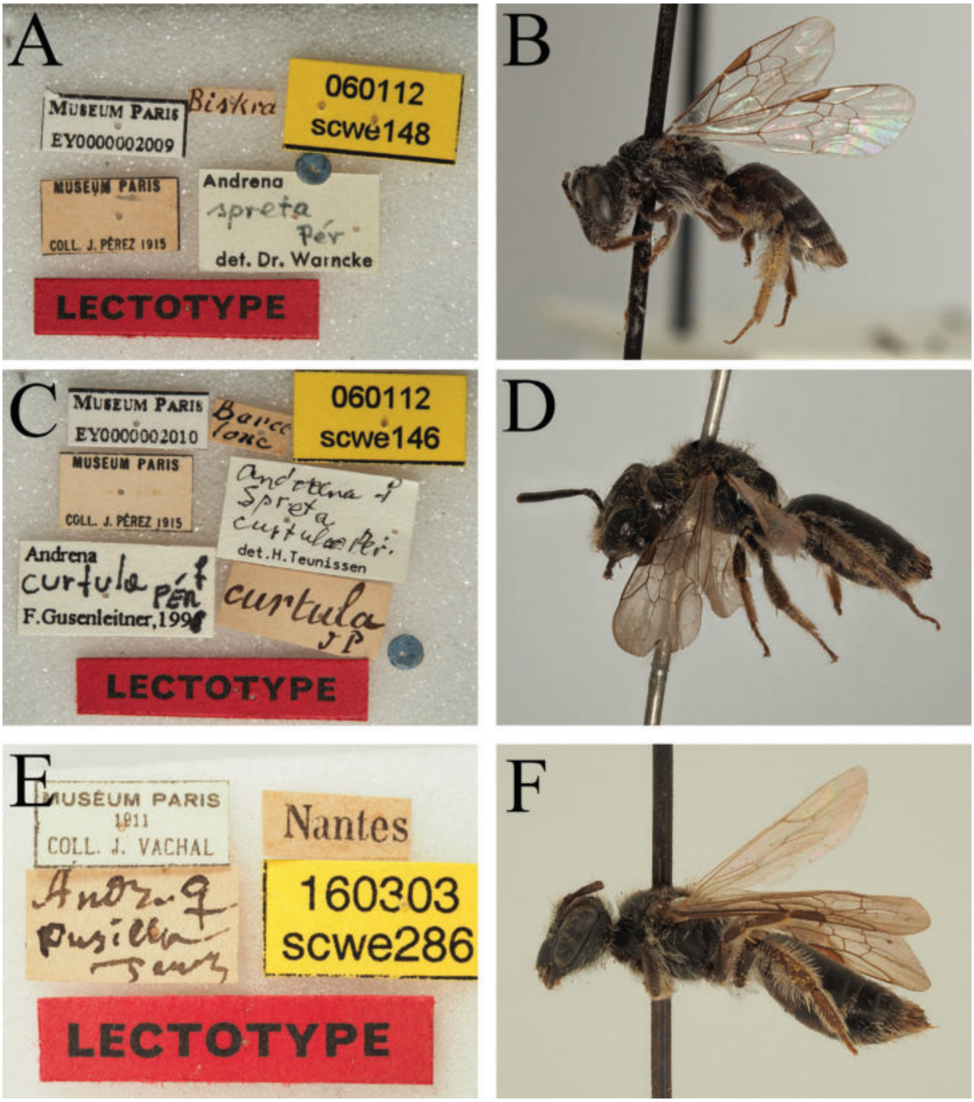

Figure 21. *Andrena* (*Micrandrena*) *spreta* Pérez, 1895, female lectotype **A** label details **B** profile; *Andrena* (*Micrandrena*) *curtula* Pérez, 1903, female lectotype **C** label details **D** profile; *Andrena* (*Micrandrena*) *pusilla* Pérez, 1903, female lectotype **E** label details **F** profile.

pretation, treating *A. pauxilla* as a distinct species, though Amiet et al. (2010) followed the position of Schwarz et al. (1996). Dardón (2010) and Dardón et al. (2014) accepted only a broad *A. spreta* taxon, including *A. curtula*, *A. pusilla*, and *A. pauxilla*, recognising *A. spreta* s. str. and *A. spreta pusilla* in an Iberian context. The situation is therefore unclear, both for the number of species present in this complex, and their distributions.

Analysis of barcodes provides unambiguous support for the existence of three distinct species (Fig. 18), *A. spreta* including *A. curtula*, *A. pusilla*, and *A. pauxilla* sp.

resurr. Specimens of *A. spreta* from Israel, Morocco, Portugal, Spain formed a clear clade with bootstrap support of 85. These sequences were separated by an average genetic distance of 0.45% (range 0.00–1.07%). They were clearly separated from a sister clade of *A. pusilla* sequences from Belgium, France, and Germany by an average genetic distance of 4.33% (range 3.88–4.84%). The *A. pusilla* clade had low intraspecific genetic distance of 0.29% (range 0.00–0.71%). *Andrena pauxilla* was strongly differentiated and was found as sister to *A.* (*Micrandrena*) *rugulosa*, showing average genetic differentiation of 10.96% (range 10.38–11.85%) from *A. spreta* and 11.69% (range 10.75–12.59%) from *A. pusilla*. This *A. pauxilla* clade includes a specimen from the south of France (KJ837178, Lac St. Croix) that was identified as *A. curtula*, the genetic results suggest that it is misidentified. Morphologically, *A. pauxilla* is clearly differentiated from *A. spreta* and *A. pusilla* due to the absence of a gradulus at the base of the terga. Confusion is impossible in the female sex after recognition of this character; the foveae are also longer and narrower and filled with white rather than light brown hairs, the scutum is more densely and uniformly punctate when compared to *A. spreta*. Examination of the lectotypes of *A. spreta* and *A. curtula* shows no clear structural difference. The degree of shagreenation varies, but this is typical for *A. spreta* across its range; both lectotype specimens show the presence of a gradulus at the base of the terga, excluding their conspecificity with *A. pauxilla*. Due to these genetic results combined with the morphology of the lectotype specimens, the synonymy of *A. curtula* with *A. spreta* as proposed by Dardón (2010) and Dardón et al. (2014) is therefore followed, though their synonymies of *A. pusilla* and *A. pauxilla* with *A. spreta* are rejected.

A single barcode was available from Moroccan specimens from the Middle Atlas tentatively identified as *A. pauxilla* which showed an average genetic distance to European *A. pauxilla* specimens of 2.00% (range 1.48%–2.29%). This is considered to represent only separation by distance, and thus *A. pauxilla* is recorded for the first time in North Africa and unambiguously recorded in Spain. Within Spain, *A. pauxilla* appears to be principally recorded from mountain ranges such as the Sierra de las Nieves, the Sierra Nevada (Fig. 22A, B), Sierra Cazorla, Sistema Central, and Sistema Ibérico (Fig. 22C, D). *Andrena pauxilla* would therefore have a currently known distribution of Morocco, Spain, France, and Germany. On the basis of these results, *A. spreta* would appear to be a pan-Mediterranean species, and *A. pusilla* its predominantly northern counterpart (though the species descends south into Italy). The two species can be found in sympatry in the south of France (Praz, in litt.), but to date I have examined no *A. pusilla* specimens from Iberia. Due to the confusion in this group, it must be considered absent until it can be positively demonstrated to be present south of the Pyrenees.

Material examined. *Andrena curtula*: Spain: Barcelona [41.4028°N, 2.1332°E], 1♀, MNHN (lectotype; Fig. 21B).

***Andrena pauxilla*: France:** Bischenberg, 28.vi.1936, 1♀, leg. M. Klein, det. E. Stöckhert, OÖLM; Hausbergen, 29.vi.1930, 1♀, leg. M. Klein, det. H.R. Schwenninger, OÖLM; **Morocco:** Fès-Meknès, Boulemane, R503, 7 km SE of Boulemane, 1900 m, 22.v.2022, 1♂, 1♀, leg. T.J. Wood, TJWC; **Spain:** Canet de Mar, 26.iii.1963, 1♀, leg. F. Vergés, det. H.R. Schwenninger, OÖLM; Cuenca, Huerta del

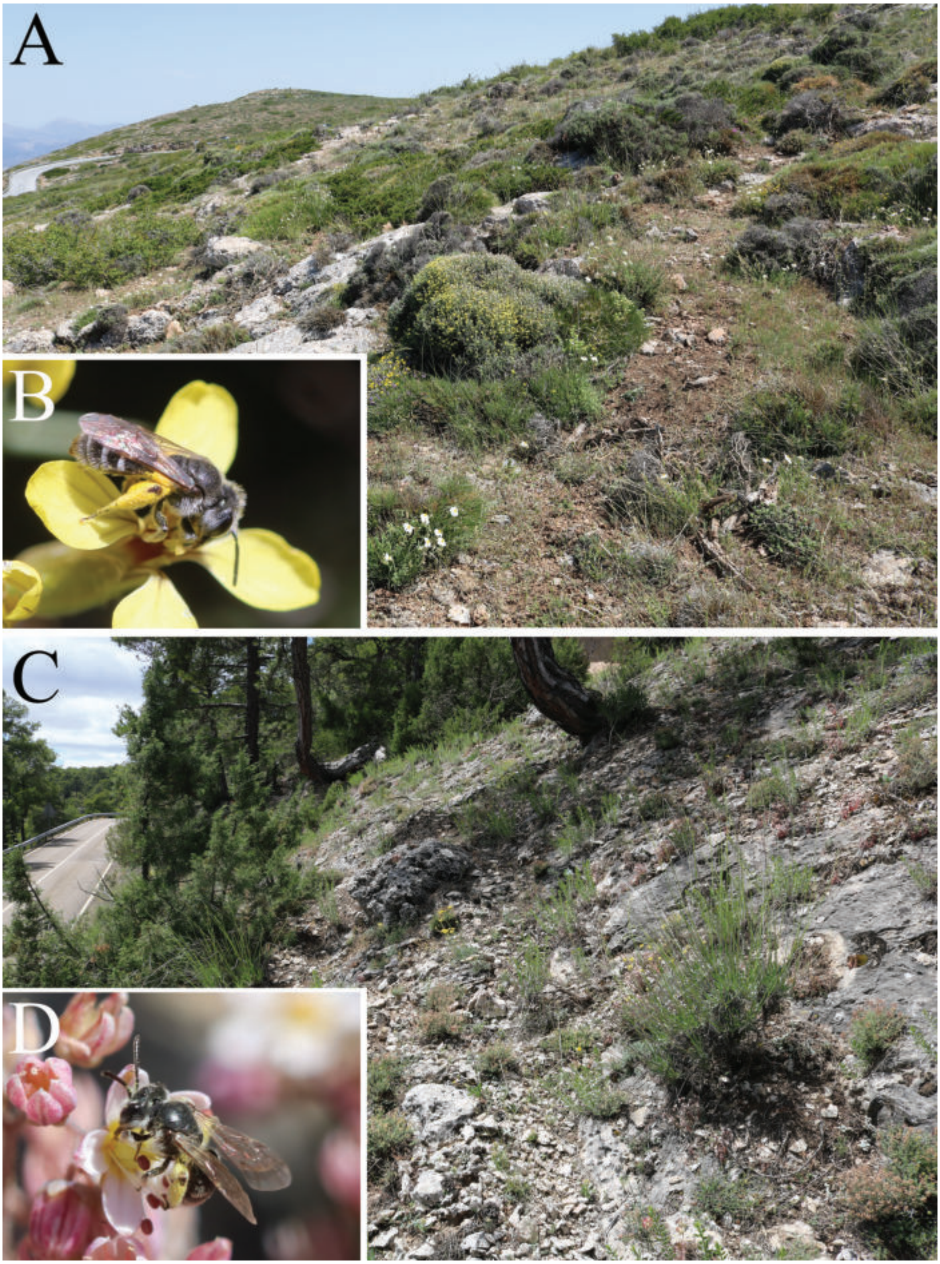

Figure 22. *Andrena* (*Micrandrena*) *pauxilla* Stöckhert, 1935 **A** habitat, Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 2100 m, 12.vi.2021 **B** female collecting pollen from *Vella spinosa* (Brassicaceae) **C** habitat, Cuenca, Mirador Valle de Valdecabras, 21.vi.2021 **D** female collecting pollen from *Sedum* spp. (Crassulaceae).

Marquesado, environs north of town, 26.vi.2021, 3♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Jardín Botánico Hoya de Pedraza environs, 1900 m, 9.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 2100 m, 12.vi.2021, 1♀, leg. T.J. Wood, TJWC; Guadalajara, Aldeanueva de Atienza, 9.vii.2021, 1♀, leg. T.J. Wood, TJWC; Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 30.v.2021, 1♀, leg. T.J. Wood, TJWC; La Cabrilla, Sierra Cazorla (Jaén), 1600 m, 3.vi.2022, leg. C.M. Herrera, CMHC; Sierra Cazorla, Puerto Llano, 1800 m, 11.vi.2022, 1♂, 3♀, leg. J. Valverde, CMHC; Teruel, Guadalaviar, Rambla de los Ojos, 27.vi.2021, 1♀, leg, T.J. Wood, TJWC; Teruel, Villar del Cobo, Barranco de los Oncenachos, 27.vi.2021, 6♀, leg, T.J. Wood, TJWC; Cuenca, Mirador Valle de Valdecabras, 21.vi.2021, 2♀, leg, T.J. Wood, TJWC.

***Andrena pusilla*: France:** Nantes [47.2233°N, -1.5542°W], 1♀, MNHN (lectotype; Fig. 21C).

***Andrena spreta*: Algeria:** Biskra [34.8600°N, 5.6995°E], 1♀, MNHN (lectotype; Fig. 21A).

Andrena (*Micrandrena*) *strohmella* Stöckhert, 1928 and *Andrena* (*Micrandrena*) *icterina* Warncke, 1974

Andrena strohmella was described from southern Germany and is a typically early spring species in the Central European *Andrena* fauna, with records extending south to the High and Maritime Alps in France, and west to the Bordeaux region; it has not previously been reported from the Pyrenees (Gusenleitner and Schwarz 2002). Warncke (1974) later described *A. icterina* from northern Algeria. He later indicated the presence of this species in south-eastern Spain in his distribution maps (Gusenleitner and Schwarz 2002), though he did not list its present in Iberia (Warncke 1976). Wood et al. (2020b) later reported the presence of this species in northern Morocco. In his description of *A. icterina*, Warncke draws comparison with *A. strohmella*, noting that the process of the labrum is half as broad, the clypeus is more sparsely punctate and lacking an unpunctured midline, that the terga are more strongly shagreened, and that the carinae on the dorsolateral corners of the first tergum are more weakly pronounced. Dardón (2010) and Dardón et al. (2014) did not actually examine any material of Iberian *A. icterina*, but inspection of new Iberian material has demonstrated that *A. icterina* is more widespread in Iberia than previously thought, being found from the Los Alcornocales to the Sierra de las Nieves, the Sierra Nevada, Sierra de Baza, Sierra Cazorla, and Sistema Central, and is also newly reported from northern Portugal (see below). In all of these localities it is found in mountainous areas, generally at high altitude in excess of 1000 m.

Dardón (2010) and Dardón et al. (2014) reported *A. strohmella* from north-eastern Spain, from Tarragona: Alcanar, v.2002, leg. Kadlec, OÖLM. I have not been able to locate and examine this specimen for myself in the OÖLM collection, but it is slightly problematic for ecological regions. *Andrena strohmella* is clearly a species of deciduous temperate woodland; this is reflected in its distribution across Central Europe, and in its association with flowering trees such as *Crataegus* (Rosaceae), *Prunus* (Rosaceae), and *Salix* (Salicaceae). *Andrena strohmella* has therefore not previously been reported from Mediterranean regions. The record from Alcanar does not therefore match the ecology of this species, Alcanar being a low-elevation (c. 70 m) village close to the Mediterranean coast. However, *A. strohmella* is present in north-eastern Catalonia based on recently collected specimens (Álvarez Fidalgo, in litt.), and so the species is retained on the Spanish and Iberian lists.

More broadly, morphological differences between *A. strohmella* and *A. icterina* are slight, though they do not appear to introgress based on examined specimens. Some characters such as the strength of the carinae on the dorsolateral corners of the first tergum are not completely consistent, because some specimens in Central Europe can be found in which these are very weakly produced. Genetic data will hopefully clarify the status of *A. icterina*, but unfortunately, like *A. lecana*, this taxon appears to be challenging to barcode, as all seven Iberian specimens sent for genetic analysis failed or returned corrupted sequences.

Material examined. ***Andrena icterina*: PORTUGAL:** Bragança, Serapicos, 16.v.2021, 1♀, leg. A. Soares, A. Soares Coll.; **SPAIN:** Ávila, Hoyocasero, El Pinar de Hoyocasero, 16.v.2021, 1♀, leg. T.J. Wood, TJWC; Ávila, Navalsauz, 1 km E, Alberche stream, 16.v.2021, 1♀, leg. T.J. Wood, TJWC; Cádiz prov., Vent. L. Canillas Hozgarganta-Tal b. Jimena 250 m, 14.iv.1985, 3♀, leg. W. Schacht, OÖLM; Campamento Alfaguara (Alfacar, Granada), 1420 m, 13.v.2007, 1♂, 2♀, leg. F.J. Ortiz-Sánchez, FJOS; Cortijo Tortas, Paterna del Madera (Albacete), 1310 m, 30.iv.2022, 2♂, leg. F.J. Ortiz-Sánchez, FJOS; Granada, Sierra de Baza, Prados del Rey, 2000 m, 19.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Capileira to La Cebadilla, 1500 m, 8.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Jardín Botánico Hoya de Pedraza environs, 1900 m, 2♀, leg. T.J. Wood, TJWC; Granada, Venta de los Alazores, 25.v.1982, 1♀, leg. R. Leys, RMNH; La Cabrilla, Sierra Cazorla (Jaén), 1600 m, 3.vi.2022, leg. C.M. Hererra, CMHC; Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 1600 m, 30.v.2021, 3♀, leg. T.J. Wood, TJWC; Sierra Cazorla, Puerto Llano, 1800 m, 11.vi.2022, 1♀, leg. J. Valverde, CMHC; Puerto Crucetillas, Riópar (Albacete), 1340 m, 30.iv.2022, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Sierra de Cazorla, Nava de las Correhuelas, 1.v.2021, 1♂, leg. C.M. Hererra, CMHC.

Subgenus *Notandrena* Pérez, 1890

The definition of this subgenus was expanded by Pisanty et al. (2022b) to include *Carandrena* Warncke, 1968 (type species *Andrena aerinifrons* Dours, 1873). It is important to note that several species formerly placed within the *Carandrena* fall elsewhere into an undescribed subgenus, but these are desert-living species, none of which are present in Iberia. In the context of this revision, *Carandrena* is treated as a strict synonym of *Notandrena*.

Andrena (incertae sedis) *urdula* Warncke, 1965 was described from Greece and is a rare and poorly understood taxon known only from a small number of specimens. It is reliably known only from Greece (type series), Spain (central Spain), and Morocco, as the distribution map presented by Gusenleitner and Schwarz (2002: 1201) actually refers to *A.* (*Notandrena*) *ungeri* Mavromoustakis 1952; the distribution map for *A. ungeri* (p. 1200) is actually the distribution map for *A. urdula*. A barcoded specimen from south of Madrid [WPATW351-21] does not clearly fall into the *Notandrena* group (Fig. 23); its true placement is unclear because it does not have any strong characters that lead to obvious affinities with specific groups. It is best treated as incertae sedis until more genetic data are available.

Warncke described two similar taxa in the group of small metallic green *Notandrena*, *A.* (*Notandrena*) *reperta* Warncke, 1974 and *A.* (*Notandrena*) *reperta varuga* Warncke, 1975. Warncke actually described *A. reperta* as a subspecies of *A. varuga*, but due to the order of publication, *A. reperta* has priority. Both species can be recognised because the hind tibial spur is apically curved, though this character is more pronounced in Iberian specimens. Genetically, specimens of *A. reperta* from Morocco and *A. reperta varuga* from central Spain formed a clade with a specimen of *A.* (*Notandrena*) *nigroviridula* Dours, 1873 from Morocco. All three taxa were well separated; *A. reperta* and *A. reperta varuga* by 12.84%, *A. reperta* and *A. nigroviridula* by 11.67%, and

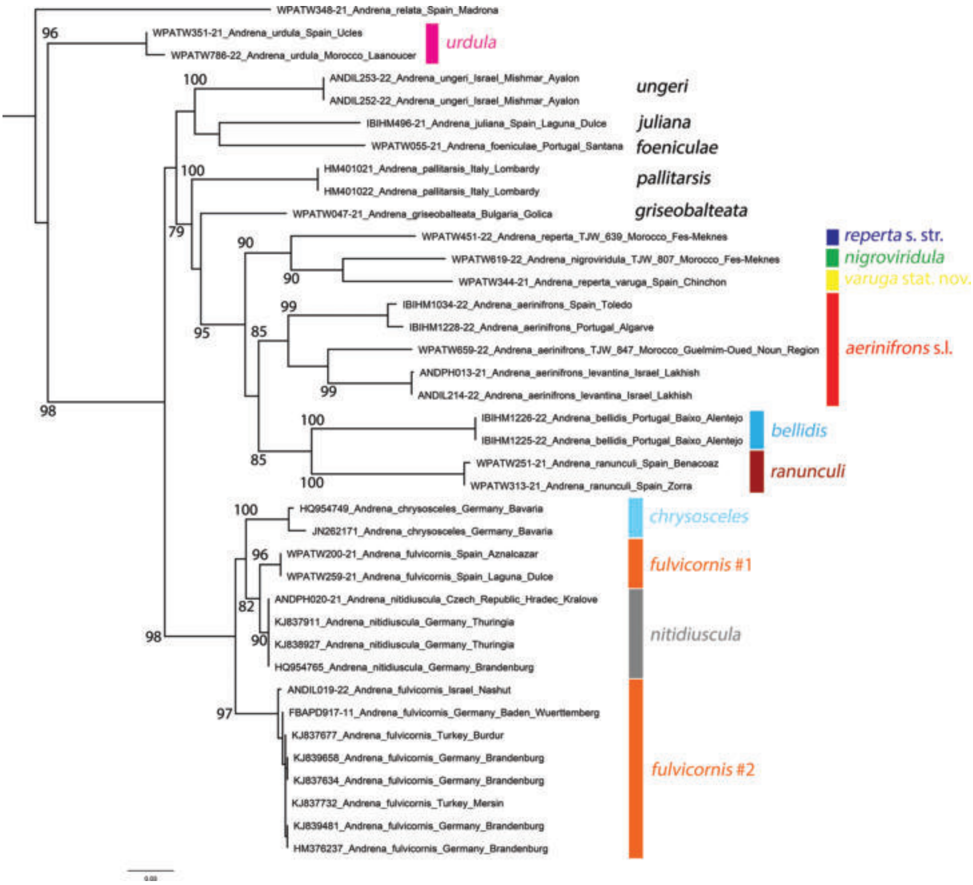

Figure 23. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Notandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (incertae sedis) *relata* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

A. reperta varuga and *A. nigroviridula* by 10.12% (Fig. 23). Moreover, *A. reperta* and *A. reperta varuga* do not form a monophyletic clade, being rendered paraphyletic by *A. nigroviridula*. On this basis, *A. varuga* stat. nov. is raised to species status. *Andrena varuga* is endemic to Spain, and *A. reperta* is found in Morocco, Algeria, and Tunisia.

Dours (1873) described *A. aerinifrons* from Algeria, and *A. aerinifrons levantina* Hedicke, 1938 was later described from the Levant. Barcode analysis shows that specimens from Israel, Morocco, Portugal, and Spain show high average intraspecific variation of 8.64% (range 0.00–11.67%). The Moroccan specimen is intermediate between the Iberian and Levantine sequences, being separated from the Iberian sequences by an average genetic distance of 9.92% (range 9.73–10.12%) and from the Levantine sequences by 10.12% (range 10.12–10.12%). Given that these sequences form a monophyletic clade, a broad interpretation of *A. aerinifrons* is taken here; a neotype can be designated for *A. aerinifrons* at a later date when the situation becomes clearer, as Dours' collection was destroyed in a fire and is not available for study (see below).

Andrena (*Notandrena*) *fulvicornis* Schenck, 1861 has been recognised as distinct from *A.* (*Notandrena*) *nitidiuscula* Schenck, 1853 (Schmid-Egger and Doczkal 1995; Schmid-Egger and Scheuchl 1997; Schwenninger 2013; Bénon and Praz 2016). Barcode analysis shows that specimens from Germany, Israel, and Turkey are indeed clearly distinct from *A. nitidiuscula*, not forming a sister clade and showing average separation of 3.79% (range 3.50–3.89%), with bootstrap support of 96. However, sequences of putative *A. fulvicornis* from Spain fall into a clade of *A. nitidiuscula* and *A.* (*Notandrena*) *chrysosceles* (Kirby, 1802). Spanish specimens are separated from *A. nitidiuscula* by 1.95% (range 1.95–1.95%), from *A. chrysosceles* by 4.67% (range 4.28–5.06%), and from the other clade of *A. fulvicornis* by 4.18% (range 3.89–4.28%). This Iberian '*fulvicornis*' is also well-supported, with bootstrap support of 96. At the present time, no taxonomic action can be taken until more genetic data are available. Morphologically, Iberian '*fulvicornis*' do not appear to be different from Central European/Turkish/Levantine specimens. Additional sequences from Iberia and France are needed; this barcode difference may be the result of an isolated population in the Iberian glacial refugium.

Subgenus *Plastandrena* Hedicke, 1933

Pisanty et al. (2022b) synonymised the subgenus *Agandrena* with *Plastandrena*, and this broader definition is used here. Some taxonomic problems within this subgenus were discussed by Wood (2023a), who found support for the species-status of *A.* (*Plastandrena*) *nigrospina* Thomson, 1872. Standard barcodes have limited utility for this group for unclear reasons, so care must be taken when interpreting results, as morphologically distinct taxa can form unclear clades, for example *A.* (*Plastandrena*) *tibialis* (Kirby, 1802). This result was reproduced here (Fig. 9), and no further discussion or action is taken; in an Iberian context, members of this subgenus appear to be identifiable using barcodes, but work is needed to revise this group at a Palaearctic scale using more powerful genetic techniques.

Andrena (*Plastandrena*) *pilipes* Fabricius, 1781 and *Andrena* (*Plastandrena*) *nigrospina* Thomson, 1872

Ortiz-Sánchez et al. (2022) reported *A. nigrospina* as new for Spain from the Sierra de Cazorla based on male specimens with their distinctive genital capsule. Wood (2023a) further reported two barcoded specimens from Spain (Sistema Central and Sistema Ibérico) belonging to *A. nigrospina*. This genetic result was further supported with the addition of more sequences from Morocco (Fig. 9), revealing that *A. nigrospina* is also present in the Middle Atlas. The *A. nigrospina* clade maintained a low intraspecific genetic distance of 0.41% (range 0.00–1.06%) from Morocco to Kyrgyzstan, and average separation from *A. pilipes* was 1.63% (range 1.06–2.35%). As this difference is still small in absolute terms, bootstrap support was moderate, with 77 for *A. pilipes* and 84 for *A. nigrospina*, but both are considered to be distinct species. Females cannot currently be consistently separated morphologically, so no characters are given in the identification key. In Iberia, *A. nigrospina* is newly reported for northern Portugal from close to the Peneda-Gerês National Park. The species is likely to be restricted to cooler parts of northern, central, and eastern Iberia where it will probably be found only in mountainous regions, or at least at elevation. More sampling and genetic study is required to define its exact range limits.

Material examined. ***Andrena nigrospina*:** **Portugal:** Minho, Ruivães, N103, 12.v.2019, 1♂, 1♀, leg. Wood, TJWC; **Spain:** Cuenca, Pajaroncillo, 3 km SW, Arroyo de Peña Quebrada, 26.vi.2021, 4♀, leg. T.J. Wood, TJWC (barcoded); Guadalajara, Bustares, 2 km N, Alto Rey, 1780 m, 1♀, 9.vii.2021, leg. T.J. Wood, TJWC (barcoded).

Andrena (*Plastandrena*) *agilissima* Scopoli, 1770 and *Andrena* (*Plastandrena*) *asperrima* Pérez, 1895

Andrena agilissima is a widespread West Palaearctic species that is well-known in Central and Southern Europe to north-western Africa. In contrast, *A. asperrima* is much less well known, having a more Mediterranean distribution in France, Spain, Morocco, Algeria, and Tunisia. Unlike *A. agilissima*, *A. asperrima* is bivoltine and is exceptionally variable in the density, size, and strength of the integumental punctation. In the female sex, the typical form has strong and dense punctures on the terga, allowing easy separation from *A. agilissima* in which the terga have small and subtle punctures. However, many specimens of *A. asperrima* can be found which have greatly reduced tergal punctation and which are therefore extremely similar to *A. agilissima*; they can be separated by the smaller body size and the sparser punctation of the scutum. This sparsely punctate form is more common in the south-west and was described from Morocco by Warncke as *A. asperrima alascana* Warncke, 1974. Overall, the two species are clearly separable by their genital capsules in the male sex.

Because of this variation, it is important to ensure that Iberian material is conspecific with North African material, since the oldest names of Pérez (1895) were described based on North African material. Warncke (1967) designated a male lectotype for

A. asperrima using a specimen from Biskra from the collection of Pic (Fig. 24A, B). This is unjustified, as it is not part of the original syntypic series, and Warncke's designation is here rejected. In Pérez's catalogue, under entry '1030 *Andrena trachodes* J.P.' [an unpublished name; Pérez sometimes changed his mind and therefore a different name to the published name can be present in the catalogue] Pérez writes that the species comes from Constantine [in Algeria], drawing comparison with *A. flessae* Panzer, 1805 (= *A. agilissima* (Scopoli, 1770)) and arguing it differs by the stronger punctation of the metasoma. Inspection of the Pérez collection shows the presence of a female

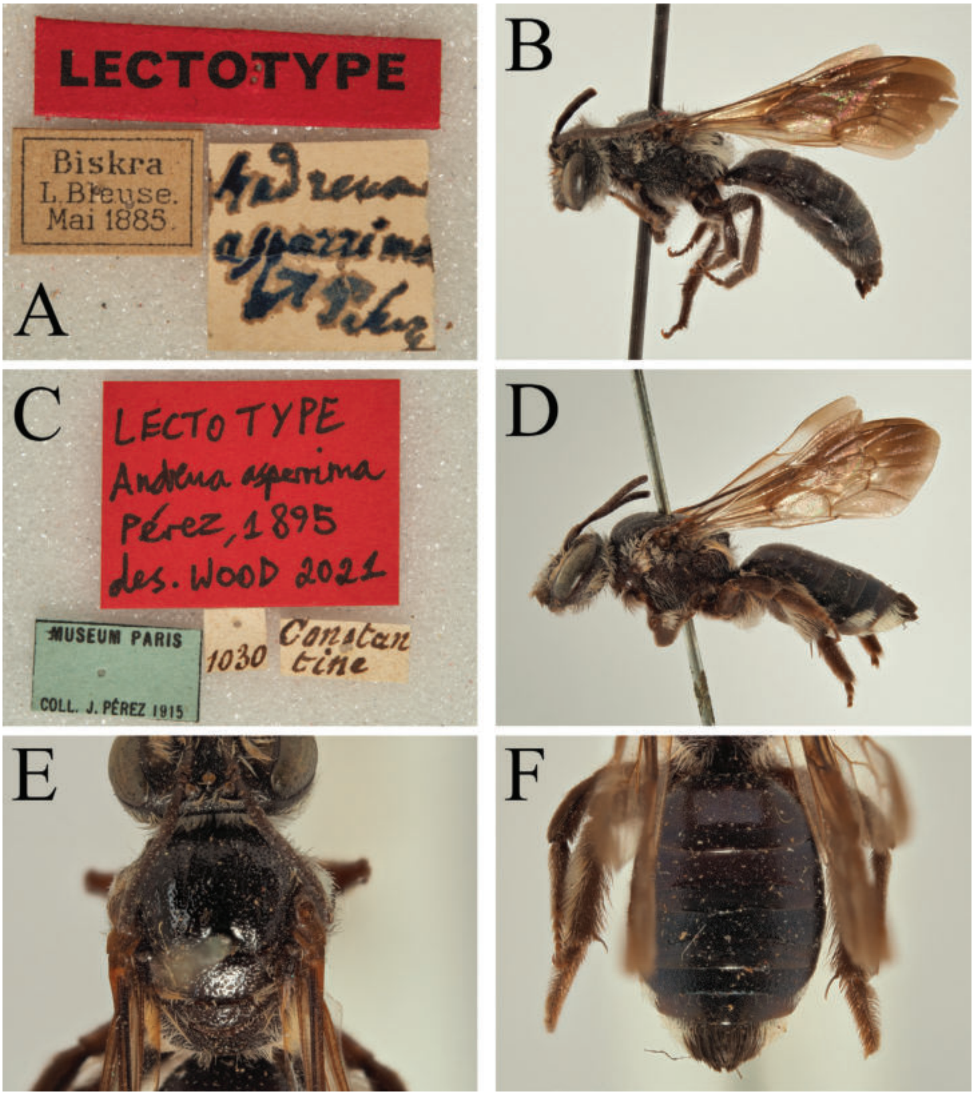

Figure 24. *Andrena* (*Plastandrena*) *asperrima* Pérez, 1895, false male lectotype **A** label details **B** profile; true female lectotype **C** label details **D** profile **E** scutum, dorsal view **F** terga, dorsal view.

specimen from Constantine which bears the label '1030', the code used by Pérez for this species. This specimen is designated as a new lectotype (Fig. 24C–F); it conforms to the concept of *A. asperrima* used by subsequent authors.

Andrena atricapilla Pérez, 1895 was also described from Algeria, but only in the male sex. Warncke (1967) listed this taxon as a synonym of *A. asperrima*, though he did not mention a lectotype. A male specimen labelled as *atricapilla* J.P. in the handwriting of Pérez is separated in the MNHN collection and labelled as a lectotype, probably by Teunissen as one of his determination labels is present. This lectotype designation was never published, and so it is here designated as a lectotype (Fig. 25). The synonymy with *A. asperrima* is maintained, as the genital capsule is typical for the species concept.

Genetic analysis of specimens of *A. agilissima* and *A. asperrima* from Croatia, Morocco, Portugal, and Spain showed two clear clades (Fig. 9). One clade contained only specimens determined as *A. agilissima* from Croatia, Portugal, and Spain. These sequences showed average intraspecific variation of 0.07% (range 0.00–0.25%), and were strongly separated from the second clade by an average genetic distance of 9.33% (range 8.74–10.20%). This second clade contained specimens identified as *A. asperrima* from Spain and Morocco, but also three specimens identified as *A. agilissima* from the Middle Atlas. There can be no doubt as to the identity of these specimens, as two are males, and their genital capsule is that of *A. agilissima* and not *A. asperrima*. However, the genetic differentiation within this clade is very low at an average of 0.42% (range 0.00–0.91%). As for *A. bimaculata* and *A. tibialis*, there is clearly genetic complexity here, as two species with distinct genital capsules have barcodes that form intermixed clades. No taxonomic action is taken on the basis of these barcoding results.

However, what can be concluded is that Iberian material of *A. asperrima* is conspecific with North African material, including the weakly punctate form that dominates in Morocco. In combination with the new lectotype designations, the invariant genital capsule, and these genetic results, the concept of Warncke (1967; 1974) and Gusenleitner and Schwarz (2002) regarding *A. asperrima* is maintained. The full synonymy is given below.

***Andrena* (*Plastandrena*) *asperrima* Pérez, 1895**

Andrena (*Plastandrena*) *asperrima* Pérez, 1895: 33, ♀♂ [Algeria, lectotype by present designation: MNHN].

Andrena (*Plastandrena*) *atricapilla* Pérez, 1895: 33, ♂ [Algeria, lectotype by present designation: MNHN].

Andrena (*Plastandrena*) *flessae* var. *elcheensis* Friese, 1922: 211, ♀ [Spain: ZMHB, not examined].

Andrena (*Plastandrena*) *hemicyanea* Cockerell, 1930: 112, ♀ [Tunisia: type lost?]

Andrena (*Plastandrena*) *asperrima alascana* Warncke, 1974: 36, ♀♂ [Morocco: OÖLM, examined].

Distribution. Spain, France, Morocco, Algeria, Tunisia.

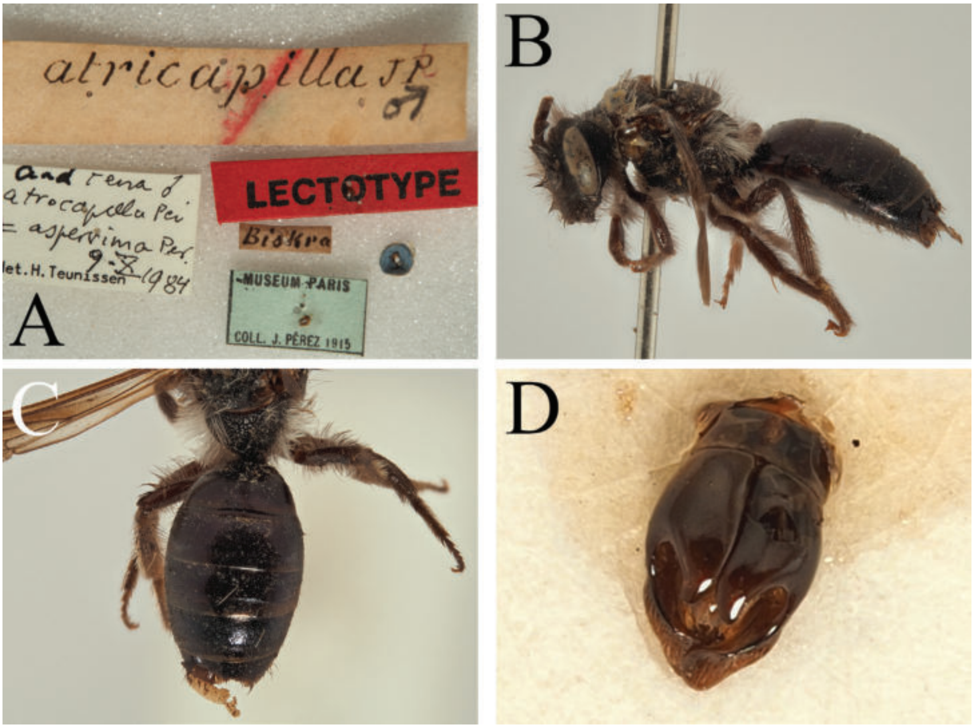

Figure 25. *Andrena* (*Plastandrena*) *atricapilla* Pérez, 1895, male lectotype **A** label details **B** profile **C** terga, dorsal view **D** genital capsule.

Material examined. **Algeria:** Constantine [36.3645°N, 6.6409°E], 1♀, MNHN (lectotype of *A. asperrima*, by present designation; Fig. 24C–F); Biskra, v.1885, 1♂, leg. Blause, MNHN (false lectotype of *A. asperrima*; Fig. 24A, B); Biskra [34.8600°N, 5.6995°E], 1♂, MNHN (lectotype of *A. atricapilla*, by present designation; Fig. 25); **Morocco:** Tizi-n-Talrhemt nr. Midelt [32.6821°N, -2.9344°E], 1900 m, 1.vi.1968, leg. M.A. Lieftinck, OÖLM (holotype of *A. asperrima alascana*).

Subgenus *Poecilandrena* Hedicke, 1933

This subgenus is strongly polyphyletic (Pisanty et al. (2022b), but these classification issues relate to eastern taxa; in Iberia, the species belong to *Poecilandrena* s. str. Warncke (1976) listed only one *Poecilandrena* species in Iberia, *A.* (*Poecilandrena*) *labiata* Fabricius, 1781. Ceballos (1956) and Pérez-Íñigo (1984) also listed *A.* (*Poecilandrena*) *potentillae* Panzer, 1809, though this species was not listed as present by Warncke and his distribution maps (Gusenleitner and Schwarz 2002) indicate that this species has a western range limit in central France.

Collection of material from the Sierra Nevada produced red-marked *Poecilandrena* females [WPATW281-21] that morphologically resemble *A. potentillae* in the reduced punctation density at the edge of the clypeus. No '*potentillae*' males with their distinctive genital capsule could be found. A female sequence clearly fell into a clade with an *A. labiata* sequence from Belgium, the two specimens separated by 2.87% (Fig. 1). The four *A. labiata* sequences from Belgium, Portugal, and Spain showed average intraspecific variation of 2.52% (range 0.78–3.92%), much lower than the average separation from *A. potentillae* sequences from Belgium, France, Germany, and Hungary of 11.81% (range 11.23–12.27%). The position is taken here that true *A. potentillae* is not present in Iberia, even though some females of *A. labiata* can resemble it morphologically. These specimens conform to the subspecific concept of *A. labiata bellina* Warncke, 1967 that was described from Madrid. Warncke (1967) noted that this form had weaker shagreenation and finer punctation than the nominate form, and I believe that this is the source of the confusion and the erroneous reports of *A. potentillae* in Iberia. *Andrena potentillae* is therefore not included in the identification key as typical female characters that can be used to separate the two species in Central Europe do not appear to work universally in Iberia.

Finally, Ortiz-Sánchez (2011, 2020) lists *A.* (*Poecilandrena*) *viridescens* Viereck, 1916 as part of the Spanish fauna. The distribution maps of Warncke (Gusenleitner and Schwarz 2002) indicate the possible presence of this species on the Spanish side of the Pyrenees. I have not examined any specimens of *A. viridescens* from Iberia, but its presence in the Pyrenees is plausible and so it is retained on the list. Several *Andrena* taxa with apparent range limits in the Pyrenees have recently been confirmed to occur in northern Spain (e.g. *A.* (*Ulandrena*) *polita* Smith, 1847 and *A.* (*Micrandrena*) *nanula* Nylander, 1848, see Álvarez Fidalgo et al. 2022), and so additional searches may well confirm the presence of *A. viridescens* as well.

Subgenus *Simandrena* Pérez, 1890

Barcode analysis returned *Simandrena* as paraphyletic (Fig. 4), but this means very little, as the subgenus is very well characterised morphologically and genetically based on UCE analysis (Pisanty et al. 2022b). No major changes in *Simandrena* taxonomy are made here, but there are a number of issues to discuss.

Warncke (1967) described *A.* (*Simandrena*) *combinata crudelis* Warncke, 1967 from Spain. Comparison of sequences shows that Iberian material is only weakly differentiated, being separated from *A.* (*Simandrena*) *combinata* (Christ, 1791) sequences from Germany by an average genetic distance of 1.12% (range 1.06–1.29%). Based on this evidence, a subspecific status is not justified.

Andrena (*Simandrena*) *vetula* Lepeletier, 1841 was recently placed in the *Simandrena*, as its unusual male morphology had led to confused previous placement (Pisanty et al. 2022b). Genetically there was a large difference between Iberian and North African sequences, separated by an average genetic distance of 6.33% (range 6.08–6.57%). *Andrena vetula* has an enormous range, from Morocco and Iberia to Central Asia (Wood and Monfared 2022). Sequences are required over this range before any taxonomic changes can be made, as morphologically there are no obvious differences between Iberian and North African specimens.

The species pair of *A.* (*Simandrena*) *confinis* Stöckhert, 1930 and *A.* (*Simandrena*) *congruens* Schmiedeknecht, 1884 continues to pose problems. Warncke (1967) treated *A. confinis* as a synonym of *A. congruens*, but others have not followed this interpretation. The two taxa can be separated morphologically in Central Europe (Schmid-Egger and Scheuchl 1997), and there are also ecological differences with *A. confinis* preferring cooler northern climates and *A. congruens* preferring warmer and drier southern climates, with overlap in Central Europe. However, in southern Europe the situation is complex and confused. Wood et al. (2021) added *A. confinis* to the Iberian list on the basis of a specimen from the Picos de Europa Mountains. Genetically, this specimen clusters with *A. confinis* sequences from Germany. However, sequences from specimens provisionally identified as *A. congruens* from northern Portugal as well as a specimen of *A. congruens* from Bulgaria render *A. congruens* paraphyletic. The genetic distance between all sequences is low. The Portuguese specimens are strongly divergent morphologically from the Spanish *A. confinis* specimen, with dense and obvious tergal punctation compared to terga which are almost impunctate, but the average genetic differentiation is low at 0.88% (range 0.60–1.15%). No major taxonomic decision is made here; much more genetic data are required for a dedicated study focused on this group. Both nominal taxa are included in the identification key.

***Andrena* (*Simandrena*) *cilissaeformis* Pérez, 1895, sp. resurr.**

Andrena (*Simandrena*) *cilissaeformis* Pérez, 1895: 42, ♀ [Spain, lectotype by present designation: MNHN]
Andrena breviscopa auctorum.

Remarks. *Andrena breviscopa* Pérez, 1895 was described in the female and male sexes from North Africa. Warncke's treatment of *A. breviscopa* is curious, because he designated a lectotype (Fig. 26) and listed the taxon as a synonym of *A. numida* Lepeletier, 1841 (Warncke 1967). However, just a few years later he listed *A. breviscopa* as a valid taxon in the subgenus *Simandrena* (Warncke 1974). Examination of the female lectotype designated by Warncke shows that his original synonymy was correct; the taxon is clearly not a *Simandrena*, and is indeed a synonym of *A. numida*.

The use of the name *A. breviscopa* to apply to the taxon present in Spain, Morocco, and Algeria is therefore incorrect. The correct name is *A. cilissaeformis* Pérez, 1895 sp. resurr. *Andrena cilissaeformis* was described from Spain, not Algeria as stated in Warncke (1967) and Gusenleitner and Schwarz (2002). This is because Pérez (1895) does not directly state the type locality (or indeed, any information about the collecting locality of any of the species described in this work), but this information is included in his personal catalogue. Warncke (1967) did not examine material of *A. cilissaeformis*, stating that whilst the label was present, material was missing. Examination of material in the MNHN has located a specimen labelled with 'Esp' [Espagne = Spain] in Pérez's handwriting (Fig. 27). This specimen was separated by Teunissen, but he never published this information. This specimen is badly damaged, but it is a *Simandrena* and

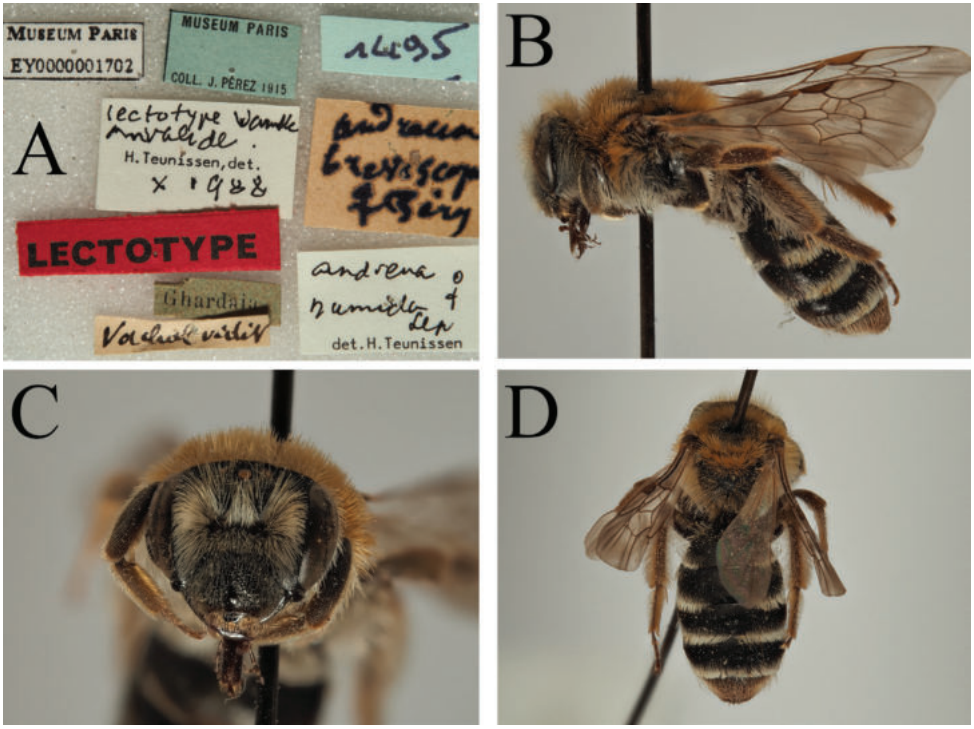

Figure 26. *Andrena* (incertae sedis) *breviscopa* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

conforms to *A. breviscopa* auctorum sensu Warncke (1974) and subsequent publications. It is designated as a lectotype to fix the name on the Iberian population. *Andrena breviscopa* is returned to its original synonymy with *A. numida*.

Distribution. Spain, Morocco, Algeria.

Material examined. ***Andrena breviscopa*****:** **Algeria:** Ghardaia [32.5047°N, 3.6419°E], 1♀, MNHN (lectotype; Fig. 26); (*Andrena cilissaeformis*): **Spain:** no collection information, 1♀, MNHN (lectotype by present designation; Fig. 27).

Subgenus *Taeniandrena* Hedicke, 1933

Large parts of this subgenus have been revised recently by Wood et al. (2021), Praz et al. (2022), Wood (2022), and Wood and Ortiz-Sánchez (2022). There is relatively little new information to present here, other than to revise the status of *A.* (*Taeniandrena*) *poupillieri* Dours, 1872, and so a reduced phylogenetic tree is presented given the results presented in these previous publications (Fig. 28). However, it is clear that there is still unfinished work to be completed in this subgenus in an Iberian context. Specifically, Praz et al. (2022) identified an unclear lineage "*sp. nov. 2*" from northern Portugal. This specimen is a male that has a genital capsule that diverges from any known Iberian

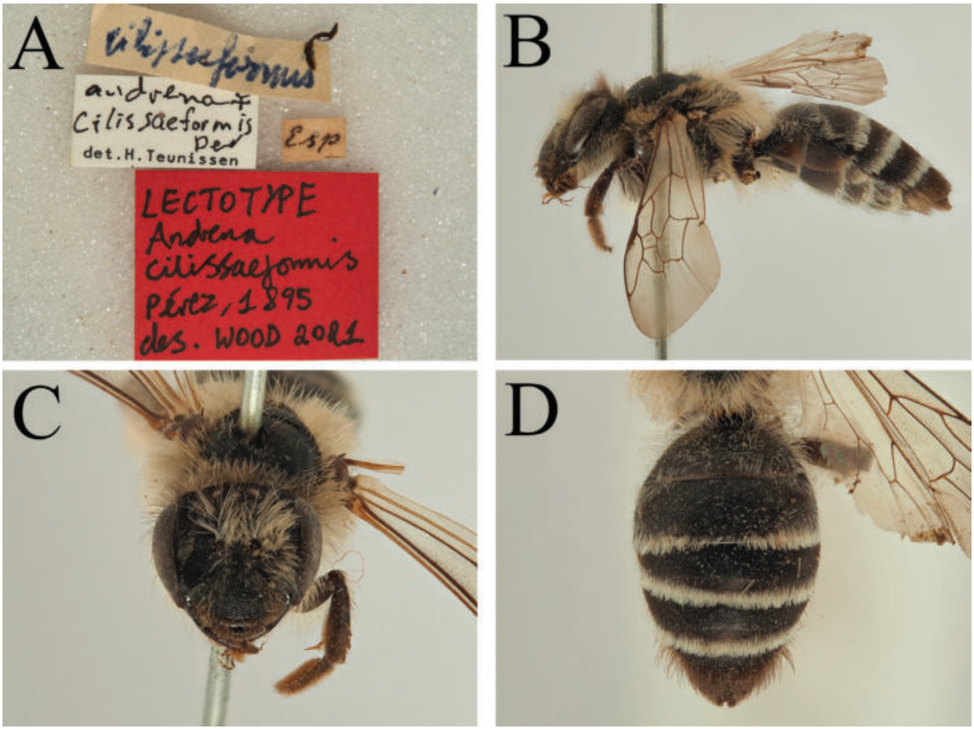

Figure 27. *Andrena* (*Simandrena*) *cilissaeformis* Pérez, 1895; female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

species. Furthermore, I have an unbarcoded male from Guadalajara province that also possesses a genital capsule that does not match any known species. These may represent additional undescribed *Taeniandrena* species endemic to the peninsula. No further action is taken until more genetic samples are available; it is extremely likely that additional barcoding will discover more diversity in this challenging and speciose subgenus.

Andrena (*Taeniandrena*) *poupillieri* Dours, 1872

Two further issues require discussion. The first is the identity of *A. poupillieri*. Praz et al. (2022) identified two potential mitochondrial lineages that could correspond to this species. Additional sampling in Morocco has clarified the situation; *poupillieri 1* sensu Praz et al. (2022) corresponds to *A.* (*Taeniandrena*) *gregaria* Warncke, 1974 and *poupillieri 2* sensu Praz et al. (2022) corresponds to the concept of *A. poupillieri* used by Warncke. As the type of *A. poupillieri* is lost, it is beneficial to designate a neotype in order to fix the concept of this species in line with the existing literature; a specimen from Algeria is chosen, as this is the original *locus typicus*. As *A. gregaria* does not occur in Iberia, it is not included in the phylogenetic tree presented here; it will be dealt with in the upcoming North African *Andrena* revision. The species *A. poupillieri* is

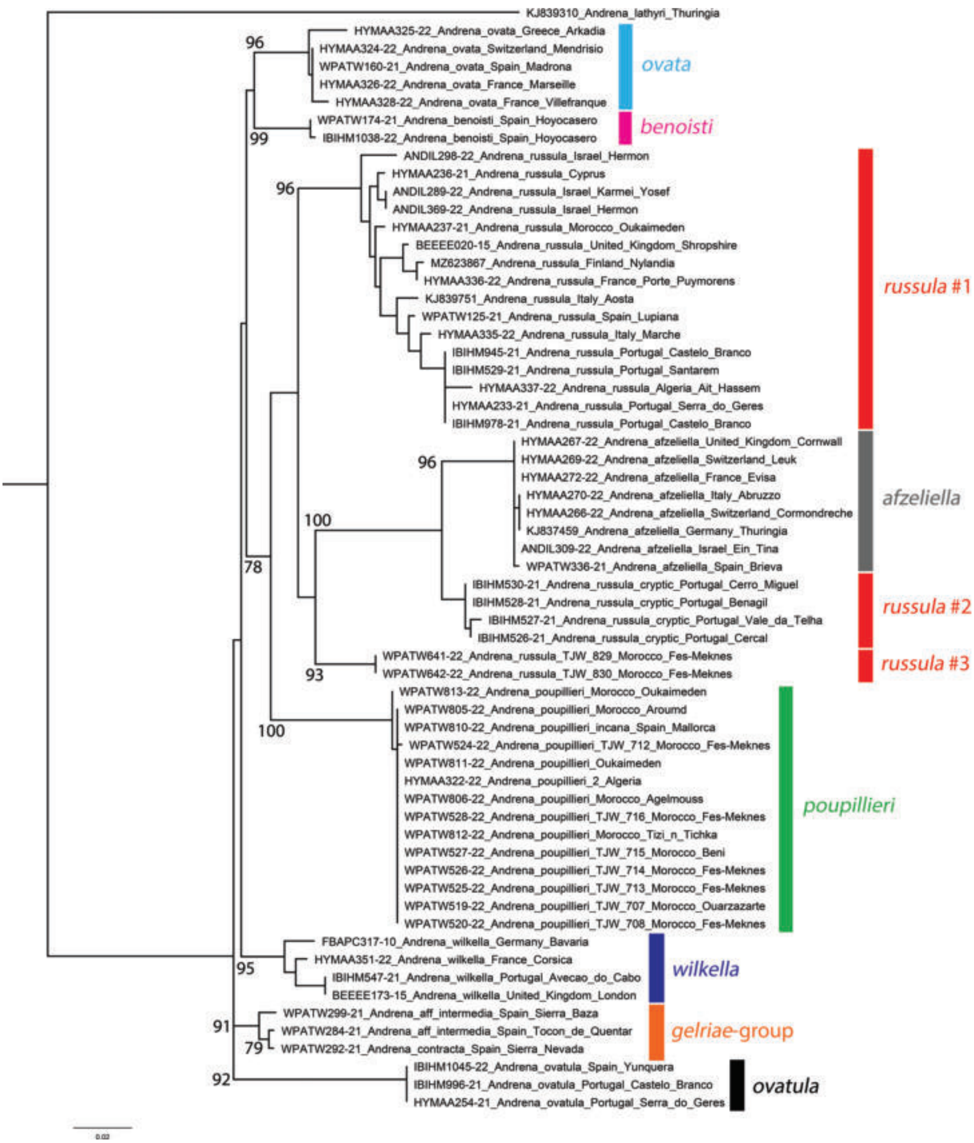

Figure 28. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Taeniandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena* (*Taeniandrena*) *lathyri* Alfken, 1900 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

commonly encountered in Morocco, and is clearly identifiable from barcodes, forming a clade with bootstrap support of 100. Separation of females from *A.* (*Taeniandrena*) *ovatula* (Kirby, 1802) can be made by the tergal punctation, this being much stronger in *A. ovatula*. Generally, the two taxa are well-separated by an average genetic distance of 6.12% (range 5.86–7.79%). Males of *A. poupillieri* can be recognised based on the genital capsule, in which the gonostyli are apically produced into acute points.

Warncke changed his mind about the status of *A. poupillieri* – in Warncke (1967), he lists the taxon as *A. ovatula poupillieri*, but then in Warncke (1975a) he described *A. poupillieri incana* from the Balearic islands, listing *A. poupillieri* s. str. from southern Iberia (Warncke 1976). In his distribution maps (Gusenleitner and Schwarz 2002), he gives a distribution of southern Iberia, the Balearic islands, north-western Africa, Libya, and Crete. Records from Crete are likely to refer to unrecognised *A.* (*Taeniandrena*) *ovata* Schenck, 1853 (Wood, unpublished data). Examination of male specimens from the extreme south of Spain shows that *A. poupillieri* is present based on the distinctive genital capsule, though as females cannot be separated morphologically from *A. ovatula* the exact range of the two species is unclear. *Andrena ovatula* reaches at least as far south at the Sierra de las Nieves in Málaga province [IBIHM1045-22], though this far south it may be restricted to mountainous areas whereas the two examined male *A. poupillieri* specimens come from the coast. More collection is required. For now, *A. poupillieri* is considered to be a rare and little-collected taxon in Iberia, probably restricted to the coast in the south and south-east of the peninsula. A single sequence for *A. p. incana* was available from Mallorca that unambiguously nests within the North African *A. poupillieri* sequences; it is identical to 12 of the North African sequences, and differs from the thirteenth by just 0.15%. As such, *A. poupillieri* including *A. p. incana* shows extremely low intraspecific variation of 0.03% (range 0.00–0.15%), and subspecific status is unnecessary for the population on the Balearic islands.

Material examined. Spain: Málaga, Estepona, 24.iii.1986, 1♂, leg. J. van Oosterhout, RMNH; Málaga, San Pedro de Alcántara, 15.iii.1986, 1♂, leg. C. v. Achterberg, RMNH.

Andrena (*Taeniandrena*) *russula* Lepeletier, 1841

Praz et al. (2022) synonymised *A.* (*Taeniandrena*) *similis* Smith, 1849 with *A. russula*, taking a broad, pan-Mediterranean approach. In an Iberian context, sequences from central and northern Iberia clearly fall into a broad *A. russula* clade along with sequences from Morocco to Cyprus and Israel and north to the United Kingdom and Finland (Fig. 28). However, in the extreme south-west of Iberia in southern Portugal, sequences from specimens that are morphologically indistinguishable from *A. russula* from the rest of Iberia form a distinct clade that falls closest to *A.* (*Taeniandrena*) *afzeliella* (Kirby, 1802). These specimens come from the south of Baixo Alentejo (Cercal) and the Algarve (Aljezur, Benagil, Moncarapacho). These sequences are consistently separated from the broad *A. russula* clade by 5.50% (range 3.68–11.11%). Two specimens from Morocco that correspond to *A. russula* form a third clade of *A. russula* s.l. At the present time, no taxonomic action is taken; these three lineages may represent different isolated populations. More powerful genetic techniques are required to resolve this problem, as for Iberian members of the *gelriae*-group (see Praz et al. 2022).

Andrena (*Taeniandrena*) *gredana* Warncke, 1975

Wood et al. (2021) elevated *A. gredana* to species status, and gave a distribution across the Sistema Central, central and northern Portugal, and northern Spain across to the

Pyrenees in the province of Huesca. Examination of material from the Hautes-Pyrénées in France approximately 80 km north-east of the Huesca site revealed the presence of *A. gredana* in France. The species is therefore not endemic to the Iberian Peninsula, though it is likely to have a French range restricted to high altitude sites in the Pyrenees.

Material examined. France: Hautes-Pyrénées, Eget Cité, 4.v.2017, 1♂, leg. R. Rudelle, R. Rudelle Colln.; **Spain:** Huesca, San Juan de la Peña, 14.v.1995, 1♂, leg. H. & J.E. Wiering, RMNH (see also records in Wood et al. 2021).

Subgenus *Truncandrena* Warncke, 1968

This subgenus contains species that often vary extensively in the colouration of their pubescence, sometimes display minimal variation in structural characteristics in the female sex, and can sometimes only be reliably identified in the male sex. These identification difficulties have led to a large number of subspecific concepts in the literature, the integrity of which must be examined using molecular data. There are a number of taxonomic changes to make which affect the Iberian and more broadly West Mediterranean fauna.

Andrena (*Truncandrena*) *doursana* Dufour, 1853 sensu lato

This nominal species is highly variable across its range which was previously considered to be from Morocco and Iberia to Turkey and the Levant. *Andrena doursana* was originally described from Algeria, and Warncke (1975a, 1975b, 1980) described the subspecies *A. d. citreola* Warncke, 1975 from Spain, *A. d. agadira* Warncke, 1980 from southern Morocco, *A. d. bengasia* Warncke, 1980 from Libya, and *A. d. mizorhina* Warncke, 1975 from Turkey. Pisanty et al. (2022b) elevated the eastern subspecies *A.* (*Truncandrena*) *doursana mizorhina* to species status, leaving populations in Iberia and north-western Africa to Libya.

The differentiation between these remaining subspecies relies on the colour of the female pubescence, as there are no structural differences in the males; indeed, the subspecies *A. d. agadira* and *A. d. bengasia* were described only from the female sex. *Andrena d. citreola* is bright, and has predominantly white hairs on the face and a light brown terminal fringe with scattered white hairs laterally. *Andrena d. agadira* is much darker, with dark facial hairs and a uniformly dark terminal fringe. Wood et al. (2020b) found the undescribed female of a similar species endemic to Morocco, *A.* (*Truncandrena*) *alchata* Warncke, 1974, which is structurally very similar to the female of *A. d. agadira*, but these authors were unable to conclude if the two taxa were synonymous.

Analysis of barcodes from southern and northern Morocco and Iberia shows that female specimens identified as *A. doursana* s. str., *A. d. agadira*, and *A. d. citreola* did not form differentiated clades (Fig. 29). Light forms from southern Portugal [IBIHM1223-22] and the Moroccan Anti-Atlas near Tazenakht [WPATW505-22] were separated, and dark forms from south-western Morocco near Guelmim [WPATW506-22] and Tiznit [WPATW503-22] were clustered closer to the light specimen from Tazenakht. The light specimen from Portugal was clustered close to

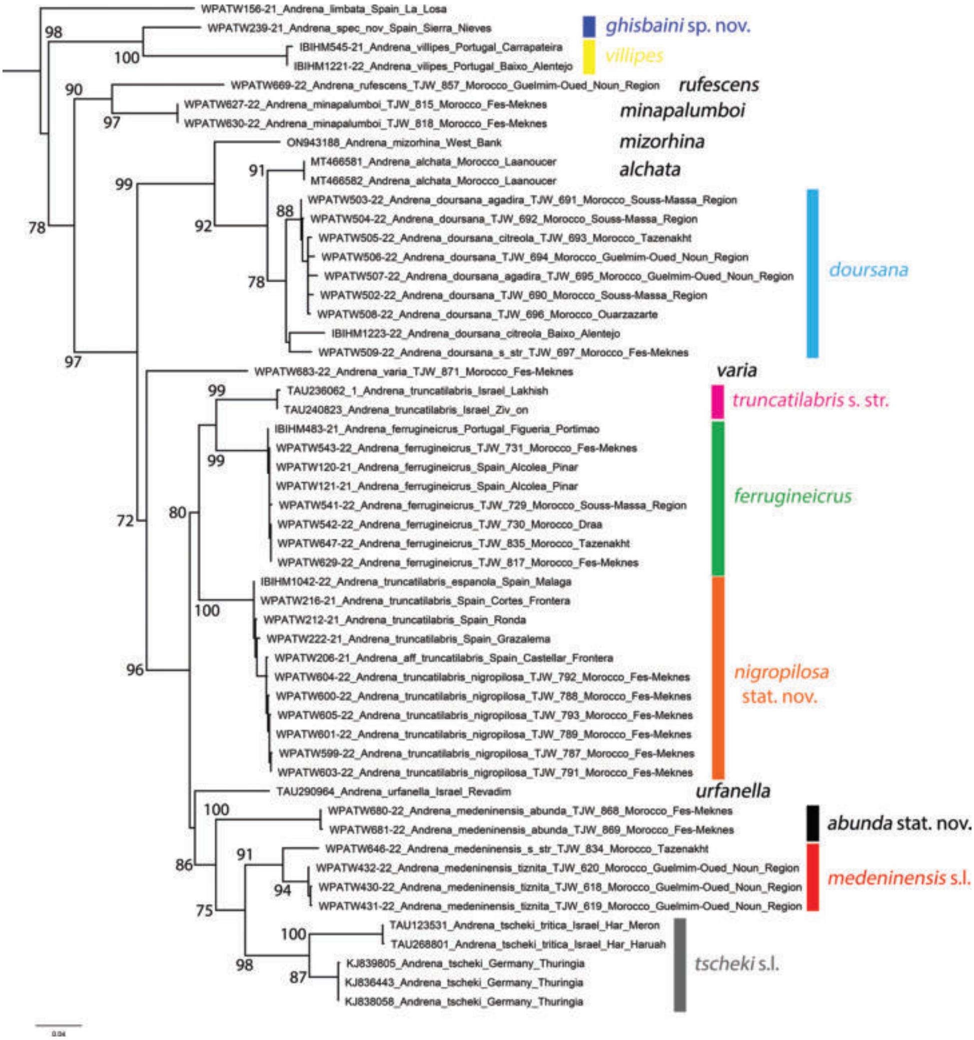

Figure 29. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Truncandrena* Warncke, 1968 based on the mitochondrial COI gene. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

a specimen of *A. doursana* s. str. from the Middle Atlas near Taza [WPATW509-22]. This pattern strongly suggests simple separation by distance, with geographically closer specimens displaying more similar barcode sequences. Accepting a broad *A. doursana* species concept, these sequences showed an average intraspecific distance of 2.79% (range 0.29–5.93%).

More broadly, this *A. doursana* clade had bootstrap support of 78, and was sister to the *A. alchata* sequences generated by Wood et al. (2020b), a species that has a clearly different male morphology. *Andrena alchata* has bootstrap support of 91, and was separated from *A. doursana* by an average of 6.29% (range 5.62–8.03%). Finally, the single sequence of *A. mizorhina* was strongly separated from *A. doursana* by an average of 10.45% (range 10.18–10.94%). These genetic results justify the decision of Pisanty et al. (2022b) to elevate *A. mizorhina* to species level, the findings of Wood et al. (2020b) who identifed the female of *A. alchata*, and the original description of *A. d. agadira* by Warncke as a subspecies, correctly associating dark specimens from south-western Morocco with *A. doursana*. Given the variation in colour forms observed here, no subspecies framework is employed, and so the Iberian taxon is referred to simply as *A. doursana*.

***Andrena* (*Truncandrena*) *medeninensis* Pérez, 1895 sensu lato**

Andrena medeninensis was described from Tunisia, and like *A. doursana*, it nominally displays great variation across its range from Morocco and Iberia to Turkey and the Levant. Warncke (1967, 1974, 1980) described several subspecies, *A. m. donata* Warncke, 1967 from Spain, *A. m. abunda* Warncke, 1974 from Morocco, *A. m. tiznita* Warncke, 1980 from south-western Morocco, and *A. m. usura* Warncke, 1967 from Turkey. Wood (2023b) synonymised *A. m. usura* with *A. pareklisiae* Mavromoustakis, 1957, leaving the North African and Iberian populations.

Sequences of *A. medeninensis* s. str. and *A. m. tiznita* formed a clade with bootstrap support of 91 (Fig. 29). However, the single available sequence of *A. medeninensis* s. str. differed from *A. m. tiznita* sequences by an average of 4.80% (range 4.70–4.85%), *A. m. tiznita* forming a subclade with bootstrap support of 94. However, *A. m. abunda* was strongly separated from this clade of *A. medeninensis* s.l. by an average genetic distance of 10.19% (range 9.97–10.57%). This *A. m. abunda* clade had bootstrap support of 100, and was sister to an *A. medeninensis* s.l. + *A. tscheki* Morawitz, 1872 s.l. clade. *Andrena abunda* stat. nov. is therefore raised to species status; it restricted to Algeria and Morocco. Morphologically, it is extremely similar to *A. medeninensis* s.l., but has much darker pubescence. In the female sex (the male is unknown), the only clear structural difference is that A3 exceeds the length of A4+5+6, whereas in *A. medeninensis* s.l. A3 is shorter than A4+5+6.

As it was unfortunately not possible to sample the Iberian subspecies *A. m. donata*, and no genetic sequences are available from Tunisia, the *locus typicus* for *A. medeninensis* s. str., no further taxonomic action is taken here. Given the large genetic difference displayed by *A. abunda* despite almost no morphological differentiation (at least in the female sex), it is difficult to comment on the Iberian subspecies which simply appears to be a colour variant of this nominally widespread species.

***Andrena* (*Truncandrena*) *truncatilabris* Morawitz, 1877, *Andrena* (*Truncandrena*) *truncatilabris espanola* Warncke, 1967, and *Andrena* (*Truncandrena*) *truncatilabris nigropilosa* Warncke, 1967**

Andrena truncatilabris is a widespread species that was originally described from the Caucasus from what is today Armenia (Astafurova et al. 2021). The species is nominally distributed across the Mediterranean basin, from Morocco and Iberia to the Urals and Iran (Gusenleitner and Schwarz 2002). However, in the east it descends only to the Levant and does not enter the eastern part of North Africa. In the west, Warncke (1967) described two subspecies: *A. t. espanola* from Spain and *A. t. nigropilosa* from Algeria that differed from *A. truncatilabris* s. str. in the structure of their clypeus and their male genital capsule, though Warncke noted that the difference between the two subspecies was minimal, pointing to the darker pubescence of North African specimens as a point of difference.

Sequences from specimens from Spain and Morocco showed almost no genetic differentiation, with an average intraspecific distance of 0.99% (range 0.00–1.85%; Fig. 29). They were strongly separated from *A. truncatilabris* s. str. sequences from northern Israel by an average genetic distance of 9.66% (range 9.12–10.12%). *Andrena truncatilabris* s. str. formed a clade with bootstrap support of 99, and was sister to *A.* (*Truncandrena*) *ferrugineicrus* Dours, 1872, whereas *A. t. nigropilosa* + *A. t. espanola* formed a clade with bootstrap support of 100 that was sister to the *A. truncatilabris* s. str. + *A. ferrugineicrus* clade.

Given this genetic difference, it is clear that specimens from Iberia and north-western Africa are both conspecific and distinct from *A. truncatilabris* s. str. Given this distribution, the use of the name *A. t. espanola* is undesirable, and so *A. nigropilosa* stat. nov. is elevated to species status and *A. t. espanola* syn. nov. is synonymised with it as a subjective junior synonym, as the two names were described in the same publication. The updated synonymy is therefore as follows:

Andrena (*Truncandrena*) *nigropilosa* Warncke, 1967, stat. nov.

Andrena (*Truncandrena*) *truncatilabris nigropilosa* Warncke, 1967: 225, ♀♂ [Algeria: OÖLM, examined].

Andrena (*Truncandrena*) *truncatilabris espanola* Warncke, 1967: 224, ♀♂ [Spain: OÖLM, examined] syn. nov.

Distribution. Portugal, Spain, France, Morocco, Algeria, Tunisia (newly recorded). Material from south-eastern France and northern Italy must be carefully revised, but the position is taken here that the Maritime Alps represent a barrier between *A. nigropilosa* and *A. truncatilabris* s. str. This should be confirmed with genetic evidence.

Material examined. **Algeria:** S. Algeria, Laghouat [33.8082°N, 2.8316°E], iii.–iv.1929, 1♀, leg. Meyer, OÖLM (holotype of *A. t. nigropilosa*); Tlemcen, 20.iv.1910, 1♂, leg. de Bergeoin, OÖLM (paratype of *A. t. nigropilosa*); **Spain:** Sierra Nevada [37.0732°N, -3.3948°E], vi.1891, 1♀, leg. Handl., OÖLM (holotype of *A. t. espanola*); Montarco, 28.iv.1924, 1♂, leg. J.M. Dusmet y Alonso, OÖLM (paratype of *A. t. espanola*); **Tunisia:** Kef, 5 km SW Touiref, 28.iv.2012, 41, leg. C. Sevidy & A. Müller, AMC/TJWC.

Andrena (*Truncandrena*) *villipes* Pérez, 1895

Pérez (1895) described *A. villipes* from north-eastern Spain (Fig. 30), later describing the synonymous *A.* (*Truncandrena*) *squalida* Pérez, 1903 from south-western

Figure 30. *Andrena* (*Truncandrena*) *villipes* Pérez, 1895; female lectotype **A** label details **B** profile **C** face, frontal view **D** dorsal view.

France. It has a restricted distribution, known from Cistaceae-rich habitats from northern Morocco, Portugal, Spain, southern France, and north-western Italy (Gusenleitner and Schwarz 2002; Lhomme et al. 2020). Searches in the Sierra de las Nieves in southern Spain produced two particularly large and dark specimens provisionally identified as *A. villipes*. A sequence from one of these specimens is separated from *A. villipes* sequences from southern Portugal by an average genetic distance of 11.85% (range 11.85–11.85%). This new species is described and diagnosed below.

Material examined. **Spain:** Barcelona [41.4028°N, 2.1332°E], 1♀, MNHN (lectotype of *A. villipes*; Fig. 30).

Undescribed subgenera

As a result of the ground-breaking analysis of Pisanty et al. (2022b), we now have unprecedented phylogenetic resolution for the genus *Andrena*, and are now able to seriously deal with the problems inherent to the subgeneric classification system largely solidified by Warncke (1968a). Building on the work of Pisanty et al. (2022b), the Iberian fauna contains representatives of 44 described subgenera, but also representatives for nine additional clades that are currently undescribed. Some of these are dealt with here, though the *aegyptiaca*-group (Iberian representative: *A. alluaudi* Benoist, 1961) is not treated here; this lineage will be described in a planned future comprehensive revision of the subgenus.

The former *Poliandrena* Warncke, 1968

Pisanty et al. (2022b) demonstrated that *Andrena polita* Smith, 1847 falls into an expanded *Ulandrena*, and that *Poliandrena* is a strict synonym of this subgenus, and additionally that *Poliandrena* sensu Warncke contains at least five different polyphyletic clades, with the possibility of additional distinct clades when taxonomic sampling and phylogenetic analysis is more complete. Warncke, who described the subgenus *Poliandrena*, understandably used it as a 'waste-basket' for unclear taxa that displayed no clear defining characters. It is therefore necessary to split up this old grouping and to describe new subgenera.

In Iberia, representatives of all five subgenera can be found. These can be broadly summarised as the *blanda*-group, the *florea*-group, the *limbata*-group, the *oviventris*-group, and the *relata*-group. Four of these five lineages are represented in the analysis of Pisanty et al. (2022b) which is based on UCE analysis. UCE analyses are based on thousands of loci, and hence offer a high degree of confidence that groups are or are not related. Whilst single locus COI analyses cannot compare to those based on UCEs, they can demonstrate if individual species are closely related, and hence complement a UCE-informed phylogeny. No members of the *oviventris*-group were included in the analysis of Pisanty et al. (2022b), but analysis of barcodes (Fig. 31) places *A. farinosa* Pérez, 1895, *A. farinosoides* Wood, 2020, and *A. oviventris* Pérez, 1895 in a single clade with bootstrap support of 99, well-separated from *A. corax* Warncke, 1975, *A. murana* Warncke, 1975, and *A. relata* Warncke, 1975 which belong to the *relata*-group and which are morphologically the most similar to members of the *oviventris*-group. The two clades are separated by *A. limbata* Eversmann, 1852. On the basis of the analysis of Pisanty et al. (2022b) combined with these barcodes, subgenera are described for the *blanda*-group, *florea*-group, *limbata*-group, and *oviventris*-group.

No action is currently taken for members of the *relata*-group, as the status of morphologically similar species in the Eastern Mediterranean to Central Asia is unclear, and it must be genetically demonstrated if they belong to the *relata*-group or not. The members of the newly described subgenera are detailed below; in an Iberian context, the following species can be considered to be part of the *relata*-group: *A. corax*, *A. laurivora* Warncke, 1974, *A. macroptera* Warncke, 1974, *A. murana*, and *A. relata*.

The *caroli*-group

Members of this group of species have been placed in the subgenus *Campylogaster* Dours, 1873 (Warncke 1968a) that has the type species *A. erberi* Morawitz, 1871. Pisanty et al. (2022b) identified that *Campylogaster* is polyphyletic, with *A. caroli* Pérez, 1895 falling far away from *A. erberi*. *Campylogaster* therefore can probably only be

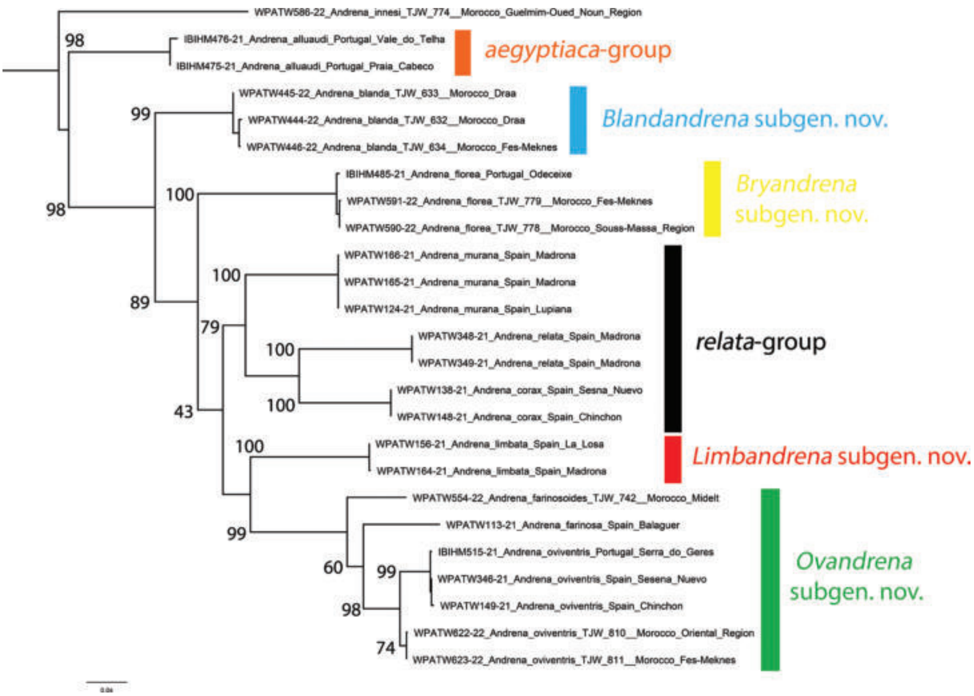

Figure 31. Phylogenetic tree (maximum likelihood) of *Andrena* from currently undescribed subgenera based on the mitochondrial COI gene. *Andrena* (incertae sedis) *innesi* Gribodo, 1894 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

applied to the species around *A. erberi* that have strongly depressed tergal margins, e.g. *A. iranella* Popov, 1940 (Iran, Turkemenistan, ?Arabian Peninsula), *A. nanshanica* Popov, 1940 (China, Mongolia), *A. chengtehensis* Yasumatsu, 1935 (China, South Korea). This subgenus therefore appears to be eastern and predominantly Asian, with a western limit of *A. erberi* in the southern Balkans. In contrast, *A. caroli* has the tergal margins flat and not noticeably depressed. Based on the analysis of Pisanty et al. (2022b) combined with this morphological difference, a new subgenus *Pruinosandrena* subgen. nov. is described below for the species around *A. caroli*. Importantly, *A. lateralis* Morawitz, 1876 and *A. incisa* Eversmann, 1852 were also placed into *Campylogaster* by Warncke (1968a). Although not sampled by Pisanty et al. (2022b), *A. lateralis* falls far away from the *Pruinosandrena* based on COI analysis (Fig. 32). Morphologically, *A. lateralis* and *A. incisa* form a species pair (that can be referred to at the *incisa*-group) that lacks many of the characters shared by members of the *Pruinosandrena* (see below), and they probably represent an additional undescribed subgenus. Without additional genetic data, no further steps are taken for this species pair at the present time.

Finally, clarity is required for the status of taxa lumped under a broad concept of *A. pruinosa* Erichson, 1835, specifically *A. pruinosa succinea* Dours, 1872 and *A. pruinosa parata* Warncke, 1967. Erichson (1835) described *A. pruinosa* from southern Spain

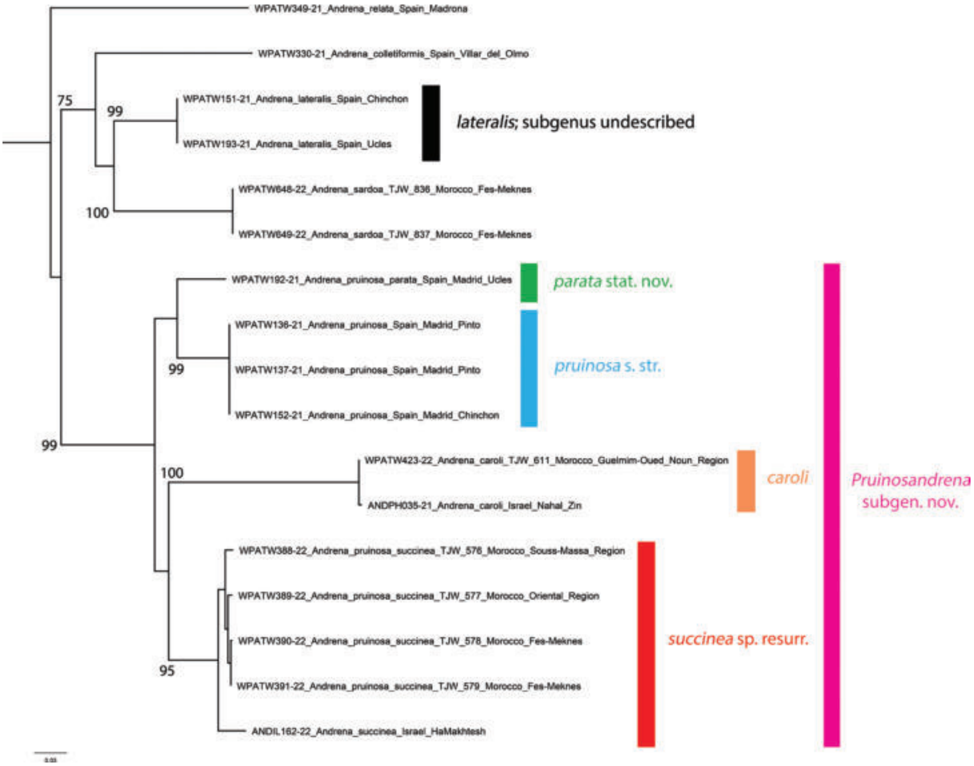

Figure 32. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Brachyandrena* Pittioni, 1948, *Lepidandrena* Hedicke, 1933, and currently undescribed subgenera based on the mitochondrial COI gene. *Andrena* (incertae sedis) *relata* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

(Andalusia); a single female labelled as 'type' is conserved in the ZMHB which may automatically be the holotype (Fig. 33), but this is ambiguous as it is unclear if Erichson described the species from multiple specimens or not. Dours (1872) described *A. succinea* from Algeria, noting the clear red colouration of the metasoma (hence the species name, *succin* = amber). Warncke (1967) used *A. succinea* as a subspecies in combination with *A. pruinosa*, arguing that males from North Africa could not be clearly separated from Spanish males. He then described *A. pruinosa parata* from south-eastern Spain, giving characters related to colouration and antennal ratios.

Genetic analysis of members of the *Pruinosandrena* demonstrates that the broad concept of *A. pruinosa* used by Warncke was overly conservative (Fig. 32). A single red-marked female specimen initially identified as *A. pruinosa* was separated by 7.45% from three additional *A. pruinosa* s. str. specimens. Inspection of Warncke's original description of *A. pruinosa parata* and comparison of the antennal ratios demonstrates that this divergent specimen has A3 clearly longer than A4+5, whereas A3=A4+5 in *A. pruinosa* s. str. The other characters mentioned by Warncke relating to colour do not

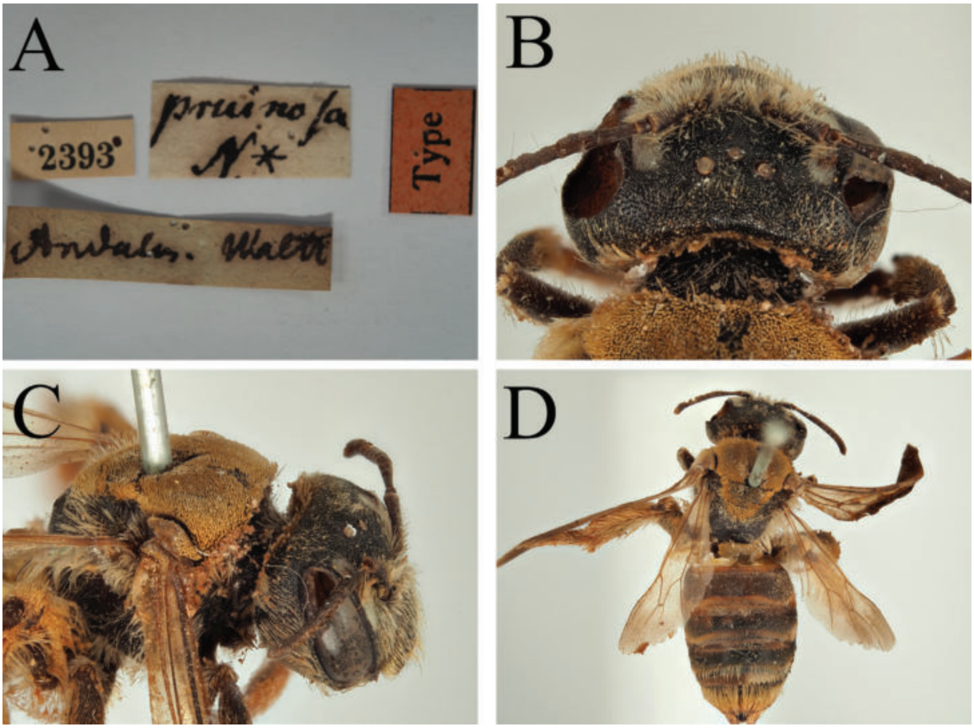

Figure 33. *Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835, female holotype/syntype **A** label details **B** head, dorsal view **C** mesosoma, dorsolateral view **D** dorsal view.

work consistently, as one of the barcoded *A. pruinosa* s. str. has the terga partially red-marked and the hind tibiae lightened orange. Though small, this morphological difference is meaningful, as the two taxa are found essentially in direct sympatry; the distance between the sampling location of barcoded specimens of *A. pruinosa* s. str. from Pinto was approximately 11 km from the Camino de Uclés sampling site for *A. pruinosa parata*. In this context, a genetic separation of 7.45% combined with the morphological difference is highly significant, and *A. parata* stat. nov. is treated as a valid species.

Andrena pruinosa succinea was strongly separated from *A. pruinosa* s. str. by an average genetic distance of 9.45% (range 8.97–10.33%). Sequences of *A. pruinosa* s. str. were identical, which is not surprising as they all came from a small part of the province of Madrid. *Andrena pruinosa succinea* samples came from a large geographic area from south-western Morocco to Israel, but still showed low average intraspecific variation of 2.06% (range 0.14–3.80%). The two clades were not sister, being separated by *A. parata* and *A. caroli*, and were supported by bootstrap support of 99 and 95, respectively. *Andrena succinea* sp. resurr. is therefore considered to be a valid species, distinct from *A. pruinosa* s. str. Morphologically, separation of males is straightforward, and it is unclear why Warncke considered the difference unclear. *Andrena succinea* males have a yellow marked clypeus (see illustrations in Wood et al. 2020b), with the yellow markings sometimes extending onto the lower part of the paraocular areas (uniformly black in *A. pruinosa* s. str. and *A. parata*) and, viewed ventrally, A4 is short, as long as broad (A4 is elongate and clearly longer than broad in *A. pruinosa* s. str.). *Andrena parata* males can easily be separated as A3 is longer than A4+5, whereas A3 is shorter than A4+5 in both *A. pruinosa* s. str. and *A. succinea*.

There are also ecological differences. *Andrena succinea* can be found in dry desert-edge steppe habitats, as opposed to *A. pruinosa* which in Iberia is found in grasslands and cold steppe that are lightly more lush, at least during the spring. For example, in Morocco, *A. succinea* can be found in stipa steppe habitat around Bou Rached (Oriental region, south of Guercif) on the eastern edge of the Middle Atlas as it transitions into the desert (Fig. 34A, B), whereas it has never been recorded from the more humid parts of the Middle Atlas that have grasslands resembling those that can be found in central Iberia (e.g. Madrid, north of Chinchón, Fig. 34C, D).

Although the type of *A. succinea* is lost, and the type for a more recently described taxon is preserved in the MNHN collection (*A. sitifensis* Pérez, 1895; Fig. 35), *A. succinea* is the name that is established in the literature, either as a species itself or in combination with *A. pruinosa* (Benoist 1961; Warncke 1967; Warncke 1974; Gusenleitner and Schwarz 2002; Wood et al. 2020b; Dermane et al. 2021). In order to conserve this use, a neotype is designated below for *A. succinea*. As a result of these numerous changes, the updated statuses and synonymies are given here:

***Andrena* (*Pruinosandrena*) *parata* Warncke, 1967, stat. nov.**

Andrena pruinosa parata Warncke, 1967: 233, ♀♂ [Spain: OÖLM, examined].

Remarks. Though described from south-eastern Spain, Warncke (1976) noted that he had examined a single specimen of *A. parata* (as *A. pruinosa parata*) from Madrid: Ribas de Jarama, but he expressed doubts as to whether or not it had been correctly labelled given the collecting localities of all other known specimens. The contemporary Camino de Uclés site is approximately 7 km from Ribas de Jarama, confirming the presence of this taxon in central Spain.

Distribution. Spain.

Material examined. Spain: Alicante [38.3628°N, -0.5093°W], 1♂, leg. G. Mercet, OÖLM (holotype); Benidorm, 2.vi.1952, 1♀, leg. J. de Beaumont, OÖLM (paratype); Fortuna [Murcia], v.1928, 1♂, leg. J. M. Dusmet y Alonso, OÖLM (paratype); Madrid, Rivas-Vaciamadrid, Canal de Manzanares to Camino de Uclés, 19.v.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW192-21].

***Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835**

Andrena pruinosa Erichson, 1835: 104, ♀ [Spain: ZMHB, examined].

Andrena lanuginosa Spinola, 1843: 137, ♀ [Spain, lectotype by present designation: MRSN].

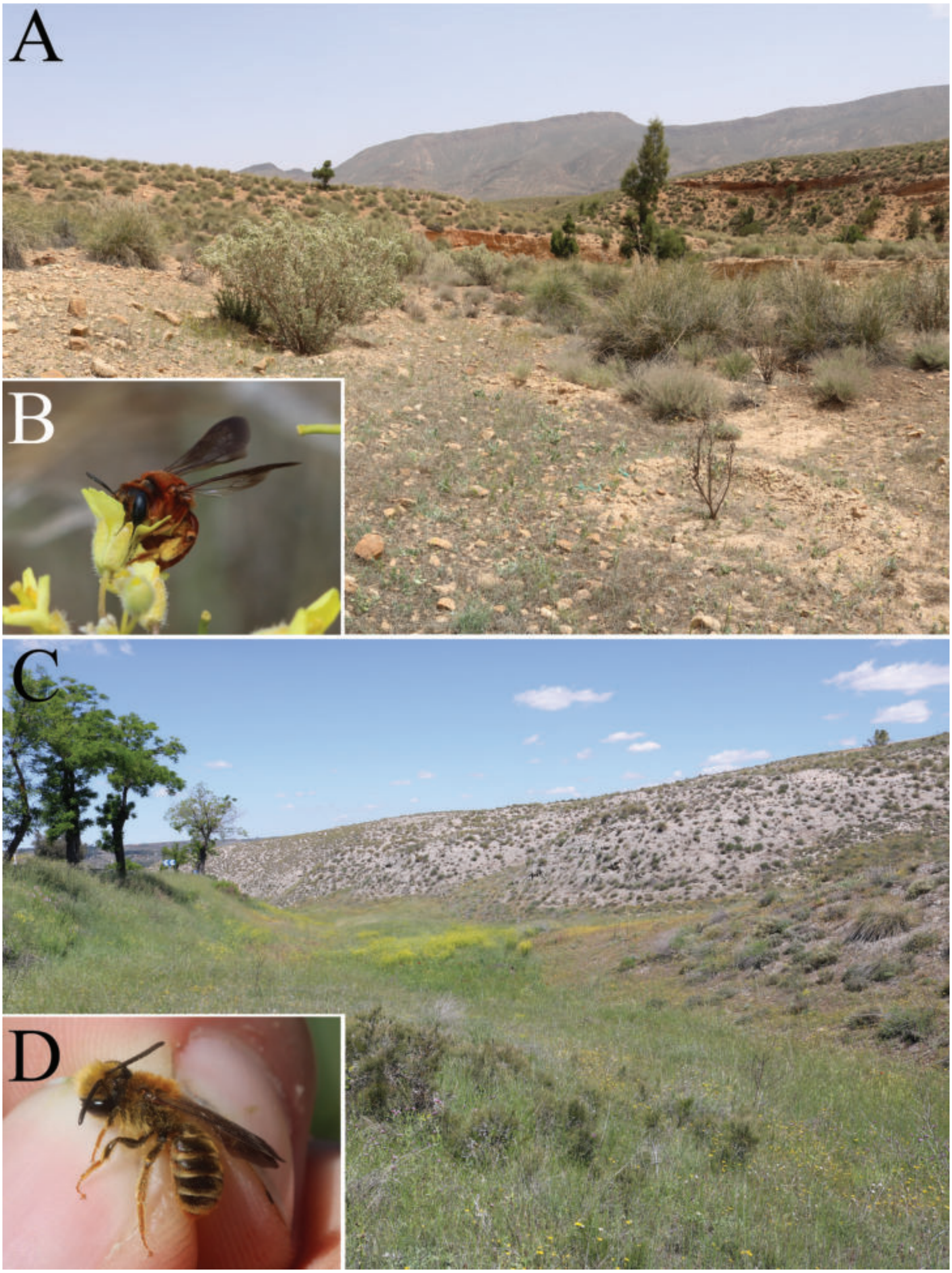

Figure 34. *Andrena* (*Pruinosandrena*) *succinea* Dours, 1872 **A** habitat, Oriental, Guercif, P5427, 2 km SW of Bou Rached, 950 m, 13.v.2022 **B** female collecting pollen from Brassicaceae spp.; *Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835 **C** habitat, Madrid, Chinchón, 6 km N, M-311, 14.v.2021 **D** male, in hand.

Remarks. Examination of the type material of both *A. pruinosa* and *A. lanuginosa* (Fig. 36) showed that both were female specimens with dark terga, conforming to the classical concept of this species. Neither represent *A. parata*, and hence the synonymy of *A. lanuginosa* with *A. pruinosa* is maintained. Spinola (1843) did not specify how many specimens he described the species from. The specimen examined here may be automatically the holotype, but as this is not clear from the original description, it is here designated as the lectotype.

Distribution. Spain.

Material examined. **Spain:** Andalusia, 1♀, leg. Waltl, ZMHB (holotype/syntype; Fig. 33); Andalusia, 1♀, leg. Ghilinni, MRSN (lectotype of *A. lanuginosa*, by present designation; Fig. 36); Madrid, Madrid, Chinchón, 6 km N, M-311, 14.v.2021, 2♂, 1♀, leg. T.J. Wood, TJWC; Madrid, Madrid, Pinto, 1 km E, Carr. la Marañosa, 13.v.2021, 1♂, 1♀, leg. T.J. Wood, TJWC.

Andrena **(*Pruinosandrena*)** ***succinea*** **Dours, 1872, stat. nov.**

Andrena succinea Dours, 1872: 424, ♀ [Algeria: type lost, neotype designated below, OÖLM].

Andrena chrysopyga Dours, 1872: 423, ♀ (nec. *Andrena chrysopyga* Schenck, 1853) [Algeria: type lost].

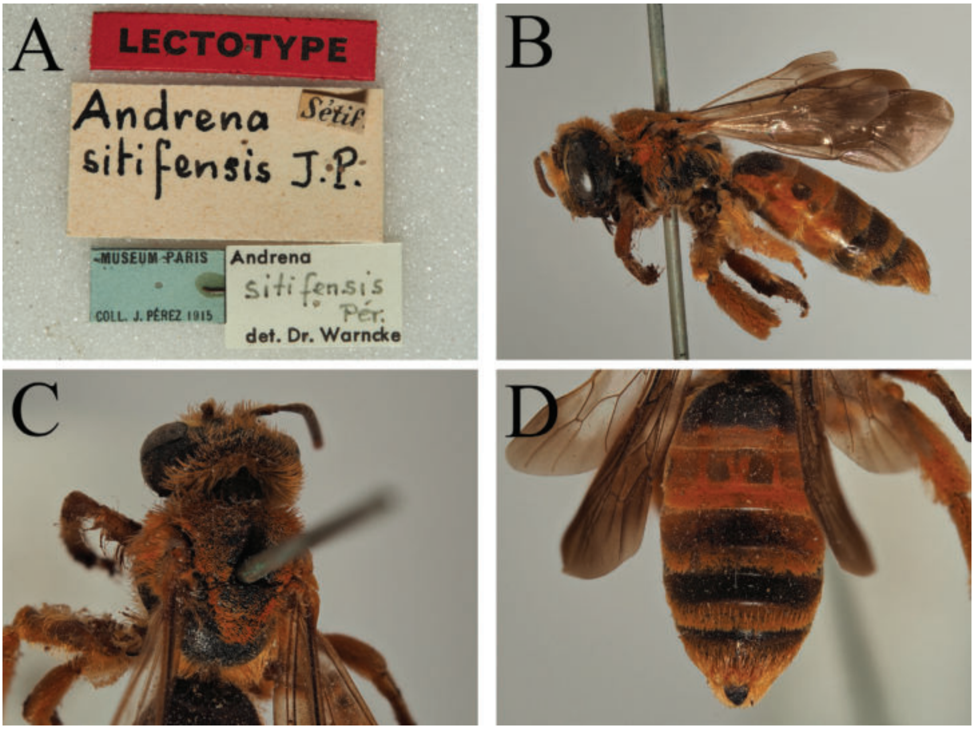

Figure 35. *Andrena* (*Pruinosandrena*) *sitifensis* Pérez, 1895, female lectotype **A** label details **B** profile **C** scutum, dorsal view **D** terga, dorsal view.

Andrena commixta Dalla Torre & Friese, 1895: 43. nom. nov. for *Andrena chrysopyga* Dours, 1872
Andrena sitifensis Pérez, 1895: 46, ♀ [Algeria: MNHN, examined]
Andrena fulvisquama Popov, 1940: 260, ♀ [Algeria: ZISP, not examined]

Remarks. The synonymy of *A. mayeti* Pérez, 1895 (described from Tunisia) with *A. succinea* reported by Warncke (1967, see also Benoist 1961) is incorrect. Examination of the female lectotype (Fig. 37) shows that *A. mayeti* syn. nov. is a synonym of *A. caroli* Pérez, 1895 (described from Algeria; Fig. 38) because the foveae are wide and there are well-developed hair bands on the tergal margins (see identification key for *Pruinosandrena* below).

Distribution. Morocco, Algeria, Tunisia, Libya, Egypt, Israel and the West Bank, Jordan, Syria, Saudi Arabia, Iran (Wood and Monfared 2022).

Material examined. **Algeria:** Setif [36.2059°N, 5.3965°E], 1♀, MNHN (lectotype of *A. sitifensis*; Fig. 35); **Morocco:** Oriental, Guercif, P5427, 2 km SW of Bou Rached, 33.8844°N, -3.6154°W, 950 m, 13.v.2022, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW389-22] (neotype of *A. succinea*, see below).

Figure 36. *Andrena* (*Pruinosandrena*) *lanuginosa* Spinola, 1843, female lectotype **A** label details **B** profile **C** head, dorso-frontal view **D** terga, dorsal view.

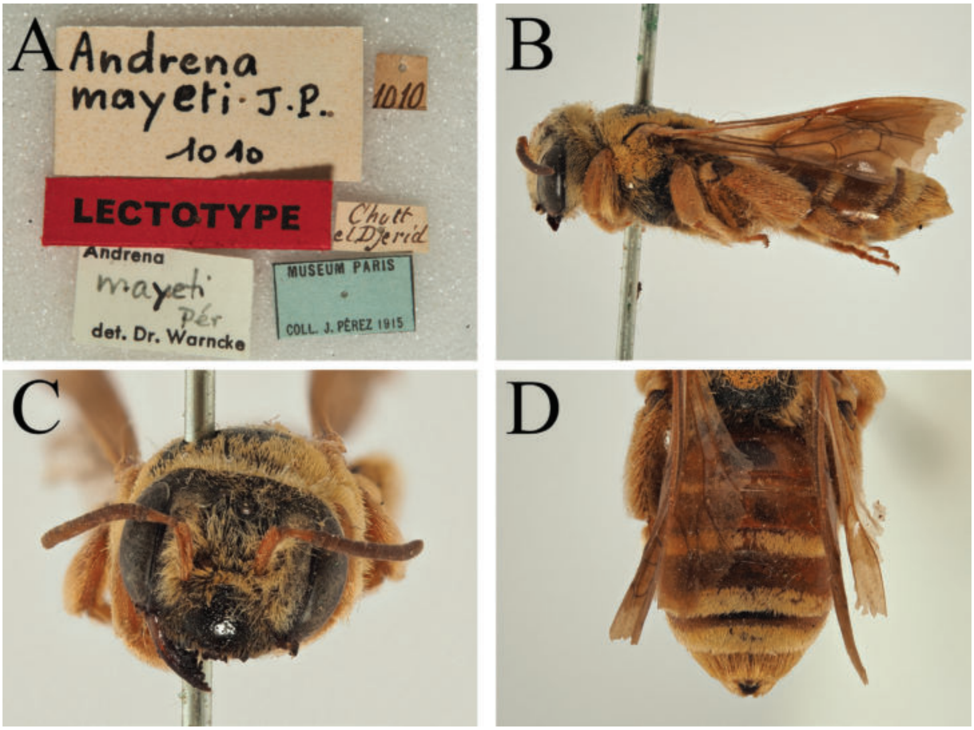

Figure 37. *Andrena* (*Pruinosandrena*) *mayeti* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

Andrena (*Pruinosandrena*) *caroli* Pérez, 1895

Andrena (*Pruinosandrena*) *caroli* Pérez, 1895: 47, ♀ [Algeria: MNHN, examined]
Andrena (*Pruinosandrena*) *mayeti* Pérez, 1895: 47, ♀ [Tunisia: MNHN, examined] syn. nov.

Distribution. Morocco, Algeria, Tunisia, Egypt, Israel.

Material examined. Algeria: Biskra [34.8600°N, 5.6995°E], 1♀, MNHN (lectotype of *A. caroli*; Fig. 38); **Tunisia:** Chott el Djerid [33.8806°N, 8.1435°E], 1♀, MNHN (lectotype of *A. mayeti*; Fig. 37).

The *numida*-group

This group of Palaearctic species was previously placed in the subgenus *Thysandrena* Lanham, 1949 by Warncke (1968a). However, true *Thysandrena* occur only in North America, and Palaearctic species fall elsewhere (Pisanty et al. 2022b). Four species are recognised in the Palaearctic; *A. hypopolia* Schmiedeknecht, 1884, *A. numida*, *A. ranunculorum* Morawitz, 1877, and *A. lunata* Warncke, 1975, though additional

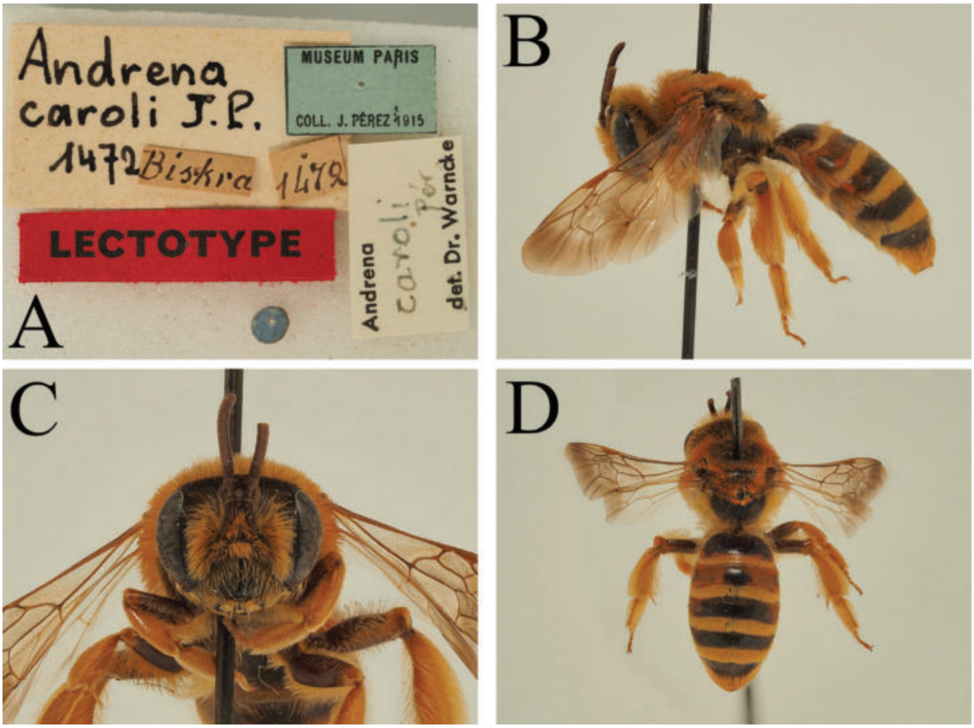

Figure 38. *Andrena* (*Pruinosandrena*) *caroli* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

genetic work is required to ensure that they all belong together; no subgenus is therefore described in the current work.

The status of *A. hypopolia* (described from southern France) has been somewhat unclear, as no major morphological differences from *A. numida* (described from Algeria) are apparent. Warncke used *A. hypopolia* in combination with *A. numida* as the subspecies for south-western Europe, using several other taxa as subspecies for populations in Central and Eastern Europe (ssp. ?*holosericea* Bramson, 1879, considered a *nomen dubium* by Gusenleitner and Schwarz 2002), southern Italy (ssp. *syracusae* Strand, 1921), and Turkey (ssp. *albiscopa* Warncke, 1967, see Gusenleitner and Schwarz 2002). No members of this group are known from the Levant.

The situation is further complicated because the type of *A. hypopolia* is lost (and could not be found amongst undesignated Schmiedeknecht type material located in the RMNH collection, see below), and the type of *A. numida* can also not be located at the MNHN. Furthermore, *A. inconspicua* Morawitz, 1871 was described from Calabria in southern Italy. Warncke (1967) treated this as *A.* (*Taeniandrena*) *russula* Lepeletier, 1841 based on the description; Gusenleitner and Schwarz (2001) then listed it as a synonym of *A. numida*, before finally Gusenleitner and Schwarz (2002) listed it as a synonym of *A. hypopolia* despite the fact that it is an older name. This is because, under the broad treatment of Warncke, *A. inconspicua* would be junior to *A. numida*. However, Gusenleitner and Schwarz (2002) treated *A. hypopolia* as a distinct species, and did not resolve the status of *A. inconspicua*, even though it is an older name than *A. hypopolia*. The lectotype of *A. inconspicua* was recently illustrated by Astafurova et al. (2021), confirming its affinity with the *numida*-group, and not the subgenus *Taeniandrena*. The use of the name *A. inconspicua* therefore depends on two things; 1) whether European and North African material are distinct, and 2) whether material from southern Italy shows a stronger affinity with the European or North African taxon.

Genetically, barcoded specimens from Iberia showed almost no differentiation from specimens from Germany (average genetic distance 0.26%; Fig. 1), thus demonstrating that the name *A. hypopolia* can be applied to both the south-western and Central European populations. However, there was a consistent separation between Moroccan and German/Iberian sequences, these separated by an average genetic distance of 3.05% (range 2.87–3.13%). A single sequence was available from Sicily. This sequence differed from German/Iberian sequences by an average genetic distance of 6.11% (range 3.87–6.82%) and from Moroccan sequences by an average of 2.39% (range 2.17–2.64%). It clustered with Moroccan sequences, with the clades Morocco+Sicily showing bootstrap support of 92 and Germany+Iberia showing bootstrap support of 86. Examination of these barcoded specimens shows that there is a subtle but consistent morphological difference, which is the density of punctures on T3 of females. In Iberian specimens, the disc of T3 is densely punctate, with punctures separated by <1 puncture diameter. In contrast, in Moroccan and Sicilian specimens, the disc of T3 is shallowly and obscurely punctate, with punctures separated by >1 puncture diameter. Examination of the female lectotype of *A. inconspicua* (Astafurova et al. 2021: fig. 24) shows that this specimen morphologically conforms to *A. numida*, with weak and obscure punctures on the disc of T3. On this basis, *A. inconspicua* is synonymised syn. nov. with *A. numida*, and *A. hypopolia* is maintained as the senior name for populations in Iberia and Central Europe. A barcoded neotype of *A. numida* is designated from Moroccan material (see below).

This action largely maintains the *status quo* of Gusenleitner and Schwarz (2002), and *A. numida* is considered to have a distribution of Morocco, Algeria, Tunisia, Libya, and Sicily and the extreme southern parts of Italy (Calabria, Campania). The inclusion of Campania derives from treatment of the taxon *A. syracusae*. This taxon was described by Strand in the male sex only as a variety of *A.* (*Simandrena*) *propinqua* Schenck, 1853. Warncke (1967) treated this as a subspecies of *A. numida* with dark facial hair. The barcoded specimen from Sicily is a female, and whilst it should represent *A. syracusae* since it was collected only 150 km west of the *locus typicus* of Syracuse, since the female of *A. syracusae* is unknown and undescribed this cannot be said for certain. I have not seen male *A. numida* material from Sicily, or the type material of *A. syracusae* itself. However, I have seen males from the island of Ischia by Naples. These conform to the concept of *A. syracusae*, with extensive dark facial pubescence, and show extremely weak and sparse punctation on T3. The island of Ischia and the nearby Sorrento Peninsula on the Italian mainland are unusual and host an *Andrena* fauna with several species that are otherwise found in Italy only in Sicily, such as *A.* (*Micrandrena*) *fumida* Pérez, 1895. On the basis of its morphology, *A. syracusae* is considered to represent only a form of *A. numida*. This should ultimately be confirmed through the direct barcoding of males with dark facial pubescence; these are expected to fall into the *A. numida* clade.

The status of *A. numida albiscopa* is unclear, but based on its distribution and morphology (T3 is clearly punctured), it is transferred to *A. hypopolia albiscopa* comb. nov. The punctures of T3 are sparser than in *A. hypopolia* s. str., and the interspaces are shinier. This is true also of *A. hypopolia* material from Central Asia (Kyrgyzstan). For now, a conservative position is taken that *A. hypopolia* ranges from Iberia to Central Asia and western Siberia, though the eastern limit and the status of material from Turkey requires validation through genetic analysis across this range.

Finally, examination of the lectotype of *A. setosa* Pérez, 1903 (Fig. 39; des. Warncke 1967) reveals that it is not a synonym of *A. numida hypopolia* as given by Warncke (1967), but a synonym (syn. nov.) of *Andrena ranunculorum*. The specimen comes from Arreau in France which is in the Hautes-Pyrénées department, and is situated immediately adjacent to mountains that ascend to 3,000 m. *Andrena ranunculorum* is known from alpine habitats in the central and eastern Pyrenees on both the French and Spanish sides, so this synonymy makes both morphological and ecological sense.

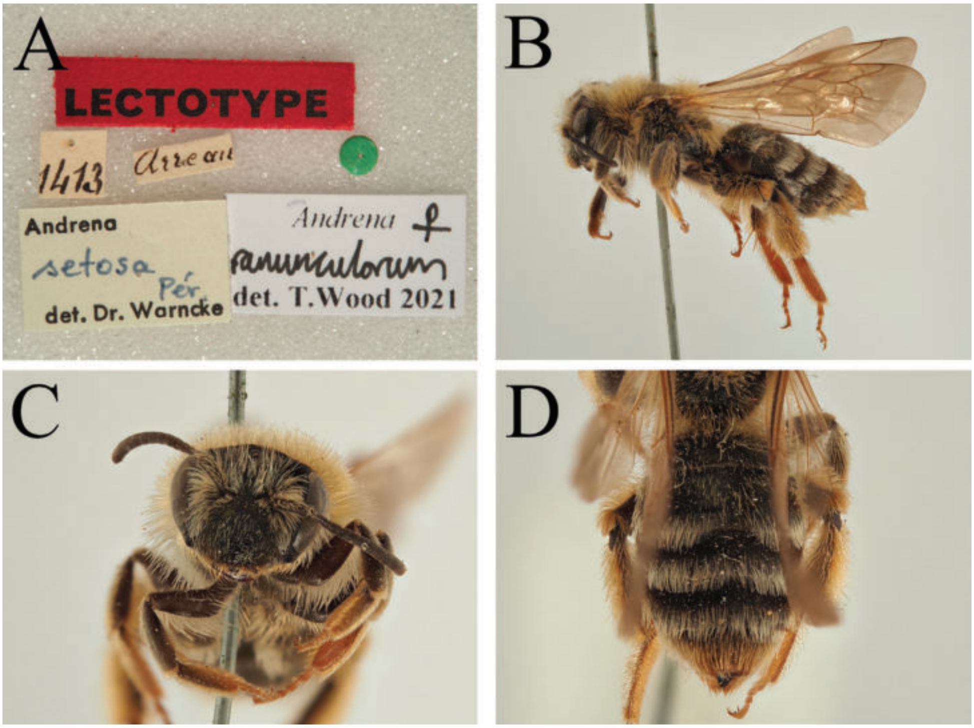

Figure 39. *Andrena* (incertae sedis) *setosa* Pérez, 1903, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

Material examined. ***Andrena ranunculorum*: France:** Arreau [42.9064°N, 0.3557°E], 1♀, MNHN (lectotype; Fig. 39).

***Andrena numida* f. *syracusae*: Italy:** Campania, Is. Iscia, Panza, 9.iv.1991, 6♂, leg. J. Gusenleitner, OÖLM/TJWC.

***Andrena fumida*: Italy:** Kampanien, Salerno, Monti Alburini (NP), SE Petina, 1100 m, 8.vi.2003, 1♀, leg. H. & R. Rausch, OÖLM; Mondello [Palermo, Sicily], 10.iv.1979, 1♂, leg. J.A.W. Lucas, OÖLM; Monte Faito (Campania), 13.v.1976, 1♂, leg. Pagliano, MRSN; Sorrento [Naples], 3.v.1970, 1♂, leg. J.P. van Lith, RMNH.

Description of new subgenera

Subgenus *Blandandrena* subgen. nov.

https://zoobank.org/E78F170A-60CC-4D38-9D56-9727B1347DDC

Type species. *Andrena blanda* Pérez, 1895.

Diagnosis. *Blandandrena* is monotypic, and hence diagnosis of *A. blanda* (Fig. 40) is *de facto* diagnosis of the subgenus. Through the combination of slightly upturned fore margin of the clypeus, fovea broad and occupying over ½ the space between the lateral ocellus and the inner margin of the compound eye, weak but distinct humeral angle, unmodified posterior face of the hind femur (without teeth, carinae, or spines), lack of squamous hairs, simple hind tibial spur (not broadened basally or medially), dark integument, black male clypeus, and essential absence of defining features it falls very close to members of the *relata*-group and to *Ovandrena* subgen. nov. that were formerly lumped together under the subgenus *Poliandrena* (see above). *Andrena blanda* females can provisionally be separated from the *relata*-group by the weakly punctate terga, punctures shallow and somewhat obscure, separated by 1–2 puncture diameters (Fig. 40D) whereas in the *relata*-group, tergal punctures are typically much stronger, clear and dense, separated by 1–2 puncture diameters but often by only 1 puncture diameter. This character works for West Mediterranean members of the *relata*-group, but additional work is needed to define this subgenus in the east, and so it is not defined and described here. *Andrena blanda* females can be separated from the *Ovandrena* by their simple scutal hairs (Fig. 40A–C; hairs semi-squamous in *Ovandrena*) and poorly delineated propodeal triangle that lacks lateral carinae (Fig. 40C; propodeal triangle clearly defined by presence of lateral carinae in *Ovandrena*; see below for additional detail).

Andrena blanda males can be separated by their black clypeus (Fig. 40F) in combination with their distinctive genital capsule (Fig. 40G). Most members of the *relata*-group have a yellow-marked clypeus, but for those with a black clypeus (e.g. *A. corax*), the genital capsule allows recognition. In *A. blanda*, the genital capsule is short and compact, more or less round, with gonocoxae with apically diverging inner margins and which are produced into short pointed teeth, and the gonostyli are apically strongly broadened and flattened, the disc being slightly broader than long. In the *relata*-group, the genital capsule is typically simple, without strongly apically broadened gonostyli, or when this is the case (e.g. *A. murana* Warncke, 1975a) then the clypeus is yellow-marked and the

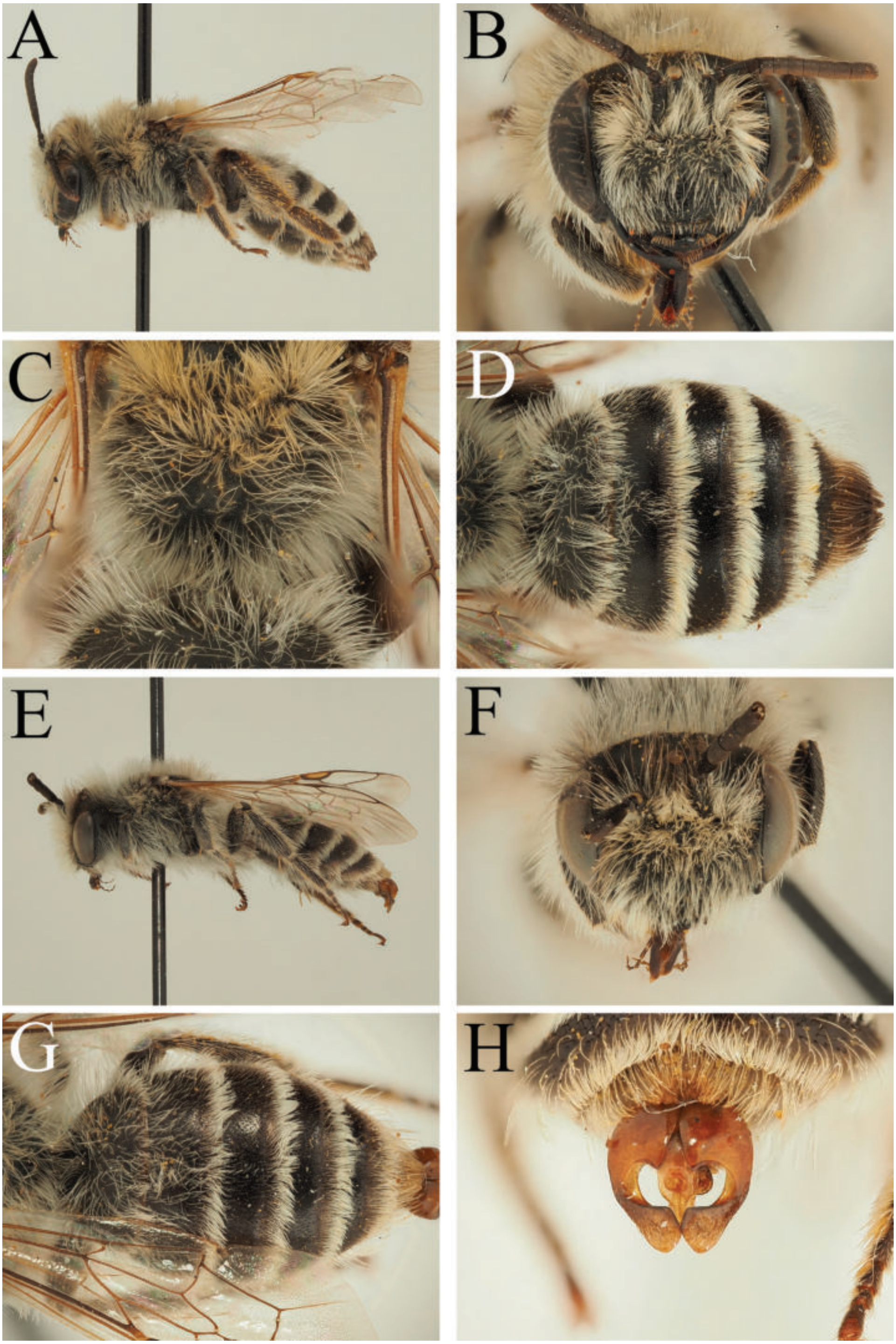

Figure 40. *Andrena* (*Blandandrena*) *blanda* Pérez, 1895, female **A** profile **B** face, frontal view **C** propodeum, dorsal view **D** terga, dorsal view; male **E** profile **F** face, frontal view **G** terga, dorsal view **H** genital capsule.

gonocoxae are not produced into pointed teeth. *Andrena blanda* can be separated from the *Ovandrena* by the genital capsule, as in *Ovandrena* the gonostyli are apically flattened and spatulate, but the disc is always longer than broad. The gonocoxae are also produced into apically projecting teeth, but the inner margins of the gonocoxae are parallel and do not diverge. The propodeal triangle of *Ovandrena* is also triangular and strongly defined by lateral carinae, whereas in *A. blanda* it is poorly defined and lacks lateral carinae.

Description. Medium-sized bees (9–10 mm) with dark integument. Head broad, 1.4 times broader than long. Gena slightly exceeding width of compound eye; ocelloccipital distance 1.5–2 times diameter of lateral ocellus, slightly broader in male sex. Facial fovea broad, occupying almost entire distance between lateral ocellus and inner margin of compound eye. Mesosoma dorsally with moderately long light brown hairs, laterally with white hairs. Pronotum laterally with humeral angle. Dorsolateral surface of propodeum with obscure and finely raised rugosity; propodeal triangle broad, poorly delineated laterally, surface with fine granular reticulation, basally with weakly raised rugosity, propodeal triangle thus defined by change in surface sculpture. Forewing with nervulus antefurcal. Hind tibial spurs simple, not broadened basally or medially. Terga weakly and obscurely punctate, punctures separated by 1–2 puncture diameters. Male genital capsule rounded, more or less circular in outline, gonocoxae with inner margins apically diverging, produced into apically projecting short pointed teeth. Gonostyli apically broadened and flattened, apical disc slightly broader than long. Penis valves relatively narrow, occupying less than half space between gonostyli.

Etymology. The name is taken from the name of the type species *A. blanda*, with *blanda* being the feminine singular of the adjective *blandus* which can mean pleasant, agreeable, smooth. It can be used to refer to the generally unremarkable nature of the species which has made it hard to assign to a particular group of species. The gender is feminine.

Included species. *Andrena blanda* (Spain, including mainland Spain and newly recorded for Fuerteventura), Morocco, Algeria, Tunisia; Gusenleitner and Schwarz 2002).

Material examined (illustrative). **Algeria:** Biskra [34.8600°N, 5.6995°E], 1♀, MNHN (lectotype des. Warncke 1967); 5 km N of Mecheria, st. 9, 7.iv.1983, 1♀, leg. R. Leys & P. v. d. Hurk, RMNH; 5 km SE of Sfissifa, st. 8, 6.iv.1983, 1♀, leg. R. Leys & P. v. d. Hurk, RMNH; **Morocco:** Drâa-Tafilalet, Tazenakht, 1 km W Anezal, c. 1600 m, 15.iv.2022, 1♀, leg. T.J. Wood, TJWC; Foum Zguid, 50 km N, 30.iii.1986, 1♂, 16♀, leg. M. Schwarz, MSC; Ifkern, 25 km E Boulemane, 25.v.1995, 10♀, leg. Mi. Halada, OÖLM; **Spain:** Fuerteventura, Costa Calma, ESE Montaña Pelada, 29.iii.2015, 3♀, leg. A. Müller, AMC/TJWC; Fuerteventura, S Costa Calma, Montañeta de los Verdes, 1.iv.2015, 5♀, leg. A. Müller, AMC; Sierra de María, 25 km W Lorca, 10.v.2003, 1♀, leg. J. Halada, OÖLM; Granada, Pantano de los Bermejales, 26.v.1982, 1♀, leg. R. Leys, RMNH.

Subgenus *Bryandrena* subgen. nov.

https://zoobank.org/54B1C9C7-8D5A-441B-B49B-DDBA8FB5FE39

Type species. *Andrena florea* Fabricius, 1793.

Diagnosis. *Bryandrena* is monotypic, and hence diagnosis of *A. florea* is *de facto* diagnosis of the subgenus. The combination of broad head (Fig. 41B, F; 1.3–1.4 times broader than long), the inner margins of the compound eyes diverging ventrally, humeral angle (stronger in male), punctate clypeus with underlying surface shiny over the majority of its area, propodeal triangle not defined by lateral carinae and comparatively smooth relative to the microreticulate dorsolateral parts of the propodeum (Fig. 41C), terga that are always at least partially red-marked (Fig. 41D, G), unmodified posterior face of the hind femur (without teeth, carinae, or spines), lack of squamous hairs, simple hind tibial spur (not broadened basally or medially), black male clypeus, and unique genital capsule (Fig. 41H; see description below) allows separation from any other *Andrena* species.

Description. Medium-sized bees (11–13 mm), integument predominantly dark, with red markings on at least one tergum, sometimes all terga extensively red marked. Head broad, 1.3–1.4 times wider than long, inner margins of compound eyes diverging ventrally. Gena slightly exceeding width of compound eye in females, clearly exceeding width of compound eye in males; ocelloccipital distance 1.5–2 times diameter of lateral ocellus. Facial fovea broad, occupying ¾ of distance between lateral ocellus and inner margin of compound eye. Pronotum laterally with humeral angle, more pronounced in male sex. Dorsolateral surface of propodeum microreticulate, with weakly raised reticulation; propodeal triangle poorly defined laterally, comparatively smooth and lacking microreticulation, basally with raised rugosity covering variable extent, never entire propodeal triangle. Forewing with nervulus interstitial. Terga regularly and densely punctate, punctures separated by 1 puncture diameter. Male genital capsule strongly elongate, gonocoxae essentially truncate with inner margin rounded, gonostyli apically produced, elongate, strongly flattened and spatulate, 3 times longer than broad; penis valves basally broad, strongly narrowing medially to become elongate and acutely pointed apically.

Etymology. The name is taken from the pollen host plant *Bryonia* (Cucurbitaceae) which ultimately derives from the Greek βϱυωνία [bruōnía]. *Andrena florea* can be found frequently almost wherever *Bryonia* species are in flower. The gender is feminine.

Included species. *Andrena florea* (West Palaearctic, from Morocco and Iberia to Iran and the Ural Mountains; Gusenleitner and Schwarz 2002).

Subgenus *Limbandrena* subgen. nov.

https://zoobank.org/E0948E05-DB8C-4AD2-B260-01D335F6EA96

Type species. *Andrena limbata* Eversmann, 1852 (illustrated by Astafurova et al. 2022).

Remarks. Historically, *A. toelgiana* Friese, 1921 has been considered the sister species to *A. limbata*, differing by the yellow clypeus in the female sex (see Gusenleitner and Schwarz 2002). However, the male is unknown. Structurally, there are no differences. Examination of specimens from Bulgaria and Turkey show a gradient of yellow colouration on the clypeus, from entirely black, with a narrow longitudinal yellow

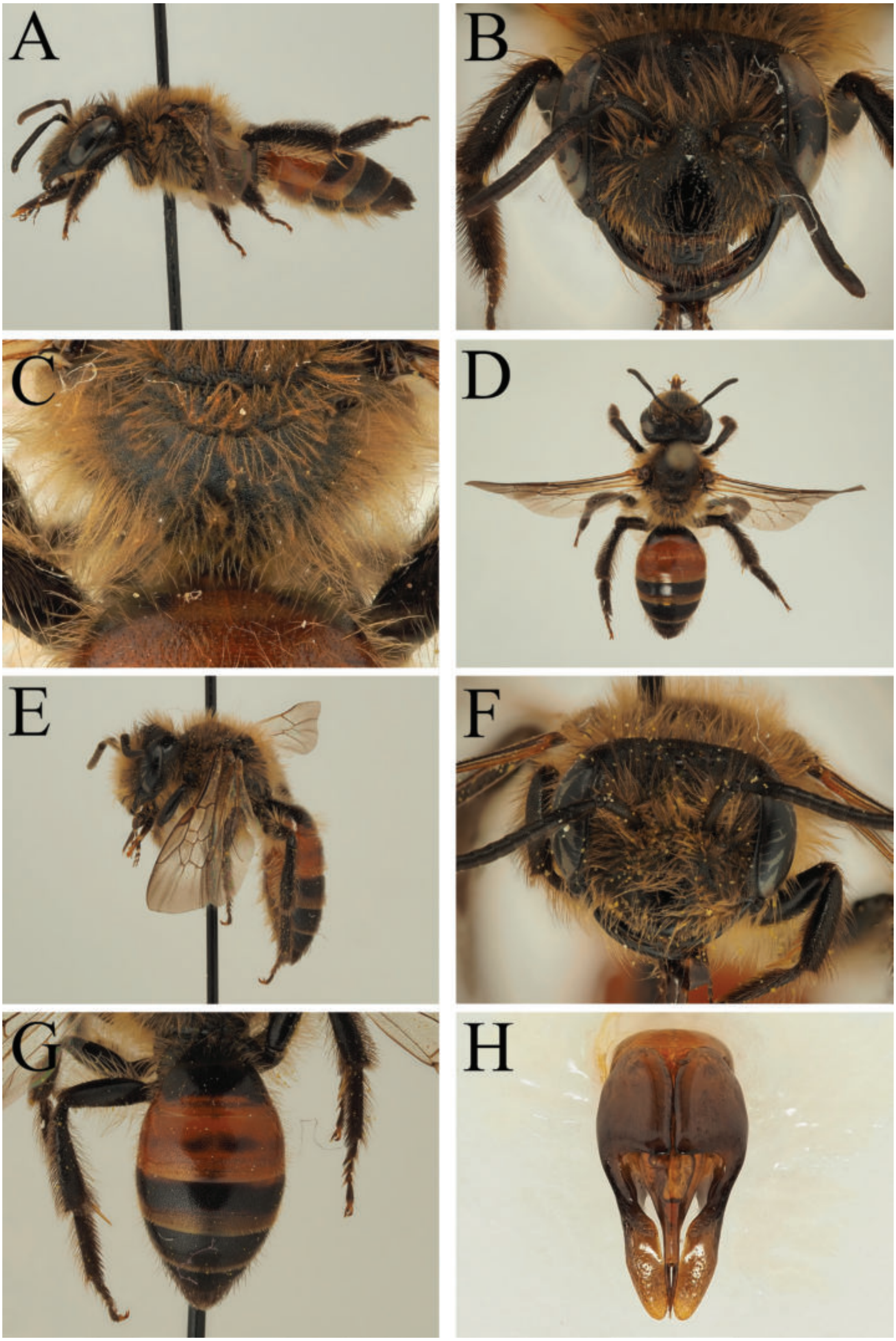

Figure 41. *Andrena* (*Bryandrena*) *florea* Fabricius, 1793, female **A** profile **B** head, frontal view **C** propodeum, dorsal view **D** dorsal view; male **E** profile **F** face, frontal view **G** terga, dorsal view **H** genital capsule.

strip, predominantly yellow-marked, and entirely yellow-marked (Fig. 42). Across this gradient there is also variation in the strength of the tergal hair bands, with material nominally conforming to *A. toelgiana* falling closer to *A. limbata* s. str. in displaying clear hair bands, whereas the subspecies *A. limbata dusmeti* Warncke, 1975 (Portugal, Spain, southern France, north-western Italy) has hair bands that are almost absent in fresh specimens (Figs 43C–H, 44A, B, E, F). On the basis of this colour gradient, absence of structural characters, and lack of a described male that could offer a distinctive difference, *A. toelgiana* syn. nov. is synonymised with *A. limbata*.

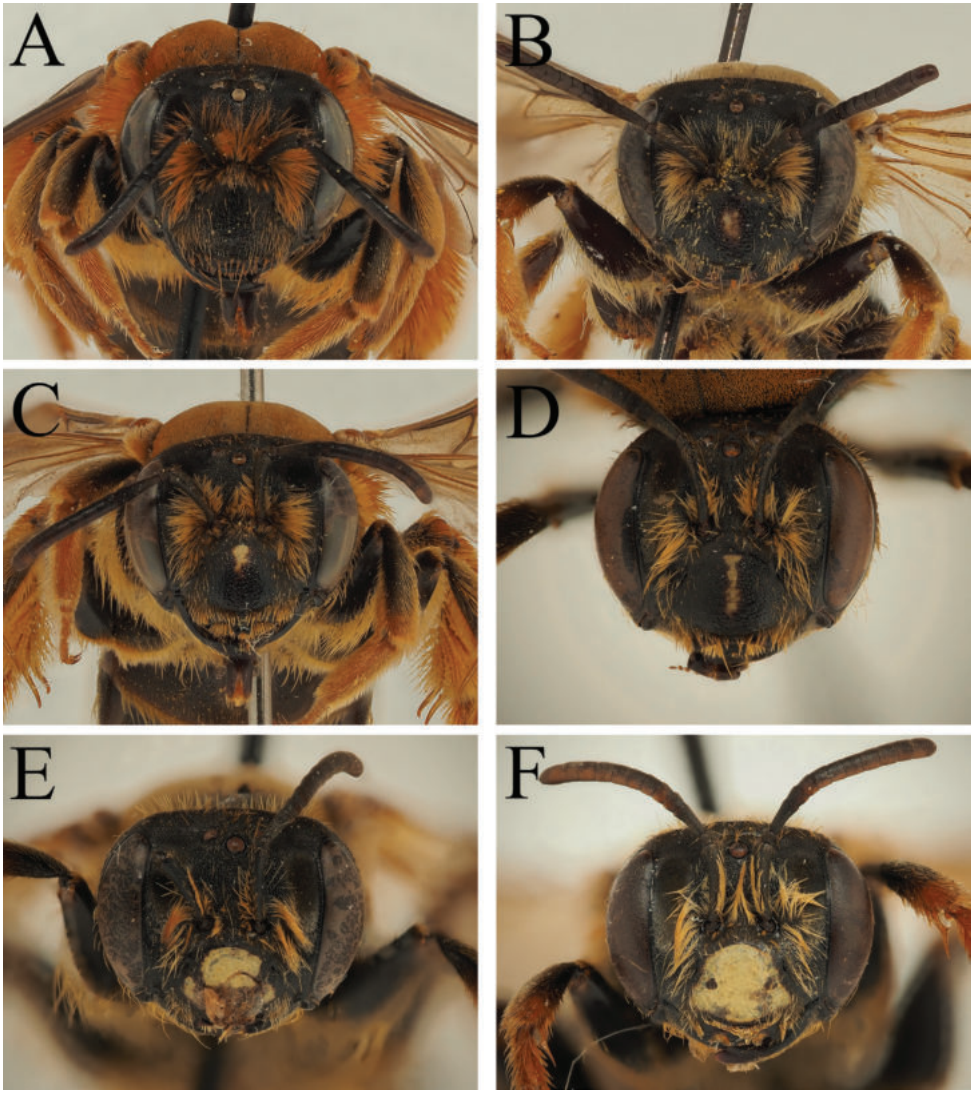

Figure 42. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852 female head in frontal view on west-east gradient **A** Spain **B** Bulgaria **C** Turkey (Gürün) **D** Turkey (Bingöl) **E** Turkey (Bingöl) **F** Turkey (Diyarbakır).

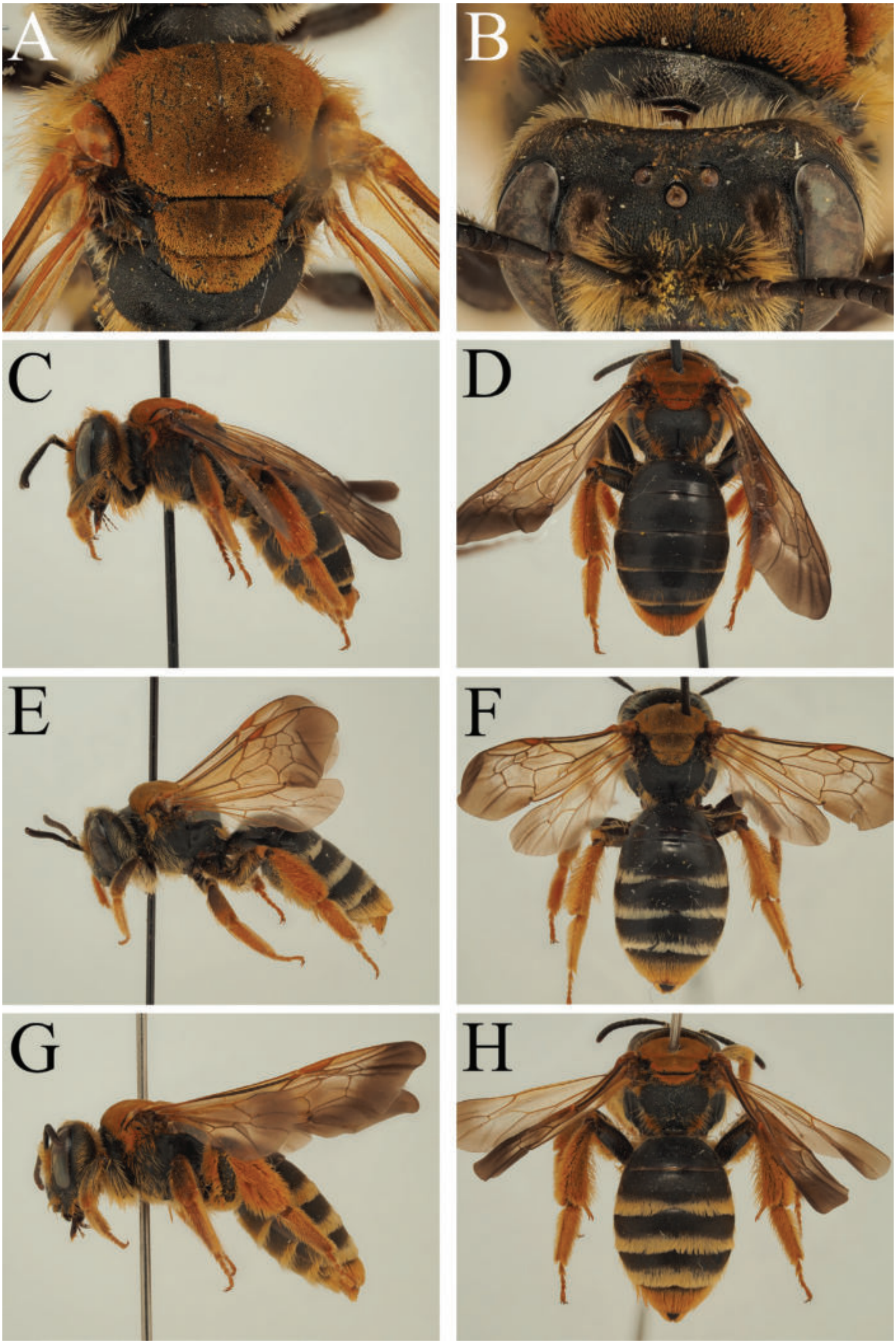

Figure 43. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852, female **A** scutum, dorsal view **B** head, dorso-frontal view; *Andrena limbata dusmeti* Warncke, 1967 female **C** profile **D** terga, dorsal view; *A. limbata* s. str. female, Bulgarian specimen **E** profile **F** terga, dorsal view; *A. limbata* s. str. female, Turkish specimen **G** profile **H** terga, dorsal view.

Diagnosis. *Limbandrena* (and, *de facto*, *A. limbata*) can be recognised in the female sex due to the combination of squamous brown hairs on the scutum, scutellum, and metanotum (Fig. 43A), the long ocelloccipital distance equal to three times the diameter of a lateral ocellus (Fig. 43B), the posterior face of the hind femur which lacks a transverse carina and transverse row of raised teeth or spines, the weakly and shallowly punctate dorsolateral surfaces of the propodeum, the laterally clearly delineated and internally finely rugose propodeal triangle (not rugosely areolate), the pronotum with at most a weak lateral angle, the more or less squarish head which is only 1.1 times wider than long, and the simple hind tibial spur that is not broadened basally or medially.

Males can be recognised by most of the same characters: the yellow clypeus (Fig. 44C, D), the relatively rounded head which is only 1.1–1.2 times broader than long (Fig. 44C, D), the long ocelloccipital distance equal to three times the diameter of a lateral ocellus, the pronotum with at most a weak lateral angle, the weakly and shallowly punctate dorsolateral surfaces of the propodeum, the laterally clearly delineated and internally finely rugose propodeal triangle (not rugosely areolate), and the genital capsule with weakly produced rounded gonocoxal teeth, gonostyli with weakly raised and rounded projection on inner margin, and penis valves with rounded lateral hyaline extensions (Fig. 44G, H). No other *Andrena* species shows this combination of characters.

Description. Medium-sized bees (11–14 mm) with dark integument with exception of yellow maculations on female (sometimes) and male clypeus (always). Head 1.1–1.2 times broader than long, compound eyes with inner margins weakly converging apically. Gena slightly exceeding width of compound eye; ocelloccipital distance long, 3 times diameter of lateral ocellus. Facial fovea moderate, occupying ½ space between lateral ocellus and compound eye. Female scutum, scutellum, and metanotum covered with short brown squamous hairs. Pronotum laterally with weak humeral angle. Dorsolateral surface of propodeum weakly and shallowly but regularly punctate, punctures separated by 0.5–1 puncture diameter. Propodeal triangle clearly delineated laterally by raised carinae, internal surface with clear pattern of fine rugosity medially, not extending over entire area. Forewing with nervulus strongly postfurcal. Hind tibial spurs simple, not broadened basally or medially, apically weakly bent. Terga densely and finely punctate, punctures separated by 0.5 puncture diameters. Male genital capsule slightly elongate, with produced and weakly rounded gonocoxal teeth. Gonostyli with weakly raised and rounded projection on inner margin. Penis valves produced into rounded hyaline extensions laterally, occupying majority of space between gonostyli.

Etymology. The name is taken from the name of the type species *A. limbata*, with *limbata* being the feminine singular of the adjective *limbatus* which means edged or fringed, probably in reference to the distinct squamous hairs on the female scutum and scutellum. The gender is feminine.

Included species. *Andrena limbata* (Europe from Portugal and Spain to Turkey, Israel, northern Iran, and the Ural Mountains; Gusenleitner and Schwarz 2002).

Material examined (illustrative). Albania: Lopan [Lapanj], 14.vi.2018, 2♀, leg. Kobe Janssen collection (Belgium); **Bulgaria:** Lozenec [Lozenets, Лозенец]/Mičurin, 24.vi.1988, 5♀, leg. B. & O. Tkalců, OÖLM; **Croatia:** Istrien, Rovinjsko Selo, 8–9.

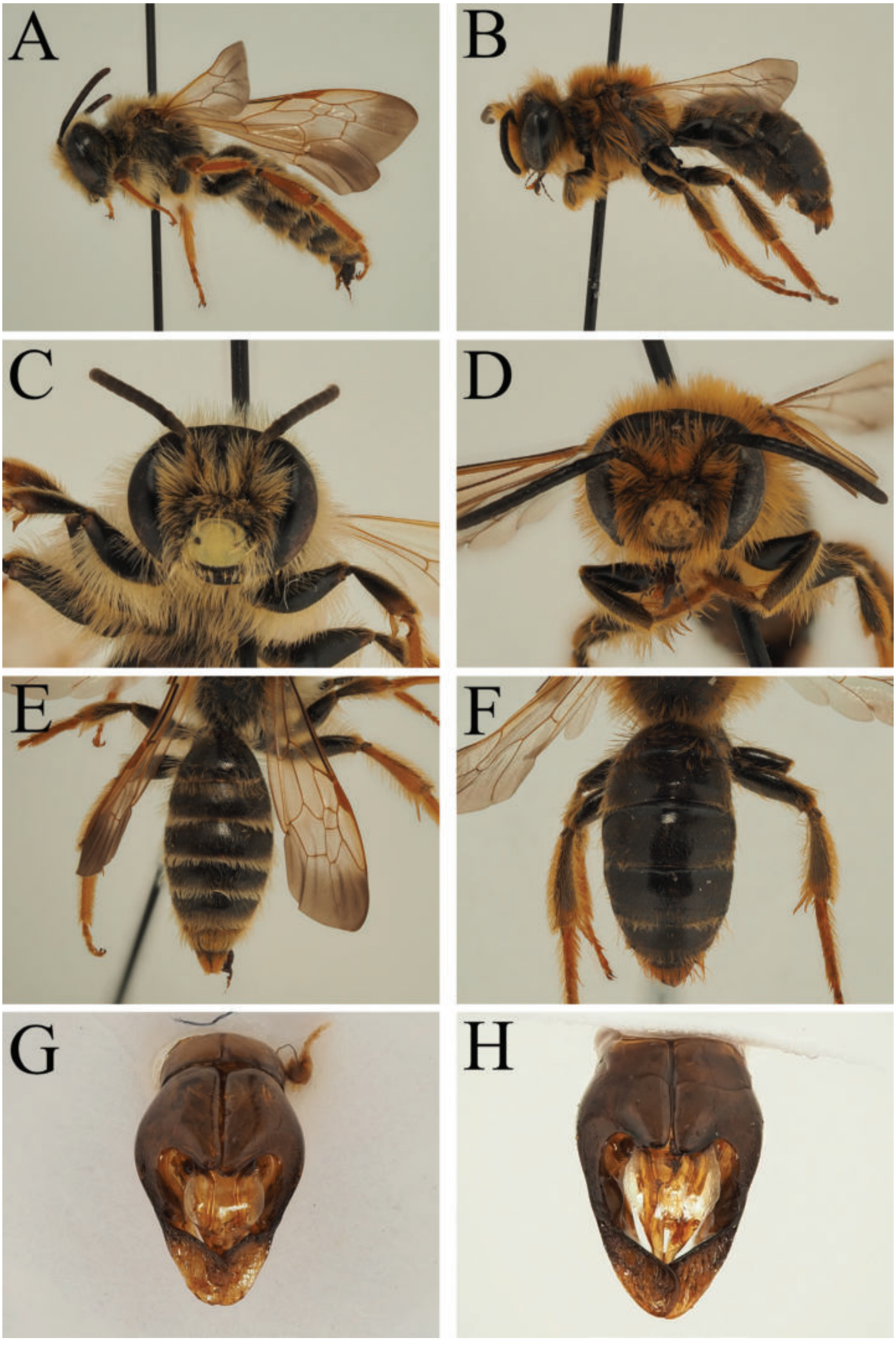

Figure 44. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852, Turkish male **A** profile **C** face, frontal view **E** terga, dorsal view **G** genital capsule; *Andrena limbata dusmeti* Warncke, 1967, Spanish male **B** profile **D** face, frontal view **F** terga, dorsal view **H** genital capsule.

vi.2012, 1♀, leg. Holzmann, OÖLM; **France:** B. d. R., Fontvieille, 28.v.1993, 4♀, leg. H. & J.E. Wiering, RMNH; **Georgia:** E Tbilisi, lori river S Sagarejo, 19.vi.2015, 3♀, leg. M. Snižek, OÖLM; **Greece:** Kos I. Kefalos, 4.v.1989, 2♀, leg. K.M. Guichard, NHMUK; Peloponnese, 12 km NWW Sparti, 26.v.2005, 1♀, leg. M. Kadlecová, OÖLM; **Italy:** Arezzo, Oliveto, 28.v.1989, 3♀, leg. H. & J.E. Wiering, RMNH; Piemonte, S. Benefetto Belbo, 10.vi.1979, 1♀, leg. Pagliano, MRSN; **Portugal:** Manteigas, Serra da Estrela [40.4009°N, -7.5396°E], 28.iv.–9.vii.1929, 1♀, leg. Kricheldorf, OÖLM (holotype of *A. limbata dusmeti*); **Spain:** Segovia, Madrona, 500 m NE, Arroyo del Hocino, 15.v.2021, 1♂, 2♀, leg. T.J. Wood, TJWC; Ávila, Hoyocasero, 1350 m, 20.v.1995, 1♂, 2♀, leg. H. & J.E. Wiering, RMNH; **Turkey:** Tanin-Tanin-Pass, 1700 m, 12.vi.1984, 1♀, OÖLM; Karatepe/Adana, 17.iv.1984, 3♂, 1♀, leg. K. Warncke, OÖLM; Akyaka, Yeşilova, 20.vi.2016, 1♀, leg. M. Kasparek, OÖLM.

Subgenus *Ovandrena* subgen. nov.

https://zoobank.org/A122C278-C33D-4790-A34A-FC270AE6A962

Type species. *Andrena oviventris* Pérez, 1895.

Diagnosis. Through the combination of slightly upturned fore margin of the clypeus, broad fovea occupying at least ½ the space between the lateral ocellus and the inner margin of the compound eye, weak but distinct humeral angle, unmodified posterior face of the hind femur (without teeth, carinae, or spines), simple hind tibial spur (not broadened basally or medially), dark integument, black male clypeus, and essential absence of defining features it falls very close to members of the *relata*-group and to *Blandandrena* that were formerly lumped together under the subgenus *Poliandrena* (see above).

In the female sex, *Ovandrena* species differ from these groups by only a single major character: the structure of the propodeal triangle (Fig. 45A, B). *Ovandrena* species have scutal hairs that are not as short and clearly squamous as in members of the *Aenandrena*, *Limbandrena*, or *Lepidandrena* Hedicke, 1933, but they are partially squamous in some species (Fig. 45C, D), whereas the scutal hairs in the *relata*-group and *Blandandrena* are typically simple, though in some species such as *A. corax* the hairs can be semi-squamous. The structure of the propodeal triangle is therefore the only character that allows consistent separation. In *Ovandrena*, the propodeal triangle is a broad and well-defined triangle (lateral margins extending almost to the lateral edges of the metanotum) that is defined by raised carinae; the internal surface is covered in raised irregular carinae of a similar width, therefore appearing homogenous and consistent (Fig. 45A, B). In the *relata*-group and *Blandandrena*, the propodeal triangle varies from smooth and undefined to weakly defined with at most irregular rugosity on its internal surface, but never approaches the condition in *Ovandrena*. The combination of these two characters therefore always allows recognition. They can also be partially recognised by the extremely dense and fine punctation of the terga, punctures separated by <0.5 puncture diameters; in comparison groups, the punctures are never this fine or this dense.

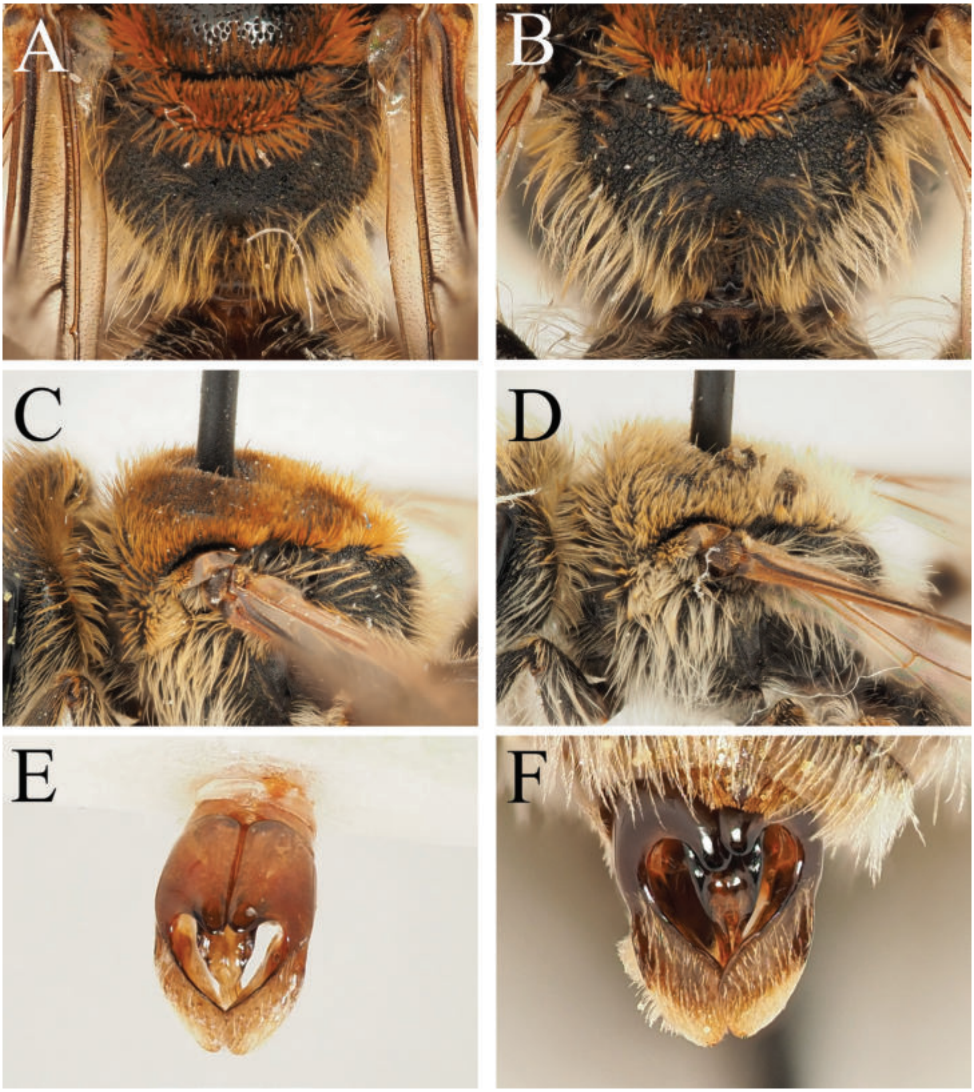

Figure 45. *Andrena* (*Ovandrena*) subgen. nov. characters. *Andrena* (*Ovandrena*) *marsae* Schmiedeknecht, 1900, female **A** propodeal triangle; *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895 **B** female propodeal triangle **C** female scutal hairs, profile view **F** male genital capsule; *Andrena* (*Ovandrena*) *farinosa* Pérez, 1895 **D** female scutal hairs, profile view **E** male genital capsule.

Males can be recognised through their combination of dark clypeus with upturned fore margin, distinctive propodeal triangle as in the female sex, pronotum with weak or strong humeral angle, A3 exceeding A4 but shorter than A4+5, and genital capsule which is compact with pronounced and rounded gonocoxal teeth (Fig. 45E, F). Members of the *relata*-group often have a yellow-marked clypeus, but for species showing a dark clypeus (e.g. *A. corax*), the clearly defined triangular propodeal triangle allows separation (smooth to at most weakly defined in the *relata*-group). Separation can be made from *Blandandrena* by the genital capsule and the propodeal triangle, as detailed in the diagnosis section for that subgenus.

Description. Small to moderately sized bees (7–11 mm) typically with dark integument, one species with red tergal markings; male clypeus always dark. Head broad, 1.3–1.4 times broader than long, compound eyes with inner margins weakly converging apically. Gena slightly exceeding width of compound eye; ocelloccipital distance short, slightly less than to slightly more than diameter of lateral ocellus. Facial fovea moderately broad, occupying ½ distance between lateral ocellus and compound eye. Female scutum, scutellum, and metanotum covered with shortish light brown to whitish semi-squamous hairs (Fig. 45C, D). Pronotum laterally with weak to strong humeral angle. Dorsolateral surface of propodeum with regular and dense network of raised reticulation; propodeal triangle wide, lateral margins extending almost to lateral edges of metanotum, laterally defined by straight raised carinae, thus strongly triangular (Fig. 45A, B). Internal surface of propodeum covered by raised irregular carinae of a similar width, therefore homogenous and consistent. Forewing with nervulus interstitial to weakly antefurcal. Hind tibial spurs simple, not broadened basally or medially. Terga densely punctate, in females punctures extremely dense and fine, separated by <0.5 puncture diameters, in males punctures slightly sparser and coarser, separated by 0.5–1 puncture diameters. Male genital capsule compact, consistent across species, with gonocoxae strongly produced into apical rounded teeth (Fig. 45E, F). Gonostyli apically spatulate, with a more or less strongly raised inner margin. Penis valves basally narrow or moderately broad, in both cases becoming narrow medially.

Etymology. The name is taken from the type species for the genus, *A. oviventris*. It derives from the Latin *ovum* meaning egg, in reference to the egg-shaped metasoma. The gender is feminine.

Included species. *Andrena farinosa* Pérez, 1895 (Spain and France), *Andrena farinosoides* Wood, 2020 (Morocco), *Andrena marsae* Schmiedeknecht, 1900 (Morocco, Algeria, Tunisia), and *Andrena oviventris* (Morocco, Algeria, Portugal, Spain, France). The subgenus is therefore currently restricted to the Western Mediterranean, and the centre of diversity is Morocco. The status of *A.* (incertae sedis) *inusitata* Pisanty, 2022 must be resolved through genetic analysis (see Pisanty et al. 2022a).

Material examined. *Andrena oviventris*: Algeria: Teniet el Had [35.8727°N, 2.0007°E], 1♀, MNHN (lectotype; Fig. 46).

***Andrena farinosa*: Spain:** Murcie [Murcia], 1♀, MNHN (lectotype).

Identification key to subgenus *Ovandrena* subgen. nov.

1 Females..**2**
– Males[1]..**5**

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[1] Note, males of these four species are extremely similar, and great care must be taken when separating them. Association with females should be made, as well as reference to their known biogeographical distributions and to confidently determined reference material.

2 Terga almost entirely red-marked, with at most slight black marks basally on T1 and two black spots laterally on T2 (north-western Africa) .... ***marsae* Schmiedeknecht**

– Terga dark, without red markings **3**

3 Scutum less densely punctate, punctures separated by at least 1 puncture diameter, surface clearly smooth and shiny between punctures (Morocco) .... ***farinosoides* Wood**

– Scutum densely punctate, punctures separated by 0.5 puncture diameters to confluent, narrow interspaces shiny **4**

4 Tergal discs glabrous, with hairs restricted to marginal areas. Larger, 10–11 mm (north-western Africa and south-western Europe).................. ***oviventris* Pérez**

– Tergal discs extensively covered with extremely short hairs, forming a velvety pubescence in addition to denser and longer hairs on tergal margins. Smaller, 8–9 mm (Spain and France only) .... ***farinosa* Pérez**

5 Larger, 9–10 mm. Tongue with outer surface of galea clearly punctate, punctures separated by 1–2 puncture diameters. Sterna with weak and sparse fringes on apical margins. Tergal punctation comparatively larger and coarser (north-western Africa and south-western Europe) .... ***oviventris* Pérez**

– Smaller, 7–8 mm. Tongue with outer surface of galea more or less smooth and shiny, without obvious punctures. Sterna with strong and dense fringes on apical margins. Tergal punctation comparatively fine **6**

6 Clypeus comparatively less densely punctate, punctures separated by 0.5–1 puncture diameters, with shiny interspaces, thus appearing shiny. Pronotum with humeral angle comparatively strong (Spain and France only) .... ***farinosa* Pérez**

– Clypeus comparatively more densely punctate, punctures separated by 0.5 puncture diameters, interspaces dull, thus appearing dull (north-western Africa) **7**

7 Viewed laterally and ventrally, tergal margins, ventrolateral parts of terga, and sternal margins usually lightened reddish orange-brown (north-western Africa)[2] .... ***marsae***

– Tergal and sternal margins dark to hyaline, never extensively lightened reddish orange-brown (Morocco only)[2] .... ***farinosoides***

Subgenus *Pruinosandrena* subgen. nov.

https://zoobank.org/62A1E8AF-01AD-4D69-8CD5-E20843A286D5

Type species. *Andrena pruinosa* Erichson, 1835.

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[2] These two species are almost identical in the male sex, and no structural characters are currently apparent.

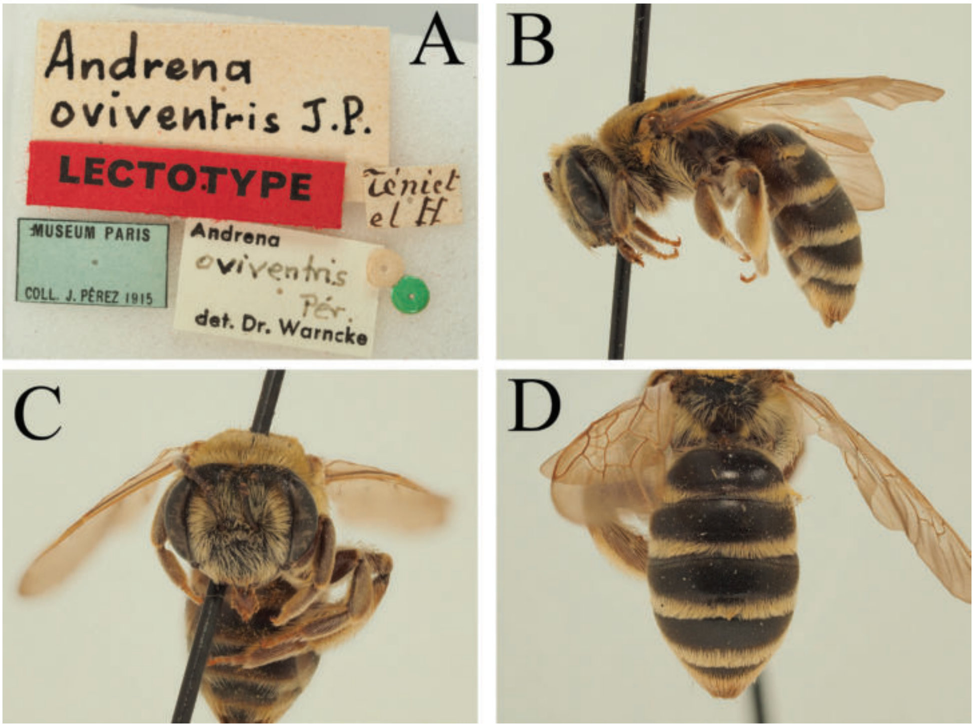

Figure 46. *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

Diagnosis. This group of species was formerly placed in the subgenus *Campylogaster* due to the unusual character of the strongly and densely punctate mesepisternum and dorsolateral parts of the propodeum (punctures separated by <0.5 puncture diameters). However, as discussed above, *Campylogaster* sensu Warncke is polyphyletic and can be broken into three distinct clades (*Campylogaster* s. str., *Pruinosandrena*, and the *incisa*-group). All three share the distinctly punctate mesepisternum and also an extremely long ocelloccipital distance exceeding three times the diameter of the lateral ocellus. However, separation is straightforward. The true *Campylogaster* have the marginal area of the terga clearly and distinctly impressed with the apical margin reflexed; the impression therefore forms a latitudinal depressed furrow. In *Pruinosandrena*, the marginal areas of the terga are flat, without any kind of depression. In the *incisa*-group, the tergal margins are flat and the mesepisternum is densely punctate, but the dorsolateral parts of the propodeum have only raised reticulation, without punctures. The propodeal triangle is also clearly delineated by raised lateral carinae, whereas these are absent in *Pruinosandrena*. The combination of extremely long ocelloccipital distance, dense punctures on the mesepisternum and dorsolateral parts of the propodeum, and flat tergal marginal areas is therefore unique and characterises *Pruinosandrena*.

Description. Medium-sized bees (10–14 mm). Integument variable, from dark with at most tergal margins lightened hyaline-yellow to entirety of metasoma and legs red-marked; male clypeus yellow-marked in one species. Head moderately broad, 1.2 times broader than long. Gena broad, exceeding width of compound eye; ocelloccipital distance extremely long, at least 3 times diameter of lateral ocellus. Facial fovea variable, from narrow to occupying entirety of distance between lateral ocellus and inner margin of compound eye. Female scutum, scutellum, and metanotum with pubescence variable, in some species with extremely short squamous hairs, hairs longer and non-squamous in other species. Pronotum laterally with humeral angle. Mesepisternum and dorsolateral parts of propodeum densely and clearly punctate, punctures confluent to separated by <0.5 puncture diameters. Propodeal triangle without lateral carinae, internal surface with dense network of irregularly raised rugosity, thus contrasting punctate dorsolateral surface. Forewing with nervulus interstitial. Hind tibial spurs simple, not broadened basally or medially. Terga typically densely and finely punctate, punctures separated by 1 puncture diameter, at least on T2–5. Male genital capsule simple, compact, with gonocoxae apically truncate to produced into weak rounded teeth. Gonostyli apically spatulate, penis valves more or less narrow, parallel-sided, occupying less than ½ space between gonostyli.

Etymology. The name is taken from the type species for the subgenus, *A. pruinosa*. The Latin word *pruinosa* is the feminine singular of *pruinosus* which means 'frosty', in reference to the squamous hairs of the mesosoma. The gender is feminine.

Included species. *Andrena caroli* (Morocco to Israel); *Andrena nilotica* Warncke, 1967 (Spain); *Andrena parata* (Spain); *Andrena pruinosa* (Spain); *Andrena sparsipunctata* Wood, 2020 (Morocco); *Andrena succinea* (Morocco to Iran and Saudi Arabia). The centre of diversity is therefore Spain + Morocco, with all six species occurring here.

Identification key to subgenus *Pruinosandrena* subgen. nov.

Note, the male of *A. sparsipunctata* is unknown. The males described by Wood et al. (2020b) are actually misidentified *A. mediovittata* Pérez, 1895; *A. sparsipunctata* is expected to be restricted to south-western Morocco. See Wood et al. (2020b) for additional useful images.

1 Females..**2**

– Males...**7**

2 In dorsal view, fovea broad, clearly occupying more than half of the distance between the lateral ocellus and the compound eye (Fig. 37C). Terga with strong apical pale hair bands that uniformly cover the entirety of the tergal depressions and obscure the underlying surface (Figs 37D, 38D; North Africa to Israel).. ***caroli* Pérez**

– Fovea narrow, occupying at most half the distance between the lateral ocellus and the compound eye (Figs 33B, 36C). Terga with or without clear hair bands; if with hair bands, then hair bands typically do not uniformly cover the tergal depressions, either weaker basally or stronger apically **3**

3 T1 with extremely sparse punctures, punctures separated by 2–4 puncture diameters. Facial fovea along its entire length separated from the inner margin of the compound eye by a distance equal to its own diameter (south-western Morocco only) .... ***sparsipunctata* Wood**

– T1 with dense punctures, punctures separated at most by 2 puncture diameters, usually by 1 puncture diameter (Fig. 59D). Fovea not strongly separated from the inner margin of the compound eye...................................**4**

4 Pubescence of scutum weakly squamous, anterior dorsolateral corners of scutum with pubescence longer, clearly exceeding width of antennae in length. Terga always predominantly red. Terga with clear apical hair bands. Punctation of T1 slightly spaced, punctures separated by 1–2 puncture diameters (eastern and south-eastern Spain only) .... ***nilotica* Warncke**

– Pubescence of scutum strongly squamous and short, anterior dorsolateral corners of scutum with pubescence short, clearly shorter than width of antennae (Figs 33C, 59C). Terga variable, red to black or any intermediate combination. Terga with or without clear apical hair bands. Punctation of T1 denser, punctures separated at most by 1 puncture diameter **5**

5 A3 exceeding A4+5 in length. Terga always extensively red-marked (central and south-eastern Spain)..***parata* Warncke**

– A3 equalling A4+5 in length. Terga variable, from almost entirely black to entirely red-marked...**6**

6 Terga usually predominantly dark (Figs 33D, 36D). Found in Spain ....***pruinosa* Erichson**

– Terga always extensively or entirely red-marked (Figs 35D, 59D). Found outside of Spain .... ***succinea* Dours**

7 Clypeus at least partly yellow-marked (North Africa to the Middle East).... .... ***succinea* Dours**

– Clypeus uniformly dark **8**

8 A3 very short, shorter than A4 (North Africa to Israel) .... ***caroli* Pérez**

– A3 at least slightly longer than A4...**9**

9 A3 exceeding A4+5 in length (central and south-eastern Spain) ....***parata* Warncke**

– A3 not exceeding A4+5 ....**10**

10 Genital capsule without clear kink in the inner margins of the gonostyli (Fig. 85E). Scutum less densely punctate, punctures separated by 0.5 puncture diameters, with shiny interspaces, predominantly shiny (eastern and south-eastern Spain only)... ***nilotica* Warncke**

– Genital capsule with clear kink in the inner margins of the gonostyli (Fig. 85F). Scutum more densely punctate, punctures almost confluent, predominantly dull (central and southern Spain) ....***pruinosa* Erichson**

Description of new species

Andrena (*Avandrena*) *juliae* Wood, sp. nov.

https://zoobank.org/C53C51E7-AA4A-43A1-85CC-6C4862ED1D19

Type material. ***Holotype*. Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 36.3273°N, -5.5986°W, 18.iii.2023, 1♀, leg. T.J. Wood, OÖLM.

***Paratypes*. Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 1♀, leg. T.J. Wood, TJWC; Cádiz, Tarifa, 1 km N, grazing fields, 23.iii.2023, 1♀, leg. T.J. Wood, OÖLM.

Description. Female. Body length: 9 mm (Fig. 47A). ***Head*:** Dark, 1.4 times wider than long (Fig. 47B). Clypeus weakly domed, with fine granular shagreen, dull, overlain by weak raised rugosity, rugosity forming weak, obscure, and interrupted raised latitudinal striations; remaining surface impunctate. Process of labrum rounded rectangular, twice as broad as long, surface smooth and shiny. Gena equalling width of compound eye; ocelloccipital distance equals diameter of lateral ocellus. Foveae moderately broad, occupying half space between compound eye and lateral ocellus, short, ventrally extending to level of antennal insertions; foveae filled with black hairs (Fig. 47C). Face medially with light brown-white hairs covering clypeus and antennal insertions, intermixing with black hairs, becoming entirely black haired along inner margin of compound eyes and frons; gena and vertex with long light brown hairs, longest hairs equalling length of scape. Antennae dark, A7–12 ventrally slightly lightened grey by presence of scales; A3 equalling A4+5+6. ***Mesosoma*:** Scutum and scutellum with fine granular shagreen, very weakly shiny, predominantly dull, underlying surface shallowly and obscurely punctate, punctures separated by 1–2 puncture diameters (Fig. 47D). Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum with fine granular shagreen, predominantly dull, shagreenation overlain by fine network of raised rugosity, not forming a linked network. Propodeal triangle short and broad, slightly depressed below level of dorsolateral parts of propodeum, with extremely fine granular shagreen, basal 2/3rds covered with raised longitudinal rugae, propodeal triangle thus strongly contrasting dorsolateral parts of propodeum (Fig. 47E). Mesepisternum with long strongly plumose hairs, hairs predominantly pale with some intermixed black hairs, hairs clearly exceeding length of scape. Scutum and scutellum with strongly plumose light brown hairs, intermixed with black hairs medially. Propodeum with long strongly plumose light brown hairs, propodeal corbicula incomplete, dorsal fringe weak and poorly defined, internal surface with numerous pale simple hairs. Legs dark, tarsi obscurely lightened reddish brown; pubescence light brown. Flocculus complete, strong, composed of strongly plumose light brown hairs; femoral and tibial scopa composed of light brown simple hairs. Hind tibial claws with strong inner tooth. Wings hyaline, stigma and venation dark orange, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas narrowly lightened hyaline-yellow (Fig. 47F). Tergal discs with scattered and small hair-bearing punctures, punctures separated by 3–4 puncture diameters, underlying surface finely shagreened, silky smooth, shiny. Tergal discs with

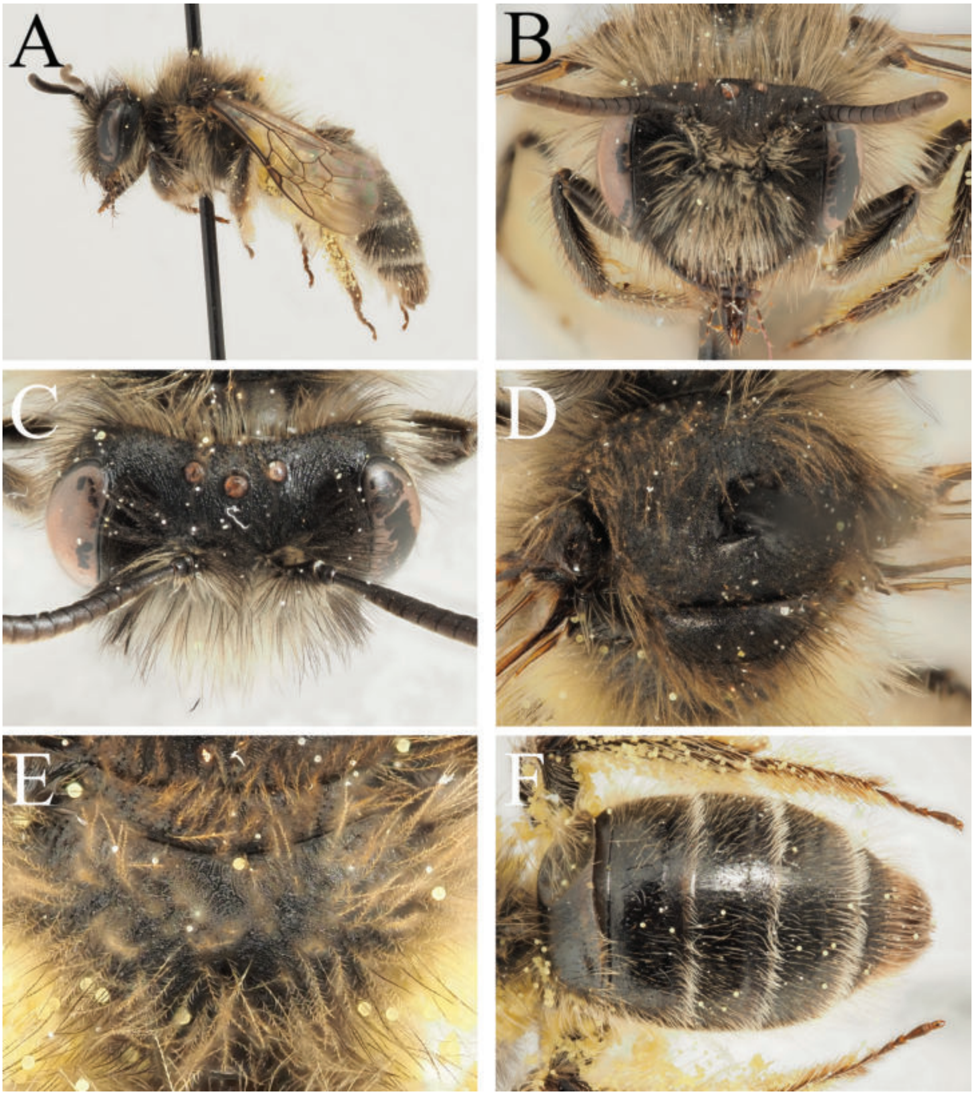

Figure 47. *Andrena* (*Avandrena*) *juliae* sp. nov. female **A** profile **B** face, frontal view **C** head, dorsal view **D** scutum, dorsal view **E** propodeum, dorsal view **F** terga, dorsal view.

sparse upstanding pale hair, T2–4 with dense apical whitish hair bands that obscure underlying surface. Apical fringe of T5 and hairs flanking pygidial plate dark brown; pygidial plate apically rounded, surface flat and featureless.

Male. Unknown.

Diagnosis. *Andrena juliae* can be recognised as belonging to the subgenus *Avandrena* due to its moderate to small body size (9 mm), short and wide head (clearly wider than long), and short and wide foveae that are only slightly longer than wide, as well as the behavioural observation that it is strongly associated with *Erodium* (Geranicaceae, see Remarks). The posterior face of the hind femora lacks spines, separating the species from *A. avara* Warncke, 1967 and *A. panurgina* De Steffani, 1889 and placing it close to *A. melacana* Warncke, 1967 and *A. erodiorum* Wood & Ortiz-Sánchez, 2022.

Andrena juliae can be separated from both species by the structure of the propodeum which has the dorsolateral parts with fine granular shagreenation that is overlain by a fine network of raised rugosity, this rugosity not forming a linked network. The propodeal triangle itself is clearly differentiated, slightly depressed below the level of the surrounding parts of the propodeum and delineated by fine carinae, the surface with fine granular shagreenation and with a network of raised longitudinal carinae covering the basal 2/3rds. In contrast, *A. erodiorum* has the dorsolateral parts of the propodeum shiny, overlain with a fine network of raised rugosity that joins together to form a clear network (Fig. 73E). The propodeal triangle is clearly delinated by raised carinae and with the entire surface covered with longitudinal carinae. In *A. melacana*, the dorsolateral parts of the propodeum are entirely covered with fine granular shagreen, without an overlay of raised rugosity, with the propodeal triangle not depressed and with even finer granular shagreen, not strongly differentiated from the surrounding areas.

The propodeum of *A. juliae* therefore sits between both comparison species and is distinct from both. It can be further separated by the pubescence of the mesepisternum which is predominantly composed of pale hairs, with approximately 30% of these hairs black (in *A. melacana* with 50–60% of the hairs of the mesepisternum black; in *A. erodiorum* with only 10% of these hairs black), by the facial foveae which occupy half of the space between the compound eye and a lateral ocellus (occupying ¾ of this space in *A. erodiorum*), by the colour of the hairs of the apical fringe of T5 and those flanking the pygidial plate which are dark brown (golden-brown in *A. erodiorum*, dark brown in *A. melacana*), and by the pubescence of the terga which are covered in sparse erect white hairs, T2–4 with dense apical hair bands of white hairs that obscure the underlying surface (in *A. melacana* terga with sparse short pubescence, only forming weak apical tergal hair bands that do not obscure the underlying surface; pubescence very similar in *A. erodiorum*).

Remarks. All specimens were collected from *Erodium* spp. The two females from Las Algamitas were collecting pollen from this genus (*Erodium* pollen can be seen in Fig. 47A). Across sampling locations in Cádiz province during March 2023, four species of *Avandrena* were active, specifically *A. avara* sensu stricto, *A. juliae*, *A. melacana*, and *A. panurgina*. All species appear to be narrowly oligolectic on *Erodium* (see below), and *A. juliae* could be found in direct sympatry with *A. avara* sensu stricto, *A. melacana*, and *A. panurgina* at the Las Algamitas site and with *A. melacana* and *A. panurgina* at the Tarifa site. *Andrena erodiorum* is currently known only from south-eastern Spain (Albacete). One *A. juliae* female showed abraded body hairs, and no males were captured, implying that the flight season may begin in early March or even late February, perhaps offering a reason as to why this species has been overlooked until now.

Etymology. Dedicated to my friend and colleague Julia Jones (University College Dublin, Ireland) who invited me on the University field course during which this new species was discovered.

Distribution. Spain (Cádiz province).

Other material examined. ***Andrena avara* s. str.: Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 1♀, leg. T.J. Wood, TJWC; Cádiz, Bolonia, El Lentiscal, 24.iii.2023, 1♀, leg. T.J. Wood, TJWC.

***Andrena melacana*: Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 3♂, 2♀, leg. T.J. Wood, TJWC; Cádiz, Tarifa, 1 km N, grazing fields, 19.iii.2023, 4♂, 6♀, leg. T.J. Wood, TJWC.

***Andrena panurgina*: Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 4♂, 3♀, leg. T.J. Wood, TJWC; Cádiz, Tarifa, 1 km N, grazing fields, 19–23.iii.2023, 6♂, 2♀, leg. T.J. Wood, TJWC.

Andrena (*Euandrena*) *isolata* Wood, sp. nov.

https://zoobank.org/08390D0E-AC36-4859-AE7E-BDD126D34BB8

Type material. ***Holotype.* Spain:** Granada, Sierra Nevada, Trevélez to Refugio La Campiñuela, 37.0239°N, -3.2656°W, 1700–2400 m, 14.vi.2021, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW368-21].

Description. Female. Body length: 9.5 mm (Fig. 48A). ***Head*:** Dark, 1.2 times wider than long (Fig. 48B). Clypeus weakly domed, densely and evenly punctate,

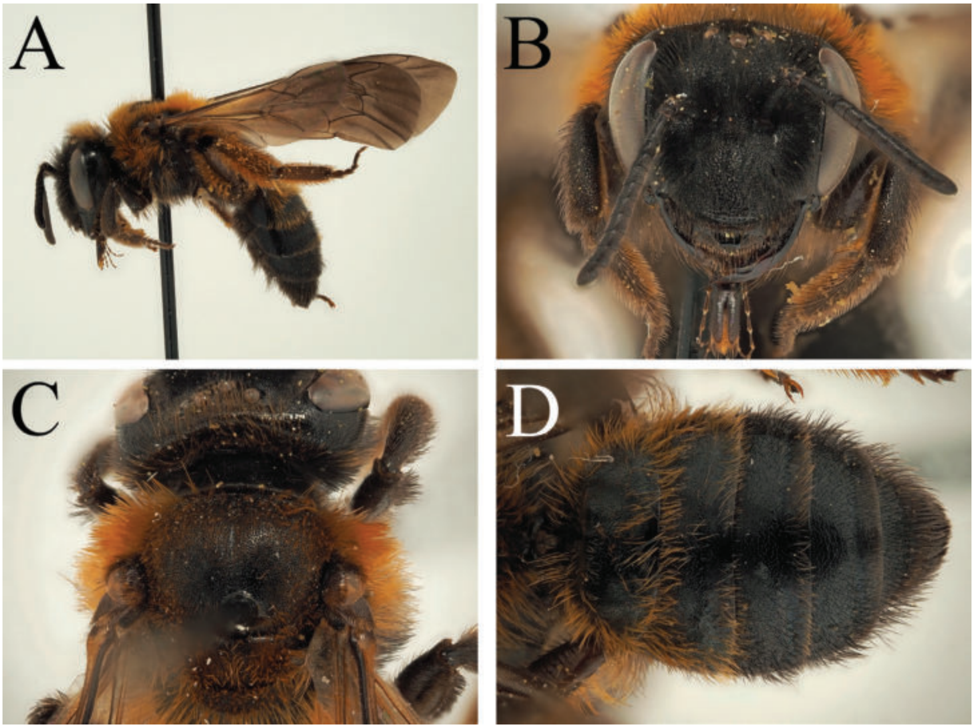

Figure 48. *Andrena* (*Euandrena*) *isolata* sp. nov. female **A** profile **B** face, frontal view **C** scutum, dorsal view **D** terga, dorsal view.

punctures separated by <0.5 puncture diameters, interspaces shiny. Process of labrum trapezoidal, twice as broad as long, apical margin with very weak emargination medially. Gena slightly exceeding width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus; vertex behind ocellar triangle densely punctate, punctures separated by 0.5 puncture diameters. Fovea dorsally narrow, occupying ⅓ of space between lateral ocellus and compound eye, ventrally reaching level of antennal insertions, here narrowing to ½ dorsal width; fovea filled with black hairs. Face, gena, and scape covered with uniformly short black hairs, vertex dorsally with predominantly golden-brown hairs with scattered intermixed black hairs. Antennae dark, A3 slightly exceeding A4+5, shorter than A4+5+6. ***Mesosoma*:** Scutum and scutellum densely punctate, punctures predominantly separated by <0.5 puncture diameters, at most by 1 puncture diameter medially, underlying surface finely shagreened and weakly shiny (Fig. 48C). Pronotum rounded. Mesepisternum microreticulate, weakly shiny to dull, with obscure raised reticulation. Dorsolateral parts of propodeum microreticulate, weakly shiny, densely and shallowly punctate, punctures separated by 0.5–1 puncture diameter. Propodeal triangle narrow, internal surface finely granulate and impunctate, basally with obscurely and weakly raised rugosity, propodeal triangle thus strongly contrasting punctate dorsolateral parts of propodeum. Mesepisternum ventrally with moderately long black hairs, becoming intermixed with golden-brown hairs medially, with entirely golden-brown hairs dorsally, hairs at most equalling length of scape. Scutum and scutellum dorsally with short golden-brown hairs, scutum medially with very short and obscure black hairs. Propodeum with long golden-brown hairs, propodeal corbicula incomplete, dorsal fringe composed of long plumose golden-brown hairs, internal surface with numerous plumose light hairs, becoming darker ventrally. Legs predominantly dark, hind femorae ventrally and posterior face of hind tibiae obscurely lightened reddish-orange; pubescence black to orange-brown. Flocculus incomplete, short, composed of weakly plumose orange hairs; femoral and tibial scopa orange, tibial scopa with at most occasional brown hairs dorso-basally. Hind tibial claws with strong inner tooth. Wings weakly infuscate, stigma and venation dark brown, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas very narrowly lightened hyaline-brown (Fig. 48D). Tergal discs regularly punctate, punctures separated by 1–2 puncture diameters, underlying surface shagreened, weakly shiny; punctures extending onto marginal areas, here weak and obscure, separated by 2–3 puncture diameters. T1–2 with orange-brown hairs basally, laterally, and apically; T2–3 with orange-brown hairs forming weak apical hair bands, not obscuring underlying surface, T4 with weak apical hair band black; discs of T3–4 with short black hairs. Apical fringe of T5 and hairs flanking pygidial plate black; pygidial plate rounded triangular, with slightly depressed and densely punctate area medially, lateral margins impunctate.

Male. Unknown.

Diagnosis. *Andrena isolata* can be quickly recognised as a *Euandrena* due to the narrow facial foveae (dorsally occupying ⅓ of space between the lateral ocellus and the compound eye) which narrow further ventrally combined with the long A3 (slightly exceeding length of A4+5) and the simple, non-plumose hairs of the tibial scopae. Its generally dark appearance with orange-brown hairs dorsally on the mesosoma and tibial scopa plus at least some black hairs on the mesepisternum place it immediately close to *A. bicolor* and allied taxa. As discussed above, the subgenus *Euandrena* is taxonomically complex, and multiple genetically distinct taxa have been lumped under *A. bicolor*. In an Iberian context, *A. isolata* is best diagnosed against *A. bicolor* s.l., *A. fortipunctata* Wood, 2021, and the distinct and probably undescribed taxon in north-western Africa identified above. Extreme care should be taken when identifying specimens morphologically, and barcodes should be used whenever possible.

In direct comparison to barcoded *A. bicolor* s.l. specimens, the only consistent character that can be identified is the structure of the clypeus. *Andrena isolata* has the clypeus densely punctate, with punctures separated by <0.5 puncture diameters, interspaces shiny but overall the clypeus only weakly shiny due to the small size of the interspaces (Fig. 48B). In *A. bicolor* s.l., the clypeal punctures are separated by an average of at least 1 puncture diameter, sometimes more, and the clypeus is therefore more strongly shiny due to the larger interspaces. The dense clypeal punctures place *A. isolata* close to *A. fortipunctata*, but the two species can be separated by the tergal structure (see illustrations in Wood et al. 2021), with the tergal margins weakly depressed with at most the apical rim lightened hyaline yellow (tergal margins strongly depressed and extensively lightened semi-translucent brown in *A. fortipunctata*), terga punctate with some punctures extending onto tergal margins, here separated by 2–3 puncture diameters (tergal margins impunctate in *A. fortipunctata*), margins of T2–3 with weak light brown hair fringes apically, T4 with entirely black hairs (T2–4 with white hair fringes emerging from junction between disc and margin, these hair fringes overlying marginal areas in *A. fortipunctata*), terminal fringe of T5 and hairs flanking pygidial plate black (terminal fringe and hairs flanking pygidial plate dark brown in *A. fortipunctata*). *Andrena isolata* is almost identical to the probably undescribed taxon from north-western Africa, but can also be separated by the structure of the clypeus. *Andrena isolata* has the clypeus densely punctate with punctures separated by <0.5 puncture diameters and with the interspaces shiny, whereas in the taxon from north-western Africa, the punctures are equally dense but the interspaces are shagreened and dull. Furthermore, this latter taxon has a short and shallow longitudinal furrow at the apex of the clypeus that is absent in *A. isolata*.

Remarks. *Andrena isolata* probably represents a relictual species that has become isolated on the Sierra Nevada from what is now a remaining North African population. Additional genetic sampling is needed to establish whether it is found away from the Sierra Nevada, but a specimen from the nearby Sierra de Baza collected at an altitude of 2000 m barcoded as *A. bicolor* s.l. [WPATW297-21]. *Andrena isolata* may well be restricted to the Sierra Nevada. Additional sampling is required to establish its ecology, including its voltinism. Its capture on *Campanula* implies that it has a similar ecology to *A. bicolor* s.l. (see Praz et al. 2019), but this requires dedicated study.

Etymology. Derived from the Latin *insulatus*, to be made into an island, *isolata* (feminine form) thus means to be isolated, in reference to its presence on the Sierra Nevada, separated from its nearest genetic relative in North Africa.

Distribution. Spain (Sierra Nevada).

Andrena (*Micrandrena*) *ortizi* Wood, sp. nov.

https://zoobank.org/F6956353-0278-4AE3-8C48-4084EDC29CCC

Type material. ***Holotype*.** **Spain:** Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 37.1239°N, -3.4322°W, 2100 m, 6.vi.2021, 1♀, leg. T.J. Wood, on *Vella spinosa* (Brassicaceae), OÖLM [BOLD accession number WPATW972-22].

***Paratypes*.** **Spain:** Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 2100 m, 6.vi.2021, 2♀, leg. T.J. Wood, on *Vella spinosa* (Brassicaceae), OÖLM/TJWC; Granada, Sierra Nevada, Puerto de la Ragua, Barranco Maja Caco, 2000 m, 10.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada 1900 m, ri. Veleta, 1.vi.1982, 1♀, leg. R. Leys, RMNH; Granada: Órgiva N, 1300 m, 26.vi.1988, 1♀, leg. M. Schwarz, OÖLM.

Description. Female. Body length: 7 mm (Fig. 49A). ***Head*:** Dark, 1.1 times wider than long (Fig. 49B). Clypeus long, apical margin clearly ventrally exceeding level of line between lower margins of compound eyes, surface weakly domed, irregularly punctate, punctures separated by 1–3 puncture diameters, impunctate longitudinal midline present; underlying surface basally finely shagreened and weakly shiny, shagreenation becoming weaker apically, here almost smooth and shiny. Process of labrum narrowly trapezoidal, slightly broader than long, apical margin narrowly truncate. Gena slightly exceeding width of compound eye; ocelloccipital distance equalling diameter of lateral ocellus. Fovea dorsally narrow, occupying ¼ space between lateral ocellus and compound eye, ventrally extending below level of antennal insertions, consistently wide along its length, filled with white hairs. Face, gena, vertex, and scape covered with sparse whitish hairs, none equalling length of scape. Antennae dark, A3 equalling length of A4+5. ***Mesosoma*:** Scutum and scutellum regularly punctate, punctures separated by 1 puncture diameter, underlying surface shagreened and weakly shiny (Fig. 49C). Pronotum rounded. Mesepisternum microreticulate, weakly shiny with finely raised reticulation. Dorsolateral parts of propodeum with dense network of reticulation; propodeal triangle laterally delineated with raised carinae, internal surface with dense network of raised rugosity. Mesepisternum, scutum, and scutellum with long whitish hairs, none equalling length of scape. Propodeal corbicula incomplete, dorsal fringe composed of long whitish plumose hairs, internal surface with scattered long simple whitish hairs. Legs dark, pubescence whitish to light brownish. Flocculus complete, composed of short weakly upturned plumose hairs; flocculus, femoral and tibial scopae white, tibial scopae with some brown hairs dorso-basally. Hind tibial claws with inner tooth. Wings hyaline, stigma dark brown, venation brown, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas very narrowly lightened hyaline-brown. Tergal discs densely and clearly punctate, disc of T1 with punctures separated

Figure 49. *Andrena* (*Micrandrena*) *ortizi* sp. nov. female **A** profile **B** face, frontal view **C** scutum, dorsal view **D** terga, dorsal view.

by 1 puncture diameter, T2–3 with punctures separated by 0.5 puncture diameters, underlying surface shagreened and weakly shiny (Fig. 49D). Marginal areas impunctate, with rectangular shagreen; marginal areas long, on T1 occupying ¼ of tergum, on T2 occupying ½ of tergum, on T3 occupying 2/3rds of tergum, on T4 occupying almost all visible tergum. T2–4 with long sparse plumose hairs arising from base of marginal area, covering but not obscuring marginal area; T3–4 apically with dense short apical fringe of white hairs laterally, obscuring underlying surface. Apical fringe of T5 and hairs flanking pygidial plate dark brown with occasional whitish hairs laterally; pygidial plate rounded triangular, with obscurely raised medial ridge, otherwise featureless.

Male. Unknown.

Diagnosis. *Andrena ortizi* can quickly be recognised as a *Micrandrena* due to its small body size, dark integument, and entirely rugose propodeal triangle. Due to the comparatively (for a *Micrandrena*) long face and clypeus (head overall only 1.1 times wider than broad; apical margin of clypeus clearly ventrally exceeding level of a line drawn between the lower margins of the compound eyes), narrow facial fovea (dorsally occupying ¼ of space between the lateral ocellus and the compound eye, consistently wide along its length, and densely punctate scutum (punctures separated by <1 puncture diameter) they are comparable to *A. rugulosa* Stöckhert, 1935 (Switzerland to Lebanon and the Caucasus), *A. atlantea* Wood, 2021 (High and Middle Atlas Mountains in Morocco), and an undescribed *Micrandrena* species from the Middle Atlas (see above).

Andrena ortizi can be separated from *A. rugulosa* by the scutum which is slightly less densely punctate, punctures separated by 1 puncture diameter (punctures separated by 0.5 puncture diameters in *A. rugulosa*), the underlying surface of the scutum being finely shagreened and shiny (scutum is densely shagreened and dull in *A. rugulosa*), the tergal discs are strongly and clearly punctate (tergal discs obscurely punctate in *A. rugulosa*), and the marginal areas of T2–4 occupy at least ½ the visible length of the tergum, on T3–4 clearly occupying over ½ this length (marginal areas typically occupying ⅓ length of tergum, at most occupying ½ tergum on T4 in *A. rugulosa*). *Andrena ortizi* is more similar to *A. atlantea*, sharing a similarly less densely punctate and weakly shiny scutum, but the same character of wide tergal margins can be used to separate them, with the marginal areas occupying at most ⅓ of the length of the tergum in *A. atlantea*. Finally, *A. ortizi* is most similar to the undescribed *Micrandrena* from the Middle Atlas, and the width of the tergal margins can again be used to separate them, with the tergal margins occupying at most ⅓ of the disc of T2 and ½ of the discs of T3–4. Additionally, *A. ortizi* has the disc of T2–3 clearly and densely punctate, whereas in the undescribed *Micrandrena* the discs of T2–3 are at most obscurely punctate, with punctures disappearing into the background microreticulation. *Andrena ortizi* also has a strongly isolated distribution, separated from the Swiss Alps (*A. rugulosa*) by c. 1,300 km and the high altitude parts around Ifrane and Azrou in the Middle Atlas (*A. atlantea*, the undescribed *Micrandrena* species) by c. 400 km.

Remarks. At the Mirador Monte Ahí de Cara (Fig. 50A, see also Fig. 22A), this species was collected foraging for pollen on the spiny yellow species *Vella spinosa* (Brassicaceae) in open habitat just above the tree line. *Andrena ortizi* appears to be endemic to the Sierra Nevada. Searches at elevations lower than 2000 m did not detect the species during 2021 surveys, so the collection nominally made at 1300 m near Órgiva may not be representative – the slopes above Órgiva (southern slopes of the Sierra Nevada) ascend rapidly, the collector may well have climbed to a higher altitude when collecting this specimen. The morphological similarity between *A. rugulosa*, *A. ortizi*, and *A. atlantea* suggests a pattern of geographical isolation in montane habitats, though only *A. ortizi* and *A. atlantea* show a close genetic relationship based on the COI sequences.

Etymology. Dedicated to the Spanish naturalist and hymenopterist Francisco Javier Ortiz-Sánchez who has worked extensively on the Iberian bee fauna for many years, including that of the Sierra Nevada.

Distribution. Spain (Sierra Nevada).

Andrena (*Truncandrena*) *ghisbaini* Wood, sp. nov.

https://zoobank.org/E5ABB0AB-EE49-4CCC-91B4-9A9A99AD2A5C

Type material. ***Holotype*. Spain:** Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 36.6621°N, -5.0362°W, 1600 m, 30.v.2021, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW239-21].

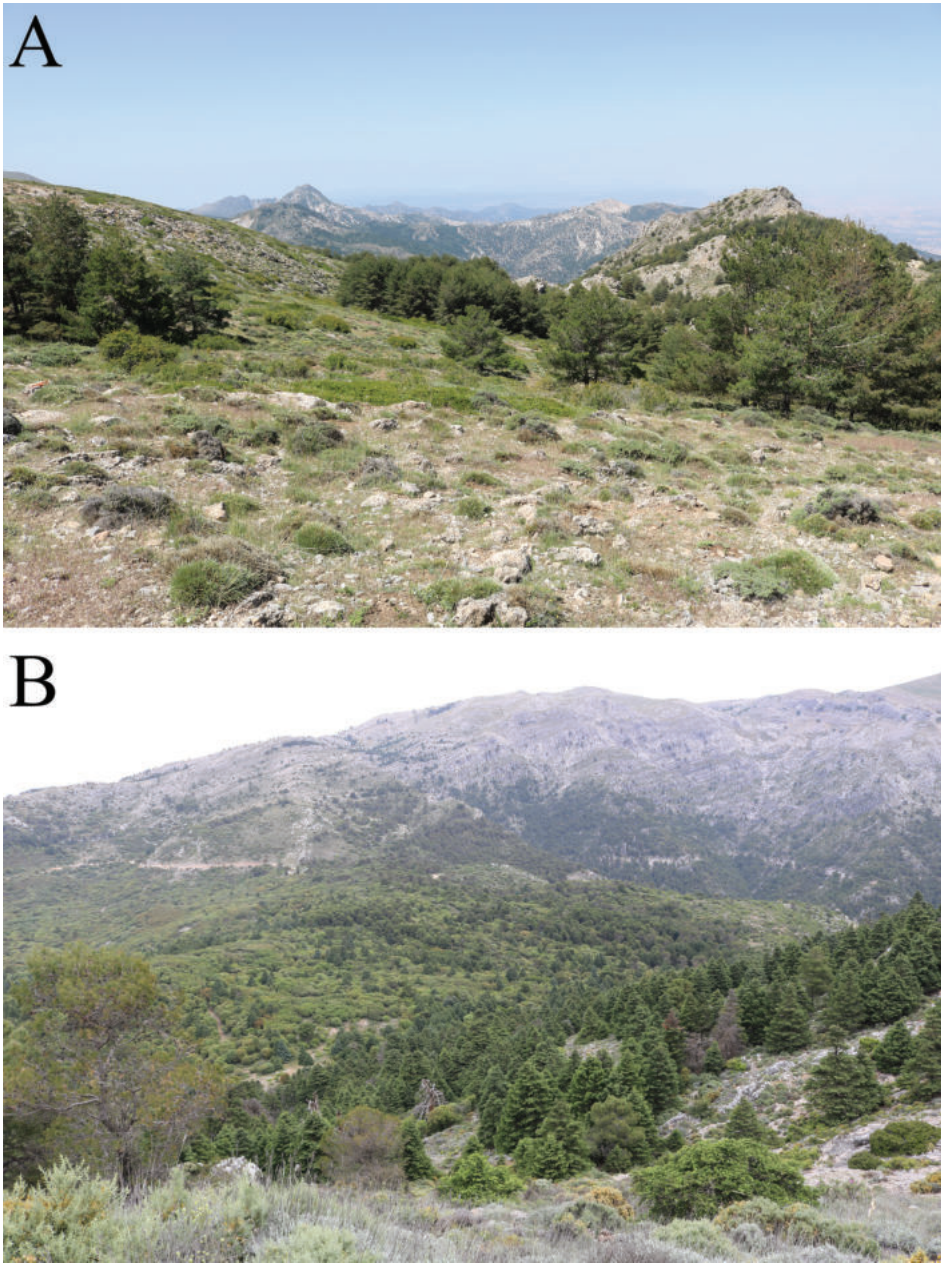

Figure 50. Habitat context **A** *Andrena* (*Micrandrena*) *ortizi* sp. nov., Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 2100 m, 12.vi.2021 **B** *Andrena* (*Truncandrena*) *ghisbaini* sp. nov., Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 1600 m, 30.v.2021.

Paratypes. **Spain:** Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 1600 m, 30.v.2021, 1♀, leg. G. Ghisbain, TJWC; Málaga – Elvira, 11.ii.1981, 4♂, leg. H. Teunissen, RMNH.

Figure 51. *Andrena* (*Truncandrena*) *ghisbaini* sp. nov. female **A** profile **B** face, frontal view **C** terga, dorsal view **D** tibial scopa, profile view.

Description. Female. Body length: 15–16 mm (Fig. 51A). ***Head*:** Dark, 1.2 times wider than long (Fig. 51B). Clypeus weakly domed, clearly punctate, punctures separated by 0.5–1 puncture diameters with exception of median longitudinal impunctate line, narrow basally, broadening apically, thus elongate triangular; underlying surface finely shagreened, weakly shiny. Process of labrum broadly trapezoidal, twice as broad as long, apical margin clearly emarginate. Gena broad, almost two times width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Fovea dorsally occupying slightly more than ½ space between lateral ocellus and compound eye, extending ventrally to lower margins of antennal insertions, filled with black hairs. Gena ventrally and laterally with long light brown hairs, longest equalling length of scape, hairs becoming black on vertex, scape, and majority of face, with shorter light brown hairs around antennae insertions. Antennae basally dark, A4 apically, A5–12 ventrally extensively lightened orange; A3 exceeding A4+5, shorter than A4+5+6. ***Mesosoma*:** Scutum and scutellum with extremely shallow and obscure punctures, punctures separated by 0.5–1 puncture diameters, punctures disappearing into underlying fine granular shagreen, surface dull to very weakly shiny. Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum with fine granular shagreen, weakly shiny, with fine and scattered raised hair-bearing punctures, punctures separated by 2–3 puncture diameters; propodeal triangle broad, with extremely fine granular shagreen, without hair-bearing punctures, propodeal triangle thus defined by change in surface sculpture from dorsolateral parts of propodeum. Mesepisternum and propodeum with long finely plumose light brown hairs, clearly exceeding length of scape; scutum and scutellum medially with long black hairs and occasional isolated pale hairs covering majority of disc, laterally becoming intermixed with light brown hairs. Propodeal corbicula incomplete, very weakly defined, dorsal fringe not differentiated from hairs of internal surface, both parts composed of long finely plumose long light brown hairs. Legs dark, apical tarsal segments lightened dark reddish, pubescence dark brown. Flocculus complete, composed of long weakly plumose and upturned light brown hairs; femoral scopae composed of light brown simple hairs; tibial scopa long, hairs exceeding apical width of hind tibia, hairs dorsally dark brown, ventrally golden orange (Fig. 51D). Hind tarsal claws with inner tooth. Wings hyaline, stigma dark brown, venation dark brown to orange, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas narrowly lightened hyaline-yellow; discs with extremely fine granular shagreen, weakly shiny, with fine and scattered hair-bearing punctures, punctures separated by 3–4 puncture diameters (Fig. 51C). Disc of T1 with long light brown hairs, exceeding length of scape, decreasing in length over T2–3, disc of T3 with intermixed short light brown and black hairs, becoming predominantly black on discs of T4–5. T2–4 with weak apical fringes of short light brown hairs, not obscuring underlying surface. Apical fringe of T5 and hairs flanking pygidial plate dark brown, pygidial plate rounded triangular, with weakly raised medial area, otherwise featureless.

Male. Body length: 13–14 mm (Fig. 52A). ***Head*:** Dark, 1.3 times wider than long (Fig. 52B). Clypeus weakly domed, entirely yellow-marked with exception of two dark rounded spots medio-laterally. Clypeus punctured, punctures separated by 0.5–1 puncture diameters with exception of median longitudinal impunctate line, essentially non-existent basally, broadening apically, thus elongate triangular; underlying surface finely shagreened, weakly shiny. Process of labrum broadly rectangular, 2.5 times wider than long, apical margin weakly emarginate, surface smooth and shiny. Gena broad, 2 times width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Gena ventrally and laterally with long light brown hairs clearly exceeding length of scape, becoming intermixed with black hairs on vertex. Face medially with extensive whitish to light-brownish hairs on clypeus, antennae insertions, and scape intermixed with black hairs along inner margins of compound eyes and scape. Antennae basally dark, A4–13 ventrally lightened orange; A3 longer than A4, shorter than A4+5; A4 rectangular, longer than broad, slightly shorter than A5. ***Mesosoma*:** Mesosoma structurally as in female; pubescence as in female. Legs basally dark, apical tarsal segments and hind tibiae lightened dark reddish-brown, pubescence dark brown to orange brown. Hind tarsal claws with inner tooth. Wings hyaline, stigma orange, venation dark brown to orange, nervulus interstitial. ***Metasoma*:** Terga structurally as in female. Discs of T1–4 with long light brown hair, on T1 clearly exceeding length of scape, becoming progressively shorter to T4; T5–6 with short black hairs on disc (Fig. 52C). T2–4 with weak apical hair fringes apically, not

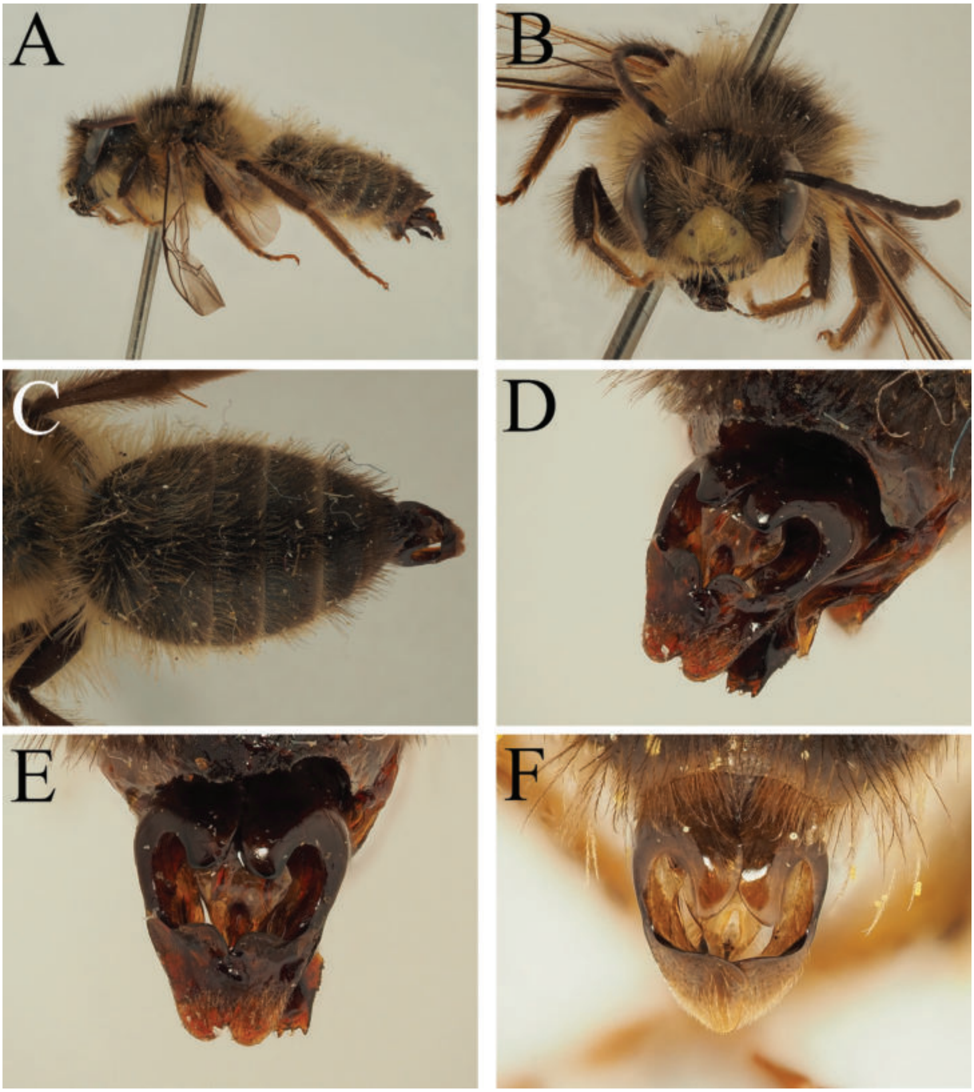

Figure 52. *Andrena* (*Truncandrena*) *ghisbaini* sp. nov. male **A** profile **B** face, frontal view **C** terga, dorsal view **D** genital capsule, dorsolateral view **E** genital capsule, dorsal view; *Andrena* (*Truncandrena*) *villipes* Pérez, 1895 male **F** genital capsule, dorsal view.

obscuring underlying surface. S8 columnar, apex rounded, ventral surface covered with short brown hairs. Genital capsule slightly elongate, gonocoxae produced into strong apical teeth, teeth pointed with apical margins diverging (Fig. 52D, E). Gonostyli basally narrow, apically produced and flattened into rounded triangular plates, internal margin strongly raised and reflexed. Penis valves basally broad, occupying more than ½ space between gonostyli, with narrow laterally produced hyaline extensions; penis valves strongly narrowing apically.

Diagnosis. *Andrena ghisbaini* can be recognised within *Truncandrena* due to its characteristically smooth and finely granulate propodeal triangle which contrasts with the similarly granulate dorsolateral parts of the propodeum which bear fine and scattered raised hair-bearing punctures, the rounded pronotum, the linear malar space, the large body size (>13 mm), yellow male clypeus, and typical genital capsule with the inner margins of the flattened apical parts of the gonostyli strongly raised. It can be placed closest to *A. villipes* Pérez, 1895 (Fig. 30) due to the antennae that are ventrally extensively lightened orange, the intermixed light and dark pubescence of the face, with pale hairs medially and dark hairs laterally, the intermixed light and dark pubescence of the scutum, with dark hairs medially and lighter hairs laterally, by the entirely yellow-marked male clypeus, and by the penis valves basally broad with lateral hyaline extensions, valves strongly narrowing apically.

The immediate difference between the two taxa is size, with *A. villipes* averaging 12–13 mm in length in females and 11–12 mm in males, compared to 15–16 mm and 13–14 mm respectively in *A. ghisbaini*. Structurally, *A. ghisbaini* females can be separated by the bicoloured scopa, black dorsally and orange ventrally (Fig. 51D; *A. villipes* with scopa unicolourous orange, Fig. 30B), the longer face, clypeus clearly projecting ventrally well below a line drawn between the lower margins of the compound eyes (*A. villipes* with face shorter, clypeus only slightly projecting below this line in direct comparison), the clypeus clearly punctured with a longitudinal impunctate midline that broadens apically (*A. villipes* with clypeus obscurely and shallowly punctate, without obvious impunctate midline), and the reduced pale pubescence of the face, with light hairs restricted to the area around the antennal insertions (*A. villipes* with extensive pale hairs covering majority of face and clypeus, with black hairs predominantly along the inner margins of the compound eyes).

In the male sex, *A. ghisbaini* can be separated by the same clypeal punctation character (stronger in *A. ghisbaini* with clearer impunctate midline), but this is slightly more subtle than in the female sex. Direct comparison of the genital capsule shows that flattened apical part of the gonostyli are more strongly elongate and longer than broad, thus appearing triangular (Fig. 52D, E; in *A. villipes* with the flattened apical part of the gonostyli more rounded, about as long as broad, Fig. 52F), the inner margins of these parts more strongly and acutely raised, slightly reflexed (in *A. villipes* with the inner margin less strongly raised and not reflexed).

Remarks. The two females from the Sierra de las Nieves (Fig. 50B) were collected from *Cistus albidus* Linnaeus (Cistaceae). Like *A. villipes* (Table 1), this species is likely to be oligolectic on Cistaceae. Additional surveys are needed to clarify the limits of its range. Male specimens from Elvira in the Naturalis collection were incorrectly determined by Teunissen as *A. maroccana* Benoist, 1950 which is a synonym of *A. leptopyga* Pérez, 1895.

Etymology. Dedicated to my friend and colleague Guillaume Ghisbain (Mons, Belgium) who accompanied me during fieldwork in Málaga province, and who is an accomplished hymenopterist in his own right.

Distribution. Spain (Málaga province).

Table 1. Host plant use and dietary classification for selected Iberian *Andrena* species. *n*, total number of pollen loads; *N*, number of pollen loads from different localities. Plant taxa: ADO, Adoxaceae; AMA, Amaryllidaceae; API, Apiaceae; ASP, Asparagaceae; AST, Asteraceae; BOR, Boraginaceae; BRA, Brassicaceae; CAM, Campanulaceae; CAP, Caprifoliaceae; CAR, Caryophyllaceae; CIS, Cistaceae; CRA, Crassulaceae; EUP, Euphorbiaceae; FAB, Fabaceae; FAG, Fagaceae; FRA, Frankeniaceae; GER, Geraniaceae; HYP, Hypericaceae; PAP, Papaveraceae; PLA, Plantaginaceae; PLU, Plumbaginaceae; RES, Resedaceae; RHA, Rhamnaceae; ROS, Rosaceae; SAL, Salicaceae; SAP, Sapindaceae; SCR, Scrophulariaceae. Countries: BE, Belgium; BG, Bulgaria; DZ, Algeria; ESP, Spain; FRA, France; IL, Israel; IR, Iran; MA, Morocco; PT, Portugal; SY, Syria; TJ, Tajikistan; TN, Tunisia.

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Aciandrena Warncke							
A. fulica Warncke	12	7	ESP (10), PT (2)	BRA 99.6, CIS 0.4	91.7	100.0	Broadly oligolectic (Brassicaceae)
A. vacella Warncke	2	2	ESP (2)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
aegyptiaca-group							
A. alluaudi Benoist	4	3	MA (2), PT (2)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
Aenandrena Warncke							
A. aeneiventris Morawitz	15	7	ESP (15)	API 100.0	100.0	100.0	Possibly broadly oligolectic (Apiaceae)
A. hedikae Jäger	22	10	ESP (11), MA (9), PT (2)	API 100.0	100.0	100.0	Possibly broadly oligolectic (Apiaceae)
A. hystrix Schmiedeknecht	9	5	ESP (8), PT (1)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
Avandrena Warncke							
A. avara Warncke	2	2	ESP (2)	GER 100.0	100.0	100.0	Broadly oligolectic (Geraniaceae)
A. melacana Warncke	6	2	ESP (6)	GER 100.0	100.0	100.0	Broadly oligolectic (Geraniaceae)
A. panurgina De Steffani	11	5	ESP (4), FRA (4), PT (3)	GER 93.6, AST 5.0, BRA 1.4	81.8	100.0	Broadly oligolectic (Geraniaceae)
Blandandrena subgen. nov.							
A. blanda Pérez	27	9	ESP (8), MA (19)	RES 100.0	100.0	100.0	Narrowly oligolectic (*Reseda*, Resedaceae)
Brachyandrena Pittioni							
A. colletiformis Morawitz	6	4	ESP (5), PT (1)	API 100.0	100.0	100.0	Possibly broadly oligolectic (Apiaceae)
A. miegiella Dours	5	4	ESP (2), MA (2), TN (1)	API 99.8, AST 0.2	80.0	100.0	Possibly broadly oligolectic (Apiaceae)
Chlorandrena Pérez							
A. abrupta Warncke	1	1	PT (1)	AST 100.0	100.0	100.0	Probably broadly oligolectic (Asteraceae; Asteroideae)
A. cinerea Brullé	22	15	ESP (6), FRA (3), PT (12), TN (1)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
A. curtivalvis Morice	1	1	ESP (1)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
A. elata Warncke	13	5	ESP (13)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Asteroideae)
A. leucolippa Pérez	22	10	ESP (12), FRA (10)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Asteroideae)
A. rhenana Stöckhert	8	4	ESP (2), PT (6)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
A. senecionis Pérez	21	15	ESP (11), FRA (3), MA (3), PT (4)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
Chrysandrena Hedicke							
A. fertoni Pérez	4	3	ESP (4)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Cordandrena Warncke							
A. vaulogeri Pérez	10	5	ESP (3), MA (7)	BRA 61.8, ROS 22.6, AST 9.6, FAB 6.0	30.0	80.0	Polylectic s. str.
Cryptandrena Pittioni							
A. ventricosa Dours	39	10	ESP (29), FRA (10)	FAB 92.8, API 6.1, others 1.1	76.9	97.4	Polylectic with a strong preference (Fabaceae)
Didonia Gribodo							
A. mucida Kriechbaumer (1st generation)	3	3	ESP (1), PT (2)	ASP 100.0	100.0	100.0	Possibly narrowly oligolectic (*Muscari*; Asparagaceae)
A. mucida Kriechbaumer (2nd generation)	12	8	BG (2), ESP (9), MA (1)	CAP 100.0	100.0	100.0	Broadly oligolectic (Caprifoliaceae)
Euandrena Pérez							
A. lavandulae Pérez	5	5	ESP (3), FRA (1), PT (1)	FAB 27.6, CIS 24.3, SCR 20.7, PLA 10.3, AST 8.3, CAM 4.7, GER 2.9, CAR 1.2	20.0	20.0	Polylectic s. str.
Graecandrena Warncke							
A. nebularia Warncke	5	3	ESP (1), MA (4)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
A. verticalis Pérez	30	21	ESP (20), MA (8), PT (2)	BRA 56.3, API 43.8	53.3	53.3	Mesolectic (Apiaceae & Brassicaceae)
incisa-group							
A. lateralis Morawitz	7	3	ESP (3), IR (1), TJ (3)	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)
Leucandrena Hedicke							
A. leptopyga Pérez	19	12	DZ (1), ESP (1), MA (12), PT (5)	RES 90.8, BRA 6.6, BOR 1.8, SCR 0.7	78.9	94.7	Polylectic with a strong preference (*Reseda*, Resedaceae)
A. tunetana Schmiedeknecht	4	4	DZ (1), ESP (2), MA (1)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
Melanapis Cameron							
A. fuscosa Erichson	18	12	ESP (15), FRA (1), IL (1), PT (1)	BRA 52.4, API 15.5, PAP 12.7, AST 9.5, ROS 6.1, EUP 3.1, others 0.7	50.0	72.2	Polylectic s. str.
Melandrena Pérez							
A. albopunctata (Rossi)	15	7	ESP (14), MA (1)	AST 47.4, API 25.3, CAP 11.2, BRA 6.4, FAB 3.9, PAP 3.1, others 2.7	20.0	86.7	Polylectic s. str.
A. assimilis Radoszkowski	15	6	ESP (4), FRA (11)	AST 34.8, ROS 21.1, API 21.0, PLU 7.9, AMA 6.6, SAL 2.7, others 6.1	6.7	73.3	Polylectic s. str.
A. bicolorata (Rossi)	8	5	ESP (2), PT (6)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. florentina Magretti	9	5	MA (1), PT (8)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. morio Brullé (including *A. hispania* Warncke)	9	8	ESP (3), PT (6)	CIS 69.6, API 17.2, AST 10.0, others 3.2	22.2	77.8	Polylectic s. str.
Micrandrena Ashmead							
A. ampla Warncke	21	10	ESP (10), FRA (10), PT (1)	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)
A. bayona Warncke	2	2	ESP (2)	API 50.0, BRA 50.0	50.0	50.0	Probably polylectic
A. djelfensis Pérez	20	13	ESP (3), MA (7), PT (10)	CIS 99.9, FAB 0.1	95.0	100.0	Broadly oligolectic (Cistaceae)
A. fabrella Pérez	22	13	ESP (8), FRA (1), MA (5), PT (8)	CIST 99.9, AST 0.1	90.0	100.0	Broadly oligolectic (Cistaceae)

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
A. icterina Warncke	9	6	ESP (9)	BRA 69.1, CIS 10.6, SAL 10.3, EUP 5.8, others 4.2	22.2	88.9	Polylectic s. str.
A. longibarbis Pérez	13	8	ESP (2), MA (8), PT (3)	BRA 99.6, AST 0.4	92.3	100.0	Broadly oligolectic (Brassicaceae)
A. nana (Kirby)	51	28	ESP (33), FRA (1), MA (8), PT (9)	API 71.2, BRA 28.6, EUP 0.2	68.6	74.5	Polylectic with a strong preference (Apiaceae)
A. nitidula Pérez	39	18	ESP (16), MA (21), PT (2)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. omnilaevis Wood	6	5	ESP (2), PT (4)	CRA 100.0	100.0	100.0	Probably narrowly oligolectic (*Sedum*, Crassulaceae)
A. orana Warncke	17	3	DZ (9), MA (5), PT (3)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. pauxilla Stöckhert	11	5	ESP (11)	CRA 82.1, BRA 17.9	81.8	81.8	Possibly polylectic with a strong preference (*Sedum*, Crassulaceae)
A. spreta Pérez	19	11	ESP (15), MA (3), PT (1)	BRA 93.1, AST 3.0, EUP 2.8, FAB 1.2	78.9	100.0	Polylectic with a strong preference (Brassicaceae)
A. tenuistriata Pérez	39	27	ESP (17), FRA (3), MA (6), PT (13)	BRA 99.8, others 0.2	94.9	100.0	Broadly oligolectic (Brassicaceae)
Nobandrena Warncke							
A. funerea Warncke	12	6	ESP (12)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
Notandrena Pérez							
A. aerinifrons Dours	25	8	DZ (3), ESP (3), MA (11), PT (8)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. bellidis Pérez	3	3	ESP (2), PT (1)	AST 38.9, RES 36.4, RAN 18.2, BOR 6.5	0.0	66.7	Polylectic s. str.
A. juliana Wood	35	2	ESP (35)	API 82.6, FRA 13.1, CIS 2.8, others 1.4	74.3	82.9	Polylectic with a strong preference (Apiaceae)
A. leucophaea Lepeletier	2	2	ESP (2)	AST 100.0	100.0	100.0	Possibly oligolectic (Asteraceae; Asteroideae)
A. nigroviridula Dours	9	8	ESP (4), MA (4), PT (1)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. varuga Warncke	3	2	ESP (3)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
numida-group							
A. hypopolia Schmiedeknecht	8	7	ESP (4), FRA (1), PT (3)	BRA 64.8, API 34.6, AST 0.6	50.0	62.5	Mesolectic (Apiaceae & Brassicaceae)
A. ranunculorum Morawitz	17	17	FRA (17)	BRA 75.8, API 10.2, ROS 5.7, FAG 5.6, AST 2.1, ADO 0.5	64.7	100.0	Polylectic with a strong preference (Brassicaceae)
Orandrena Warncke							
A. monilia Warncke	2	2	ESP (1), MA (1)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
Ovandrena subgen. nov.							
A. farinosa Pérez	9	5	ESP (9)	FAB 100.0	100.0	100.0	Broadly oligolectic (Fabaceae)
A. oviventris Pérez	28	11	ESP (9), FRA (4), MA (12), PT (3)	RES 98.3, others 1.7	82.1	100.0	Narrowly oligolectic (*Reseda*, Resedaceae)
Plastandrena Hedicke							
A. asperrima Pérez	56	29	ESP (8), FRA (5), MA (43)	BRA 77.6, RES 18.6, ROS 2.5, AST 1.3	69.6	87.5	Polylectic with a strong preference (Brassicaceae)
A. pilipes Fabricius s. str.	28	21	ESP (15), FRA (8), PT (5)	BRA 54.4, ROS 18.9, AST 13.8, CIS 6.6, API 5.7, others 0.7	35.7	57.1	Polylectic s. str.
relata-group							
A. corax Warncke	10	4	ESP (8), PT (2)	RES 99.7, AST 0.3	90.0	100.0	Narrowly oligolectic (*Reseda*, Resedaceae)
A. laurivora Warncke	3	1	MA (1)	RES 100.0	100.0	100.0	Probably narrowly oligolectic (*Reseda*, Resedaceae)

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
A. relata Warncke	2	2	ESP (2)	RES 100.0	100.0	100.0	Probably narrowly oligolectic (*Reseda*, Resedaceae)
Rufandrena Warncke							
A. orbitalis Morawitz	9	6	ESP (2), FRA (4), PT (3)	PLA 100.0	100.0	100.0	Narrowly oligolectic (*Plantago*, Plantaginaceae)
A. rufiventris Lepeletier	3	1	MA (3)	PLA 100.0	100.0	100.0	Narrowly oligolectic (*Plantago*, Plantaginaceae)
Simandrena Pérez							
A. antigana Pérez	25	14	ESP (6), MA (7), PT (12)	BRA 99.8, others 0.2	96.0	100.0	Broadly oligolectic (Brassicaceae)
A. cilissaeformis Pérez	5	5	ESP (2), MA (3)	BRA 83.6, EUP 8.8, RHA 7.6	60.0	80.0	Probably polylectic with a strong preference (Brassicaceae)
A. propinqua Schenck	43	31	BE (4), ESP (21), FRA (5), MA (3), PT (10)	BRA 46.1, ROS 25.8, FAB 10.2, CIS 4.4, CRA 3.2, BOR 2.5, others 7.7	30.2	58.1	Polylectic s. str.
A. rhypara Pérez	4	3	MA (4)	RES 100.0	100.0	100.0	Possibly narrowly oligolectic (*Reseda*; Resedaceae)
A. vetula Lepeletier	31	16	ESP (20), FRA (2), MA (7), SY (1), TN (1)	BRA 99.8, others 0.2	93.5	100.0	Broadly oligolectic (Brassicaceae)
Truncandrena Warncke							
A. doursana Dufour	8	3	MA (7), PT (1)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. ferrugineicrus Dours	28	18	DZ (1), ESP (16), MA (2), PT (9)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. nigropilosa Warncke	23	8	ESP (16), FRA (5), MA (2)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. villipes Pérez	6	2	FRA (1), PT (5)	CIS 100.0	100.0	100.0	Probably broadly oligolectic (Cistaceae)

Description of missing sexes

Andrena (*Micrandrena*) *alma* Warncke, 1975

Description. Male. Body length 6.5–7 mm (Fig. 53A). ***Head*:** Dark, 1.2 times wider than long. Clypeus flattened, unevenly punctate with large punctures, punctures separated by 0.5–2 puncture diameters, underlying surface shagreened in basal half, polished and shiny in apical half. Process of labrum trapezoidal, slightly wider than long, apical margin slightly thickened. Gena 1.3 times width of compound eye (Fig. 53B, C); ocelloccipital distance 0.5 times diameter of lateral ocellus. Face medially with whitish hairs, scape with mixture of black and white hairs, inner margin of compound eyes with black hairs, gena ventrally with white hairs, becoming black dorsolaterally, vertex and frons with mixture of black and pale hairs, none exceeding length of scape. Antennae dark, A3 exceeding length of A4, shorter than A4+5. ***Mesosoma*:** Scutum and scutellum finely granularly shagreened and weakly shiny, shallowly and obscurely punctate, punctures separated by 2–3 puncture diameters. Pronotum with clear humeral angle. Mesepisternum and dorsolateral surfaces of propodeum with fine granular microreticulation, with regular slightly raised hair bearing punctures. Propodeal triangle with regular granular shagreen, basally and medially with obscure and finely raised rugosity, propodeal triangle thus defined by change in surface sculpture compared to dorsolat-

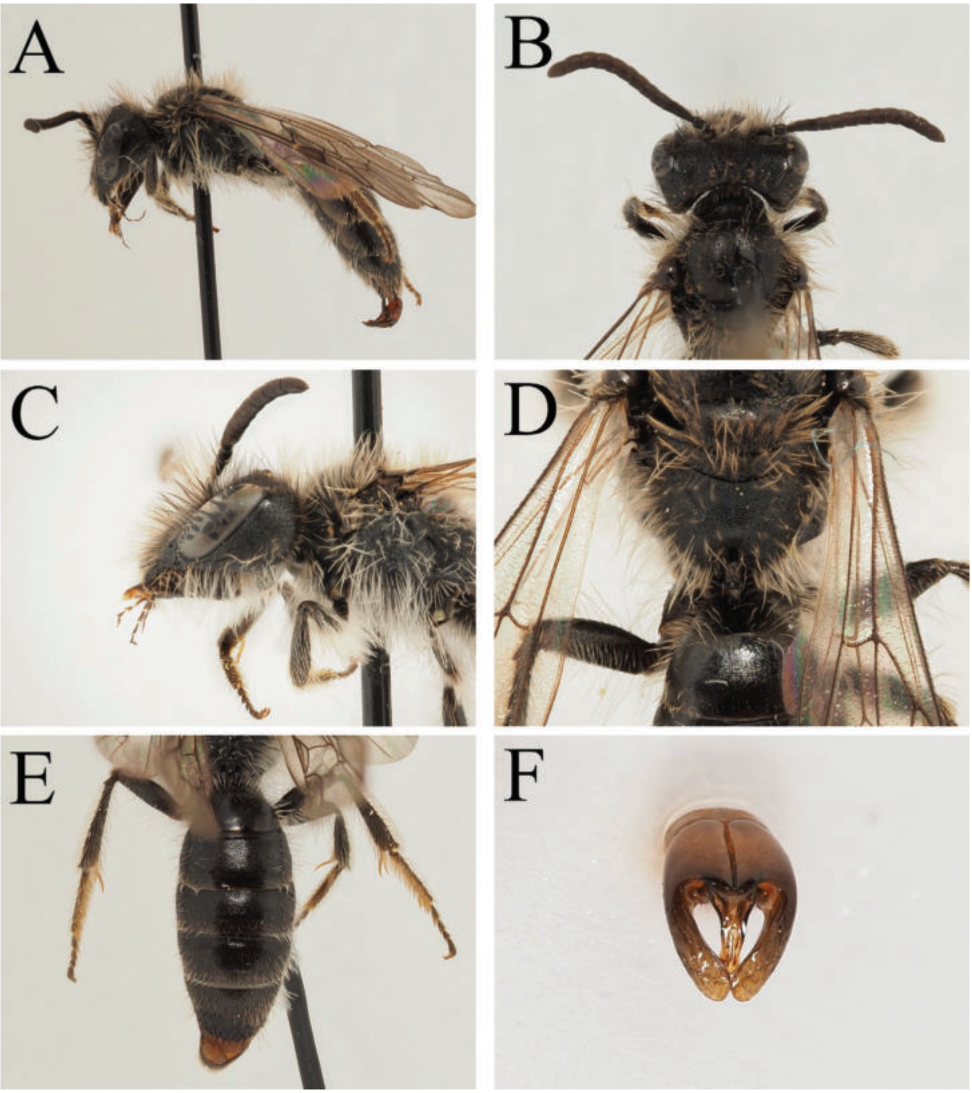

Figure 53. *Andrena* (*Micrandrena*) *alma* Warncke, 1975 male **A** profile **B** head, dorsal view **C** head, profile view **D** propodeal triangle, dorsal view **E** terga, dorsal view **F** genital capsule, dorsal view.

eral parts of propodeum (Fig. 53D). Mesosoma laterally with long white pubescence, exceeding length of scape, pubescence becoming brownish and shorter dorsally, not exceeding length of scape. Legs dark, pubescence whitish. Hind tarsal claws with inner tooth. Wings hyaline, venation and stigma dark brown, nervulus interstitial. ***Metasoma*:** Terga dark, marginal areas obscurely lightened dark hyaline brown apically (Fig. 53E). Tergal discs with obscure and weak punctures that disappear into even underlying microreticulation, surface weakly shiny. Tergal discs with sparse long light brown hairs, T2–4 laterally with weak, widely interrupted apical hair fringes. S8 columnar, slightly broadened apically, ventrally covered with short yellowish hairs. Genital capsule compact, gonocoxae apically weakly produced into short rounded teeth; gonostyli parallel-sided, spatulate; penis valves slightly broadened basally (Fig. 53F).

Diagnosis. *Andrena alma* can be recognised due to its combination of small body size, dark integument, pronotum with humeral angle, evenly shagreened and weakly shiny terga, gena exceeding the width of the compound eye (Figs 53B, C), flattened and striation-free clypeus, simple genital capsule (Fig. 53F), and smooth and granulate propodeal triangle with obscure and finely raised rugosity basally (Fig. 53D). This smooth propodeal triangle places it close to former *Distandrena* species, but the flattened and striation-free clypeus excludes *A. longibarbis* Pérez, 1895 (clypeus domed, obscurely striate) and *A. orana* Warncke, 1974 (clypeus domed and striate). The evenly shagreened terga and obscure basal rugosity on the largely granularly shagreened propodeal triangle place it superficially close to *A. djelfensis*, but this species can easily be separated by the distinctive genital capsule with elongate and strongly medially bent gonostyli, whereas the genital capsule is simple and lacking distinctive features in *A. alma*. Finally, *A. alma* has a distinctly broadened gena that slightly but distinctly wider than the width of the compound eye, an unusual character in *Micrandrena*. This allows separation from *A. abjecta* which has the gena equalling the width of the compound eye. Collectively, these characters make recognition of *A. alma* straightforward, though as the males of *A. tenostra* and *A.* aff *mica* are unknown, diagnosis may become more challenging in the future. A level of caution should therefore be applied when identifying material from the extreme south and south-east of Spain.

Distribution. Central and southern Portugal and Spain.

Material examined. **Portugal:** Algarve, Monte Gordo, Retur, Praia do Cabeço, 29.iii.2022, 1♂, leg. T.J. Wood, TJWC; Algarve, Tavira, Cacela Velha, 28.iii.2022, 1♂, leg. T.J. Wood, TJWC; **Spain:** Almodóvar del Campo (Ciudad Real), 700 m, 24.iii.2005, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Santa Ana la Real, Sierra Aracena (Huelva), 630 m, 13.iv.2006, 2♂, leg. F.J. Ortiz-Sánchez, FJOS; El Hongo (P.N. Doñana), 30.iii.2018, 1♂, leg. F. Molina, EBDC.

Andrena (*?Euandrena*) *ramosa* Wood, 2022

Description. Male. Body length 8–10 mm (Fig. 54A). ***Head*:** Dark, 1.05 times wider than long (Fig. 54C). Clypeus long, weakly domed, unevenly punctate, punctures separated by 0.5–2 puncture diameters, underlying surface strongly shagreened to microreticulate in basal half, becoming smooth and shiny in apical half. Process of labrum trapezoidal, 3 times wider than long, ventral surface smooth and polished. Gena equalling width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Face medially and gena ventrally with long yellowish hairs, face laterally, frons, and scape with long black hairs, mixing medially on face with yellowish hairs, longest exceeding length of scape. Antennae dark, A3 exceeding length of A4, shorter than A4+5, A4 slightly longer than wide, A5–13 elongate, clearly longer than wide. ***Mesosoma*:** Scutum and scutellum obscurely punctate, punctures separated by 1–2 puncture di-

Figure 54. *Andrena* (?*Euandrena*) *ramosa* Wood, 2022 male **A** profile **B** head, profile view **C** head, frontal view **D** scutum, dorsal view **E** terga, dorsal view **F** genital capsule.

ameters, disappearing into extremely strong underlying granular microreticulation, surface dull (Fig. 54D). Pronotum rounded. Mesepisternum and dorsolateral surface of propodeum with fine granular microreticulation, with finely raised network of reticulation that gives impression of large shallow punctures. Propodeal triangle narrow, surface with fine granular shagreen, basally and medially with finely raised rugosity, propodeal triangle thus defined by change in surface sculpture compared to dorsolateral parts of propodeum. Mesosoma with long, densely branches and plumose yellowish hairs clearly exceeding length of scape, black plumose hairs intermixed around wing bases, on scutum, and propodeum. Legs dark, pubescence brownish to black. Hind tarsal claws with inner tooth. Wings hyaline, stigma dark brown, venation dark to light brown, nervulus weakly antefurcal. ***Metasoma*:** Terga dark, apical rim of marginal areas very narrowly lightened hyaline brown (Fig. 54E). Tergal discs with obscure hair-bearing punctures, disappearing into background sculpture, becoming more strongly defined laterally, underlying surface shagreened and weakly shiny. T1–3 with long but loose plumose yellowish-brown hairs, these becoming black on T4–5. S8 relatively short, rectangular, apically truncate, ventrally covered with dark brown hairs. Genital capsule moderately elongate, gonocoxae apically weakly produced into short rounded projections, gonostyli more or less parallel-sided, spatulate (Fig. 54F). Penis valves occupying ½ space between gonostyli, slightly narrowing towards their apexes.

Diagnosis. The male of *A. ramosa* is morphologically most similar to *A.* (*Euandrena*) *solenopalpa* due to the long head (only marginally wider than long) and clypeus that is shiny at least in its apical half. The two species are easily separated by the mouthparts, as in *A. ramosa* the mouthparts that protrude in front of the head are at most as long as the head (viewed frontally or laterally, Fig. 54B), whereas in *A. solenopalpa* the mouthparts are extremely long, the labial palpi alone exceed the length of their head, the part of the mouthparts protruding in front of the head therefore collectively greatly exceed the length of the head. The clypeus of *A. solenopalpa* is also more extensively shiny, the gonostyli have their outer margin emarginate and are apically produced into narrow points, and A3 slightly exceeds the length of A4+5, whereas in *A. ramosa* the clypeus is shiny only in its apical half, the gonostyli are spatulate and apically truncate, and A3 only slightly exceeds A4, and is shorter than A4+5. The two species do not occur in sympatry, with *A. ramosa* restricted to south-western Spain, whereas *A. solenopalpa* is found in central and eastern Spain to southern France.

Distribution. South-western Spain (Cádiz, Sevilla).

Remarks. The phylogenetic placement of *A. ramosa* remains somewhat obscure even following the discovery of the male sex and generation of a barcode sequence. A 658-bp fragment was generated from the female type specimen [BOLD accession number: IBIHM524-21], but this did not fall unambiguously close to any species or subgenus. The most similar sequences belonged to the subgenus *Euandrena*, specifically to *A. symphyti* (90.26%), *A. montana* Warncke, 1973 (90.31%), *A. fulvida* Schenck, 1853 (89.98%), and *A. rufula* Schmiedeknecht, 1883 (89.84%). Morphologically, *A. ramosa* does not fall nicely into *Euandrena*, as the female sex has foveae which are narrow but which do not narrow ventrally. However, *Euandrena* are part of the most highly derived clade of *Andrena* (Pisanty et al. 2022b), and subgeneric classification in this clade has been highly problematic due to the lack of clear delineating characters. *Andrena ramosa* does not belong to *Margandrena* Warncke, 1968 due to the lack of a strong humeral angle on the pronotum. It does not belong to the *crocusella*-group due to the lack of a humeral angle and the lack of lateral projections on the male penis valves (in addition to the lack of barcode similarity), and whilst it has strongly plumose pollen collecting hairs comprising the propodeal corbiculae and femoral scopae, those of the tibial scopae are simple, and the foveae do not narrow below which makes placement in *Chrysandrena* Hedicke, 1933 difficult. *Andrena ramosa* is therefore best considered to be affiliated with the subgenus *Euandrena*, pending investigation with more powerful genetic techniques. It clearly possesses a unique and unusual morphology within the West Palaearctic *Andrena* fauna.

Examination of additional material from the province of Cádiz has shown that *A. ramosa* is commonly encountered in the Parque Natural Los Alcornocales area. Here it can be encountered between January and March, and is most frequently observed on *Erica* (Ericaceae; Pérez Gómez in litt.). However, the pollen host is still obscure, since none of these bees have been observed collecting pollen. Moreover, Ericaceae pollen is small, with the grains typically having a diameter of 25 µm. The widely spaced and strongly branched and plumose pollen collecting hairs of *A. ramosa* (described and illustrated by Wood et al. 2022a) would not seem to be an adaptation to the collection of small Ericaceae pollen grains, and indeed this adaptation is absent in the Ericaceae specialist *A.* (*Cnemidandrena*) *fuscipes* (Kirby, 1802) which has simple pollen collecting hairs. Further study is required; the assumption remains that *A. ramosa* collects pollen from a plant species with large pollen grains, thus necessitating these branched and plumose hairs.

Material examined. Spain: Carretera Marrufo, Herriza (Cádiz; 3 km E Puerto de Gáliz), 11.xi.2020, 1♀, leg. Á. Pérez Gómez, APGC; Sevilla, Los Pinares de Aznalcázar [37.2782°N, -6.2356°E], 10.iii.2020, 1♀, leg. F. Molina, OÖLM (holotype); Cádiz, Sierra de Montecoche, 31.i.2022, 4♂, 1♀, leg. Á. Pérez Gómez, APGC/TJWC; 18.i.2021, 1♂, leg. Á. Pérez Gómez, APGC; Cádiz, Pico del Montero, 2.ii.2022, 3♂, 1♀, leg. Á. Pérez Gómez, APGC/TJWC; Cádiz, Sierra de Fates, 21.iii.2022, 1♀, leg. Á. Pérez Gómez, APGC; Cádiz, Pico del Montero, Alcalá de los Gazules, 26.iii.2022, 1♂, leg. Á. Pérez Gómez, APGC.

Additional designation of lectotypes

Andrena (*Aenandrena*) *hystrix* Schmiedeknecht, 1883

Andrena (*Aenandrena*) *hystrix* Schmiedeknecht, 1883: 618, ♀ [France, lectotype by present designation: RMNH].

Remarks. Schmiedeknecht (1883) described several *Andrena* species from material that had been sent to him by Pérez. In each case, he indicated this in his title, e.g. 'Andrena hystrix Perez in litt' [sic]. For several of these species, the location of type material has been unclear, as they mostly did not seem to be in the MNHN in the Pérez collection (see Le Divelec 2021), or elsewhere (see Gusenleitner and Schwarz 2002). Searches in the RMNH unexpectedly uncovered specimens of four species described by Schmiedeknecht with labels written in Pérez's distinctive handwriting. The exact providence of these specimens is unclear, but the RMNH collection is known to contain material from Schmiedeknecht's collection (F. Bakker, pers. comm.). A lectotype was designated for one of these species (*A.* (*Andrena*) *mitis* Schmiedeknecht, 1883) in a previous publication (Wood 2023a); the others are designated here.

Schmiedeknecht (1883) described *A. hystrix* from female specimens from Hungary (*Hungaria*) and southern France (*Gallia meridionali*). He did not specify a type, though Gusenleitner and Schwarz (2002) list south France as the *locus typicus*. A specimen of *A. hystrix* from Marseille is labelled with Pérez's handwriting, and this is considered to be part of the original syntypic series; it is here designated as a lectotype (Fig. 55A, B). No specimens from Hungary s.l. could be found.

Material examined. **France:** Marseille [43.3612°N, 5.3942°E], 1♀, RMNH (lectotype by present designation; Fig. 55A, B).

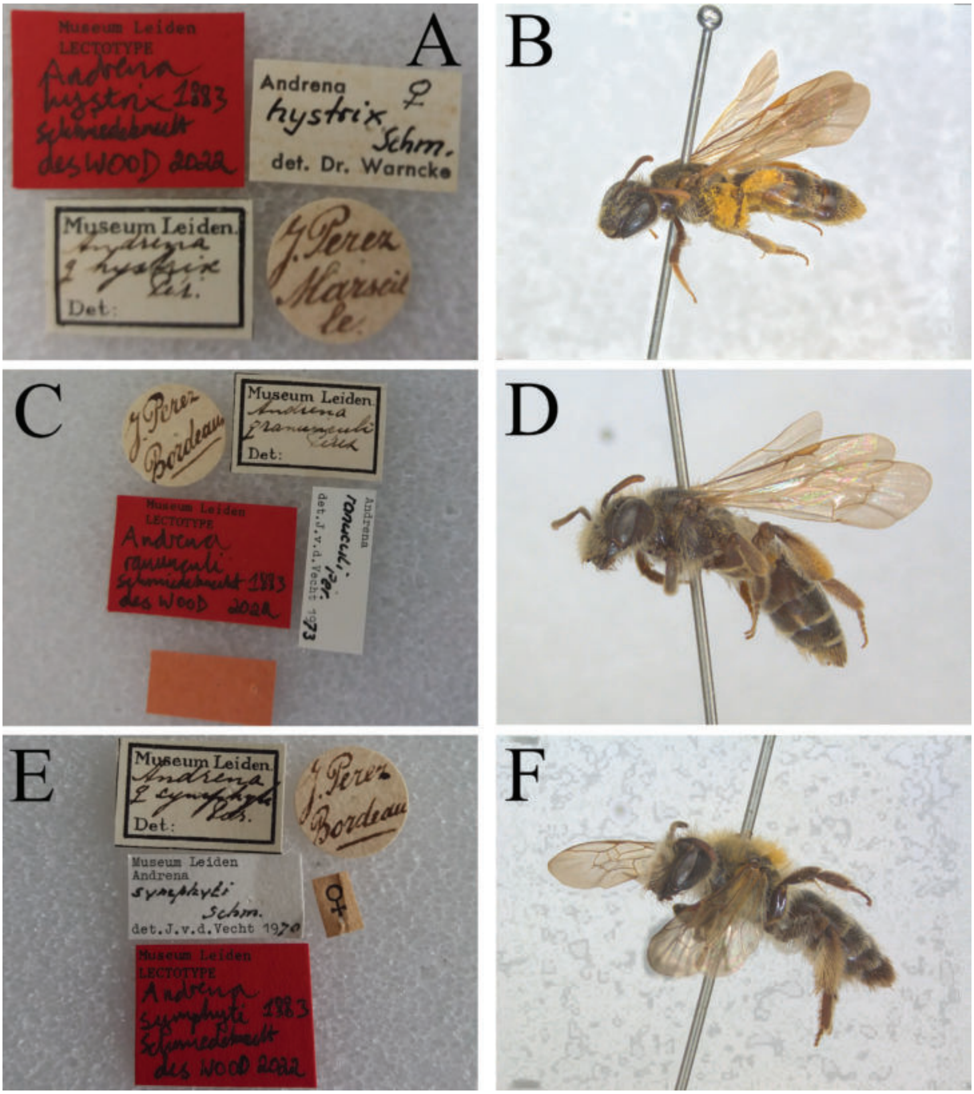

Figure 55. *Andrena* (*Aenandrena*) *hystrix* Schmiedeknecht, 1883, female lectotype **A** label details **B** profile; *Andrena* (*Notandrena*) *ranunculi* Schmiedeknecht, 1883, female lectotype **C** label details **D** profile; *Andrena* (*Euandrena*) *symphyti* Schmiedeknecht, 1883, female lectotype **E** label details **F** profile.

***Andrena* (*Notandrena*) *ranunculi* Schmiedeknecht, 1883**

Andrena (*Notandrena*) *ranunculi* Schmiedeknecht, 1883: 617, ♀♂ [France, lectotype by present designation: RMNH].

Remarks. Schmiedeknecht (1883) described *A. ranunculi*, comparing it to *A. ranunculorum*. He gave the habitat as Russia (referring to *A. ranunculorum*) and southern France (referring to the specimens received from Pérez). A series of males and females labelled by Pérez as being from Bordeau [sic, = Bordeaux] were found in the RMNH. These conform to Schmiedeknecht's description, and the concept used by subsequent authors. A female is here designated as a lectotype (Fig. 55C, D).

Material examined. **France:** Bordeaux [44.8352°N, -0.5888°E], 1♀, RMNH (lectotype by present designation; Fig. 55C, D); Bordeaux, 8♂, 5♀, RMNH.

***Andrena* (*Euandrena*) *symphyti* Schmiedeknecht, 1883**

Andrena (*Euandrena*) *symphyti* Schmiedeknecht, 1883: 583, ♀♂ [France, lectotype by present designation: RMNH].

Remarks. As for the previous two species, material labelled by Pérez was found in the RMNH collection. Two females and one male labelled as being from Bordeau [sic, = Bordeaux]. Schmiedeknecht (1883) specifically states that the type material comes from Bordeaux, writing "*In Gallia prope Bordeaux a Dom. Illustrissimo Perez detecta*". A female is here designated as a lectotype (Fig. 55E, F).

Material examined. **France:** Bordeaux [44.8352°N, -0.5888°E], 1♀, RMNH (lectotype by present designation; Fig. 55E, F); Bordeaux, 1♂, 1♀, RMNH.

Designation of neotypes

***Andrena* (*Chlorandrena*) *boyerella* Dours, 1872**

Andrena (*Chlorandrena*) *distincta* Lucas, 1849 nec. Smith, 1847 [Algeria: MNHN, not examined].
Andrena (*Chlorandrena*) *boyerella* Dours, 1872: 429, ♀♂ [Morocco: OÖLM].

Neotype. **Morocco:** Fès-Meknès, Azrou, 4 km SWW of Bakrit, Cascades Bakrit, 33.0466°N, -5.2681°E, 1650 m, 17.v.2022, 1♂, leg. T.J. Wood, OÖLM [BOLD accession number WPATW495-22] (Fig. 56).

Remarks. As discussed above, Dours (1872) described *A. boyerella* from southern France and Algeria. No material is available for study, as all of Dours' types were destroyed in a fire. Given that two taxa are present in these regions, in order to fix the name *A. boyerella* on the North African population, a barcoded neotype is designated from Moroccan material (Fig. 56).

Distribution. Morocco, Algeria, Tunisia, Italy (Sicily).

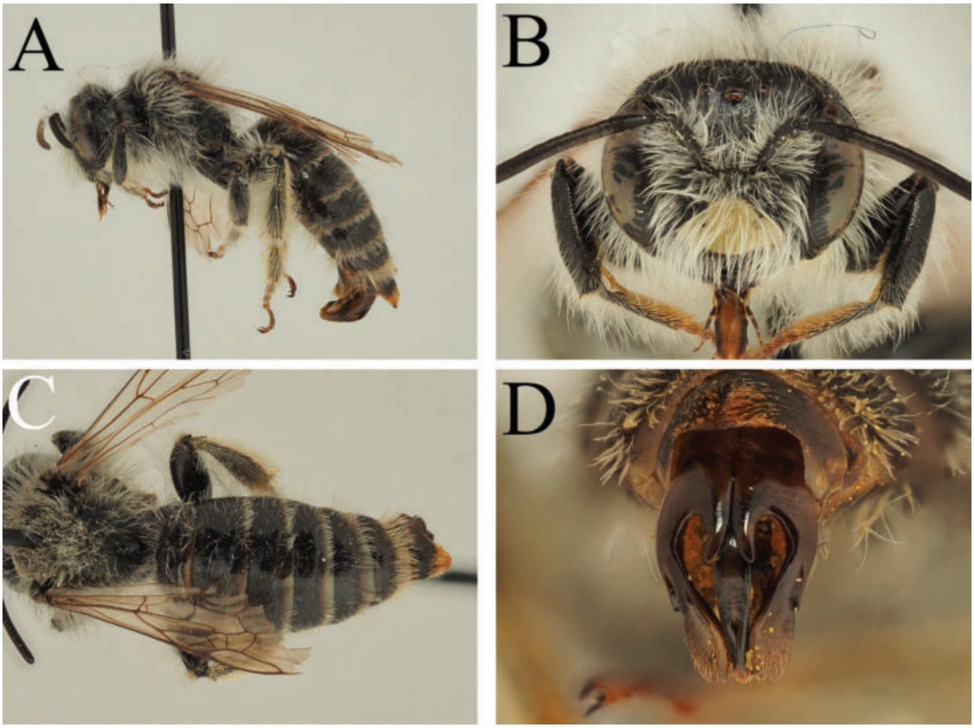

Figure 56. *Andrena* (*Chlorandrena*) *boyerella* Dours, 1872, male neotype **A** profile **B** face, frontal view **C** terga, dorsal view **D** genital capsule dorsal view.

Andrena (*Notandrena*) *griseobalteata* Dours, 1872

Andrena (*Notandrena*) *erythrocnemis* auctorum. nec. Morawitz, 1871.
Andrena (*Notandrena*) *griseobalteata* Dours, 1872: 427, ♀ [France: RMNH].

Neotype. **France:** Pyrénées-Atlantiques, Bérenx [43.4994°N, -0.8575°W], 6.vi.1987, 1♀, leg. E.A.M. Speijer, RMNH (Fig. 57).

Remarks. The correct name to apply to this distinctive taxon has been confused for many years. Through the combination of its large size (for a *Notandrena*) and densely punctate scutum it is comparable only to *A. ungeri* Mavromoustakis, 1952. The name *A. erythrocnemis* Morawitz, 1871 was used by many authors to refer to this taxon (e.g. Warncke 1967), but the lectotype of *A. erythrocnemis* is actually *A. chrysosceles* (see Proshchalykin et al. 2017; Astafurova et al. 2021). Gusenleitner and Schwarz (2002) resolved this issue by resurrecting *A. griseobalteata* to species status. Finally, Wood and Monfared (2022) removed *A. emesiana* Pérez, 1911 (southern Turkey, Syria, Iran) from synonymy with this taxon.

Although Gusenleitner and Schwarz (2002) would seem to have resolved the issue, there is no type specimen for *A. griseobalteata* due to the loss of Dours' collection. In the original description, Dours (1872: 428) listed the species from Saint-Sever in the department of Landes in south-western France, but also from Algeria. This is peculiar,

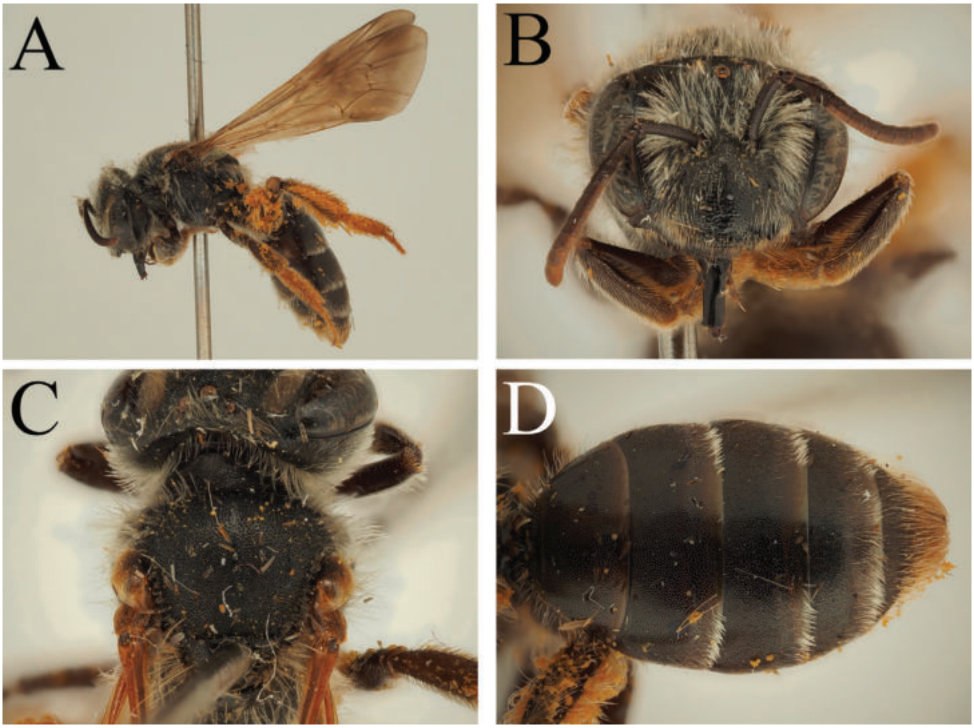

Figure 57. *Andrena* (*Notandrena*) *griseobalteata* Dours, 1872, female neotype **A** profile **B** face, frontal view **C** scutum, dorsal view **D** terga, dorsal view.

because *A. griseobalteata* is not known from North Africa. The original description also does not allow for completely unambiguous recognition of the species, though the dense punctation of the scutum is mentioned. In the interests of nomenclatural stability, a neotype from Bérenx in south-western France (36 km from Saint-Sever) is designated in order to fix the species concept for the future (Fig. 57).

Finally, though listed from Spain by Ortiz-Sánchez (2011, as *A. griseobalteata*; 2020, as *A. erythrocnemis*), the presence of this taxon in Spain is somewhat doubtful. The distribution maps of Warncke (Gusenleitner and Schwarz 2002) show dots around south-western France into the Pyrenees, but there are no unambiguous dots for Spain. However, I have been able to examine one specimen of *A. griseobalteata* from Spain, from the Sistema Central. The species is also expected to occur in the western Pyrenees; more recent material should be found to establish whether this taxon remains present in Iberia.

Material examined. **Spain:** Sierra de Gredos, 12 km SSW Hoyos del Espino, 1950–2100 m, 4.vii.1972, 1♀, leg. J.A.W. Lucas, RMNH.

Distribution. Spain, France, Italy, Croatia, Hungary, Albania, Romania, North Macedonia, Bulgaria, Greece, Turkey (western and northern Turkey; Gusenleitner and Schwarz 2002). The species is not considered to be present in North Africa, or in the Levant, as it is not found in very dry environments.

***Andrena* (*Taeniandrena*) *poupillieri* Dours, 1872**

Andrena (*Taeniandrena*) *poupillieri* Dours, 1872: 430, ♀ [Algeria: OÖLM].
Andrena (*Taeniandrena*) *poupillieri incana* Warncke, 1975a: 310, ♀♂ [Spain, Mallorca: OÖLM, examined].

Neotype. **Algeria:** Tizi-Ouzou, Tigzirt, 36.8877°N, 4.1140°E, 6 m, 31.iii.2017, 1♀, leg. H. Ikhlef, OÖLM [BOLD accession number HYMAA322-22] (Fig. 58).

Remarks. This is the taxon referred to as '*A. poupillieri* 2' by Praz et al. (2022). The taxon *A. poupillieri incana* Warncke, 1975 which was described from and restricted to the Balearic Islands is considered a simple synonym of *A. poupillieri* due to the lack of genetic differentiation observed (see above), even though the tergal punctation is slightly reduced compared to the nominate taxon. The specimen used in the analysis of Praz et al. (2022) is designated as a lectotype (Fig. 58).

Distribution. Morocco, Algeria, Tunisia, Spain (mainland and Balearic Islands). Records (Gusenleitner and Schwarz 2002) from Libya must be confirmed, though they probably do refer to true *A. poupillieri*. Records from Crete probably refer to unrecognised *A. ovata* specimens, and so *A. poupillieri* is not considered to be present there until definitive material is located.

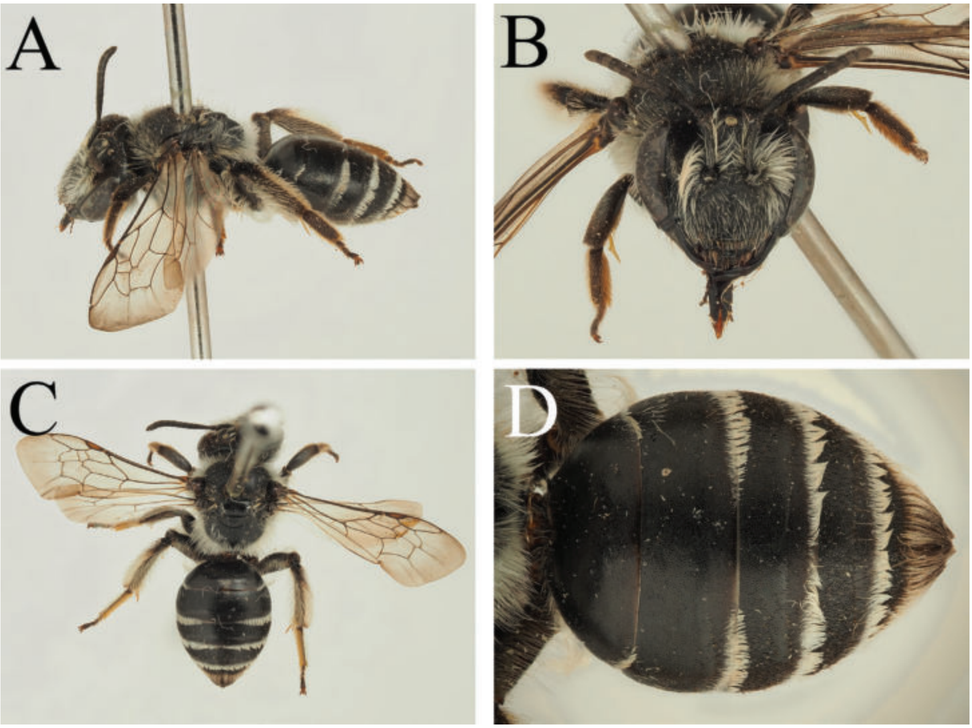

Figure 58. *Andrena* (*Taeniandrena*) *poupillieri* Dours, 1872, female neotype **A** profile **B** face, frontal view **C** dorsal view **D** terga, dorsal view.

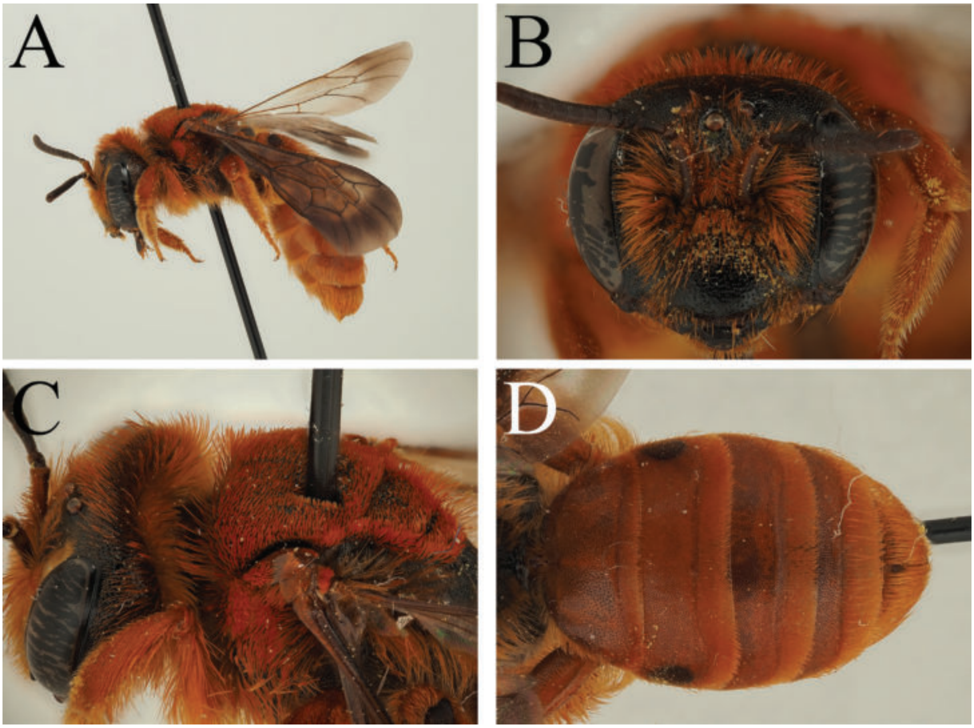

Figure 59. *Andrena* (*Pruinosandrena*) *succinea* Dours, 1872, female neotype **A** profile **B** face, frontal view **C** mesosoma, dorsolateral view **D** terga, dorsal view.

Andrena (*Pruinosandrena*) *succinea* Dours, 1872

Andrena succinea Dours, 1872: 424, ♀ [Morocco: OÖLM].

Neotype. Morocco: Oriental, Guercif, P5427, 2 km SW of Bou Rached, 33.8844°N, -3.6154°W, 950 m, 13.v.2022, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW389-22] (Fig. 59).

Remarks. As discussed above, it is preferable to designate a neotype for *A. succinea* in order to maintain nomenclatural stability. The barcoded specimen pictured in Fig. 34B is selected as a neotype (Fig. 59) in order to fix the species concept for the future.

Distribution. Morocco, Algeria, Tunisia, Libya, Egypt, Israel and the West Bank, Jordan, Syria, Saudi Arabia, Iran (Wood and Monfared 2022).

Andrena (incertae sedis) *numida* Lepeletier, 1841

Andrena numida Lepeletier, 1841: 252, ♀ [Morocco: OÖLM].

Neotype. Morocco: Fès-Meknès, Azrou, P7311, 10 km S of Ain Leuh, 1750 m, 33.2220°N, -5.3411°W, 18.v.2022, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW484-22] (Fig. 60).

Figure 60. *Andrena* (incertae sedis) *numida* Lepeletier, 1841, female neotype **A** profile **B** face, frontal view **C** dorsal view **D** T2–5, dorsal view detail.

Remarks. As discussed above, it is beneficial to designate a neotype for *A. numida* since the original type series cannot be located in the MNHN, and so that the name and genetic identity of North African populations can be fixed.

Distribution. Morocco, Algeria, Tunisia, Libya, Italy (Sicily, Calabria, Campania).

Updated faunal list

Ortiz-Sánchez (2020) lists 212 species of *Andrena* from Spain. However, given the taxonomic and faunal work that has been conducted since then, this total is slightly too low and contains mistakes resulting from taxonomic confusion and the use of variable species concepts in the literature.

Species removed from baseline list

Following the changes detailed in the previous sections, *A. boyerella*, *A. creberrima*, *A. curtula*, *A. hispania*, *A. mariana* s. str., *A. potentillae*, *A. pusilla*, and *A. truncatilabris* are removed from the Iberian fauna following their listing by Ortiz-Sánchez (2020). Four further species must also be removed, *A. similis* Smith, 1849, *A. enslinella* Stöckhert, 1924, *A. simillima* Smith, 1851, and *A. chrysopyga* Schenck, 1853. *Andrena* (*Taeniandrena*) *similis* was shown to be a synonym of *A.* (*Taeniandrena*) *russula* Lepeletier, 1841 by Praz et al. (2022). Ortiz-Sánchez (2020) listed both species as present.

Dardón (2010) and Dardón et al. (2014) listed *A.* (*Micrandrena*) aff *enslinella* as present in Spain based on the listing of Warncke (1976) and the specimen in his collection. I do not consider this to be ecologically possible, as *A. enslinella* is a species of Central and Eastern Europe to the Caucasus and Iran, having its western limit in Germany and Austria. The species appears to be absent from France (Le Divelec 2021). Given the highly interesting *Andrena* fauna in the Sistema Ibérico that contains relictual North African taxa such as *A.* (*Cordandrena*) *vaulogeri* Pérez, 1895 and the endemic *A.* (*Parandrenella*) *taxana* Warncke, 1975, further study is required, as this specimen may represent an undescribed species, as suggested by Dardón (2010).

Andrena (*Cnemidandrena*) *simillima* was listed by Ortiz-Sánchez (2020), but not by Warncke (1976). The distribution maps of Warncke (Gusenleitner and Schwarz 2002) give a single isolated dot for this species in north-eastern Spain, presumably in the eastern Pyrenees. The next closest record comes from western France (c. 400 km), with no other records for the Pyrenees. Warncke et al. (1974: carte 140) gave Bordeaux as the south-western limit for *A. simillima* (specimen leg. Pérez, coll. Warncke OÖLM). I consider the dot on the maps of Gusenleitner and Schwarz (2002) to be of doubtful providence; I have examined no material from Iberia of this species, and I could not locate a Spanish specimen in the Warncke collection. No other authors have ever recorded *A. simillima* from the Pyrenees, though *A.* (*Cnemidandrena*) *nigriceps* (Kirby, 1802) is common in this region. Males of *A. simillima* and *A. nigriceps* are extremely difficult to separate, and it is possible that this dot represents a misidentification of *A. nigriceps*. Moreover, this record is ecologically questionable, since *A. simillima* is predominantly a northern species (sensu lato, since cryptic taxa may be present) found in temperate habitats. In the absence of available specimens, the isolated nature of this record, and the identification difficulties associated with this group, I remove *A. simillima* from the Iberian fauna.

Finally, *A.* (*Melandrena*) *chrysopyga* is listed as present in Iberia. I have seen no Iberian material of this taxon which is generally very rare in collections. It is often confused with forms of *A. gravida* with light hairs in the terminal fringe. In the distribution maps of Warncke (Gusenleitner and Schwarz 2002), there are dots for *A. chrysopyga* from south-western France, but none in Iberia proper. *Andrena chrysopyga* is a species of dry grassland and steppe, extending east across the Great Eurasian Steppe to Kazakhstan. Given the absence or scarcity of steppe habitats in France, its presence in much of the country seems ecologically unlikely. Given the overly generous distribution of *A. chrysopyga* given by Warncke (e.g. the species is known only from the extreme east of Belgium yet Warncke's map indicates the presence of this taxon throughout Belgium, see Wood 2023a), the lack of available specimens, and the identification mistakes known to occur between *A. chrysopyga* and *A. gravida*, *A. chrysopyga* is not considered to be part of the Iberian fauna until such a time as validated specimens can be found or the species can be newly captured. Its historical and contemporary distribution in France must also be clarified, as I believe that most records are misidentifications of *A. gravida*.

Species added to baseline list

In addition to the species elevated above or newly described below, the following 15 *Andrena* species were explicitly added to the Iberian fauna by the following works: *A.* (incertae sedis) *laurivora*, *A.* (*Notandrena*) *juliana* Wood, 2021, *A.* (*Euandrena*) *fortipunctata* Wood, 2021, *A.* (*Taeniandrena*) *benoisti* Wood & Praz, 2021, and *A.* (*Taeniandrena*) *levante* Wood & Praz, 2021 (Wood et al. 2021); *A.* (*Plastandrena*) *nigrospina* Thomson, 1872 (Ortiz-Sánchez et al. 2022); *A.* (*Taeniandrena*) *afzeliella* (Kirby, 1802) and *A.* (*Taeniandrena*) *ovata* Schenck, 1853 (Praz et al. 2022); *A.* (*Avandrena*) *erodiorum* Wood & Ortiz-Sánchez, 2022, *A.* (*Avandrena*) *melacana* Warncke, 1967, *A.* (*Taeniandrena*) *lusitania* Wood & Ortiz-Sánchez, 2022, and *A.* (*Suandrena*) *gades* Wood & Ortiz-Sánchez, 2022 (Wood & Ortiz-Sánchez, 2022); *A.* (incertae sedis) *ramosa* Wood, 2022 (Wood et al. 2022a); *A.* (*Taeniandrena*) *contracta* Wood, 2022 (Wood 2022); and *A.* (*Andrena*) *clarkella* (Kirby, 1802) (Álvarez Fidalgo and Aguado Martín 2022).

Therefore, relative to the baseline of Ortiz-Sánchez (2020), 12 species are removed, and 28 species are added (including *Andrena* aff *mica*). In sum, the taxonomic changes and faunal updates presented here and in the referenced papers brings the Iberian *Andrena* fauna to 228 species, a substantial increase on the 175 species recorded by Warncke (1975a), with 228 species known from mainland Spain and 128 species from mainland Portugal. A full checklist can be found in Suppl. material 1.

Dietary niche of Iberian *Andrena* species

Results are presented here for Iberian species for which no or very little previous dietary data have been published. Consequently, these results are not comprehensive, but it is not considered necessary to duplicate here previous analyses that have been conducted in Central Europe (e.g. Westrich 1989) when these same species do not differ in their pollen foraging behaviour in Iberia. Pollen was analysed and removed from a total of 1,127 specimens from 76 species from 12 countries. Findings are summarised in Table 1. *Andrena* species are grouped by subgenus to highlight their often conserved patterns of pollen collection.

Demonstration of oligolecty in understudied species

For many Iberian endemic or West Mediterranean species, an oligolectic dietary niche was clearly and unambiguously demonstrated by pollen analysis. In many cases, specialised pollen use was as expected based on known subgeneric traits, such as the exclusive use of Asteraceae by the subgenus *Chlorandrena* and Brassicaceae by the subgenera *Aciandrena* and *Nobandrena* Warncke, 1968.

It is important to note some pollen collection preferences. Within the *Notandrena*, members of the former *Carandrena* are typically associated with Brassicaceae such as *A. aerinifrons* (Fig. 61A). However, two species deviate from this pattern, *A. bellidis* Pérez, 1895 and *A. leucophaea* Lepeletier, 1841. *Andrena bellidis* appears to be polylectic,

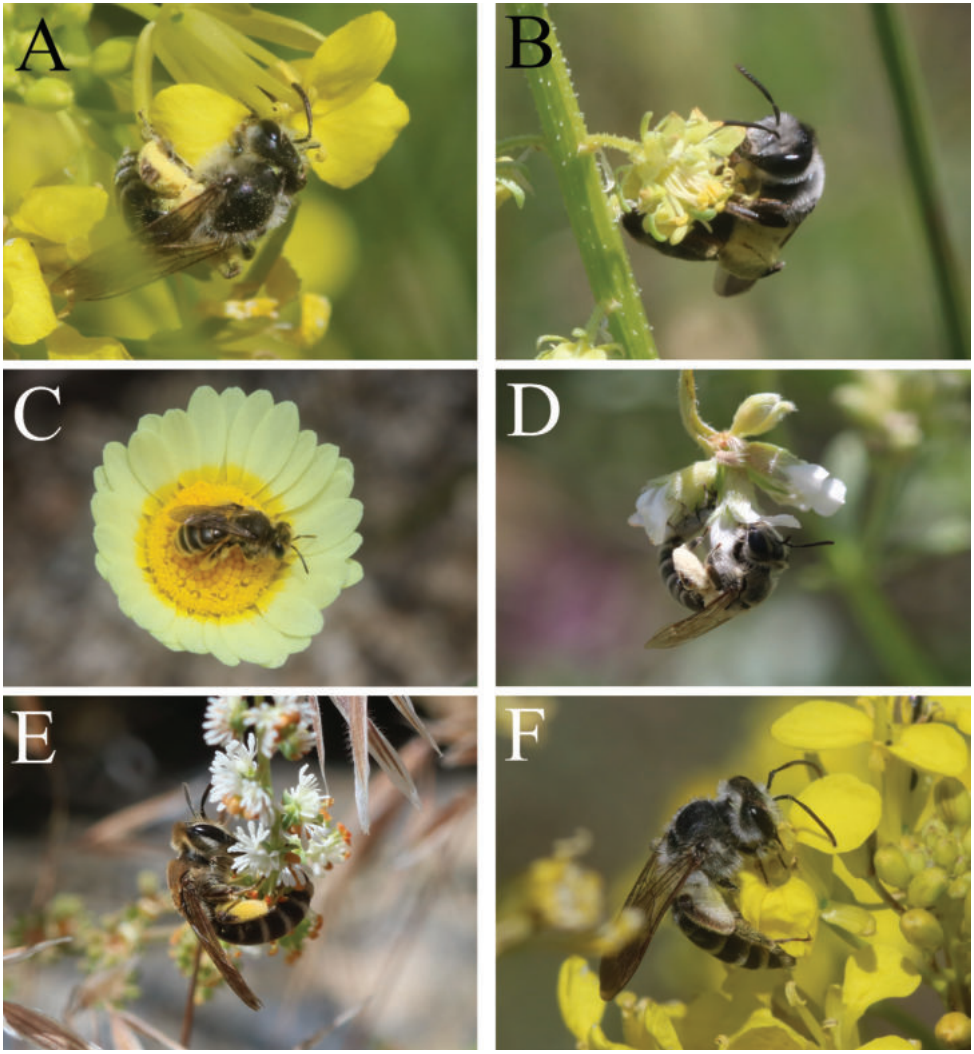

Figure 61. Pollen specialist (oligolectic) *Andrena* species in Iberia **A** *Andrena* (*Notandrena*) *aerinifrons* Dours, 1873 (Brassicaceae) **B** *Andrena* (incertae sedis) *corax* Warncke, 1967 (*Reseda*, Resedaceae) **C** *Andrena* (*Chlorandrena*) *elata* Warncke, 1975 (Asteroideae, Asteraceae) **D** *Andrena* (*Ovandrena*) *farinosa* Pérez, 1895 (*Lotus dorycnium*, Fabaceae) **E** *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895 (*Reseda*, Resedaceae) **F** *Andrena* (*Simandrena*) *vetula* Lepeletier, 1841 (Brassicaceae).

whereas *A. leucophaea* was associated with *Bellis* (Asteraceae; Asteroideae) and may be oligolectic on this subfamily. Both species fly early in the year (typically February-April) and are uncommon in collections; more study is required, but neither species is likely to be specialised on Brassicaceae.

Members of the *relata*-group appear to be specialised on *Reseda* (Resedaceae), including *A. corax* (Fig. 61B). Based on direct observations, all five Iberian members of the *relata*-group (including *A. macroptera* and *A. murana*) appear to be narrowly oligolectic on *Reseda*, but additional pollen analysis is necessary for confirmation; this being limited by the scarcity of these species in collections.

All studied members of the subgenus *Chlorandrena* are specialists of Asteraceae. However, the only published associations relate to the subfamily Cichorioideae (e.g. Westrich 1989; Schwenninger 2015). However, three Iberian *Chlorandrena* collect exclusively from Asteraceae subfamily Asteroideae: *A. abrupta*, *A. elata* (Fig. 61C), and *A. leucolippa*. These three species form a clade within the *Chlorandrena* along with *A. boyerella* which is also specialised on Asteraceae subfamily Asteroideae (data to be published in the North African revision). This situation resembles the situation within the genus *Panurgus*, members of which are specialised on Asteraceae but for which members of different lineages within *Panurgus* utilise either Asteroideae or Cichorioideae (Wood et al. 2022b).

Within the newly erected subgenus *Ovandrena*, no clear pattern was seen, as *A. farinosa* is a specialist of small-flowered Fabaceae (Fig. 61D) and *A. oviventris* is a specialist of *Reseda* (Fig. 61E). At the moment, *A. farinosa* must be considered a broad oligolege, as the identity of pollen grains removed from museum specimens cannot be identified to the genus level. In Iberia, all my observations of this species come from *Lotus dorycnium* Linnaeus (=*Dorycnium pentaphyllum* Scopoli), and so the species may be more narrowly specialised on the genus *Lotus*, but this requires additional study.

Within the subgenus *Simandrena*, central and northern European species are well-known to be polylectic (Westrich 1989). In contrast, three West Mediterranean species appear to be oligolectic, *A. vetula* (Fig. 61F) and *A. antigana* Pérez, 1895 on Brassicaceae and potentially *A. rhypara* Pérez, 1895 on *Reseda*. All three species belong to the group of *Simandrena* with a strongly shagreened and almost impunctate scutum that is distributed predominantly across the Mediterranean basin, with the highest diversity in North Africa and the Levant. Further study is required to establish the dietary niche of *A. cilissaeformis* which may be polylectic.

Most studied members of the subgenus *Truncandrena* are specialised on Brassicaceae (Westrich 1989), though this subgenus is species-poor in Central Europe and most taxa are Mediterranean and understudied. In Iberia, *A. doursana*, *A. ferrugineicrus*, and *A. nigropilosa* are also specialised on Brassicaceae. However, *A. villipes* was strongly associated with *Cistus* (Cistaceae) based on pollen analysis and direct observations, a behaviour that has not previously been demonstrated for this subgenus. As discussed above, this is likely to be the dietary niche for *A. ghisbaini*, the two species together appear basally in the COI phylogeny (Fig. 29). Additional study is required to establish whether this basal position is supported by more powerful genetic analyses.

The subgenus *Micrandrena* contains mixture of oligolectic and polylectic species in central and northern Europe, though polylectic species predominate (Westrich 1989). In Iberia, numerous species display oligolectic behaviour, specifically *A. ampla* (Apiaceae), *A. djelfensis* and *A. fabrella* Pérez, 1903 (Cistaceae), *A. longibarbis*, *A. nitidula*, *A. orana*, and *A. tenuistriata* (Brassicaceae), and *A. omnilaevis* (Crassulaceae). The dietary status of *A. spreta* is somewhat unclear, as specimens from both the spring and summer generations analysed here collected predominantly Brassicaceae pollen (93.1%). There is a bias towards spring generation specimens which are typically more abundant, and which fly at a time of year with high Brassicaceae availability. Additional samples from the summer generation are required, but the species can provisionally be considered to be polylectic with a strong preference for Brassicaceae.

There was one species for which the empirical data slightly conflicts with what I believe to be the true dietary niche. For *A.* (*Avandrena*) *panurgina*, the pollen results showed that 93.6% of collected pollen came from Geraniaceae, with the remaining pollen from Asteraceae and Brassicaceae. Following the criteria of Müller and Kuhlmann (2008), this species would not necessarily be classified as oligolectic on Geraniaceae. However, Geraniaceae pollen grains are very large, usually in excess of 50 μm, and it is possible for contaminant pollen to be present between these large grains in a way that is much less common when dealing with smaller grains which pack into scopal hairs more tightly. Behavioural observations of *A. panurgina*, including those of males which patrol around *Erodium* (Geraniaceae) plants in March and early April, strongly suggests oligolecty on Geraniaceae. All behavioural pollen-foraging observations of *A. panurgina*, along with other western *Avandrena* Warncke, 1968 species *A. avara*, *A. erodiorum*, and *A. melacana* Warncke, 1967 have been made at *Erodium* (Wood and Ortiz-Sánchez 2022; pers. obs., Álvarez Fidalgo in litt.). Consequently, the presence of Asteraceae and Brassicaceae pollen in the quantitative analysis is considered likely to be contamination, and *A. panurgina* is considered to be an oligolege of Geraniaceae along with the other western *Avandrena* species (see Pisanty et al. 2022a).

The data presented here also resolve the pollen collection preferences of the West Mediterranean *A.* (*Rufandrena*) *orbitalis* Morawitz, 1871 and *A.* (*Rufandrena*) *rufiventris* Lepeletier, 1841 which belong to the subgenus *Rufandrena* Warncke, 1968 that may contain three species, with a further species known from Syria and Hatay province in Turkey (Wood 2023b) which requires genetic confirmation of its placement. The two West Mediterranean species are instantly recognisable in the female sex because of their extraordinarily long and incredibly plumose hairs of the tibial and femoral scopae and both flocculi (see Fig. 64H). Baldock et al. (2018) identified the use of *Plantago* (Plantaginaceae) pollen by *A. orbitalis*, but did not come to a firm conclusion as to the overall dietary niche of this species. Analysis of scopal pollen loads and behavioural observations (*A. orbitalis* in the Algarve, Portugal and *A. rufiventris* in the Middle Atlas, Morocco) show that both *A. orbitalis* and *A. rufiventris* are specialists of *Plantago*. In the spring, usually in the months of March and April, both species can be seen visiting low-growing *Plantago* species. Upon arriving (Fig. 62C) at a small flower head, they grab onto its side and present the underside of their body so that falling grains will land on their venter and scopae (Fig. 62A). They will then manipulate the anthers using their fore legs and mandibles (Fig. 62D), often directly scraping pollen from the anthers using their mandibles (Fig. 62E). When the flower head is long, they will sometimes work from bottom to top, often vigorously dislodging pollen grains that can form a small but distinctly visible cloud (Fig. 62B). Pollen landing on the body is then groomed into the scopae.

As *Plantago* is wind-pollinated, it does not provide a nectar source. Nectar is therefore collected from other plants such as *Crepis* (Asteraceae), *Malva* (Malvaceae, Álvarez Fidalgo in litt.), or *Reseda* (Fig. 62F). Pollen is packed into the scopae dry, and inspection of freshly caught and pinned specimens shows that pollen rapidly falls out of the scopae with gentle manipulation, for example with an entomological pin. This

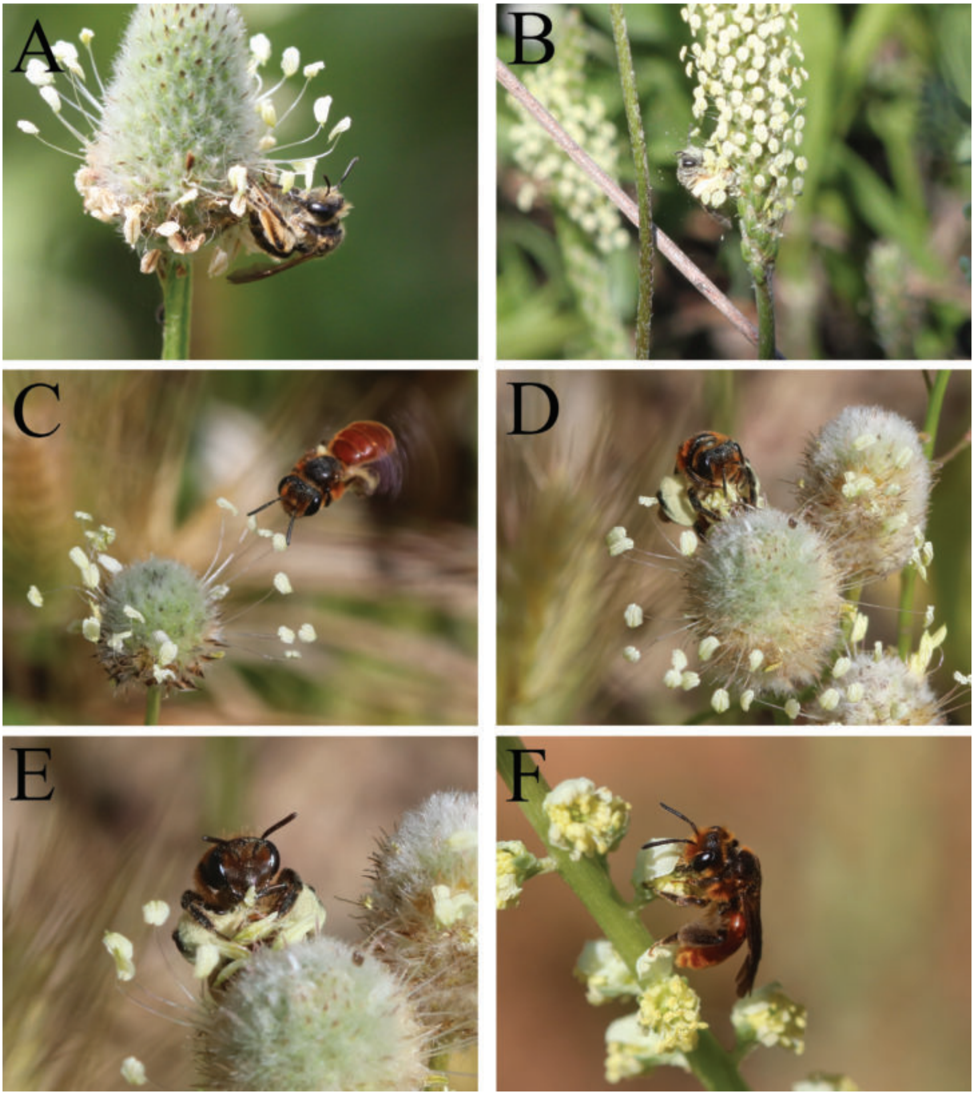

Figure 62. Use of *Plantago* (Plantaginaceae) pollen by *Rufandrena* Warncke, 1968 species. *Andrena* (*Rufandrena*) *orbitalis* Morawitz, 1871 **A** female, manipulating *Plantago* anther **B** female, vigorously collecting *Plantago* pollen; *Andrena* (*Rufandrena*) *rufiventris* Lepeletier, 1841 **C** female approaching *Plantago* flower head **D** female manipulating *Plantago* anthers with forelegs and mandibles **E** female scraping pollen from *Plantago* anther using mandibles **F** female drinking nectar at *Reseda* (Resedaceae) with empty scopae.

probably explains both why the scopal hairs are so densely and finely plumose in order to retain these small pollen grains (typically <20 μm in diameter), and also why very few specimens in museum collections have scopae that retain pollen, as dry grains are easily dislodged after specimen collection. Use of pollen from wind-pollinated plants is well-known in bees, predominantly by social polylectic species (Saunders 2018), but also by solitary species, including species belonging to genera such as *Lipotriches* Gerstaecker, 1858 (Halictidae) that can be oligolectic upon members of the Poaceae (Immelman and Eardley 2000). Whilst some *Andrena* species are known to collect pollen from wind-pollinated plants (Wood and Roberts 2017; Saunders 2018), to my knowledge this is the first time that any *Andrena* species has been demonstrated to be specialised for pollen collection on a wind-pollinated plant.

Finally, a note on the pollen collection preferences of *A. afzeliella* and *A. ovatula* is beneficial. Praz et al. (2022) demonstrated that *A. afzeliella* is polylectic with a strong preference for Fabaceae, and *A. ovatula* is oligolectic on Fabaceae. Additional detail and context can be provided based on observations in Iberia which help to explain their differing distributions and ecologies. *Andrena afzeliella* typically visits herbaceous Fabaceae, such as *Trifolium pratense*. It visits honestly, and does not manipulate the flowers beyond what is typically expected in an 'honest' visit. It can be found commonly on the open steppe habitats of Old Castile, for example in Segovia, Castroserna de Abajo, Buitreras y Cuevas (25.vii.2021, Fig. 63A, B). In contrast, *A. ovatula* prefers areas with an Atlantic influence that host members of the tribe Genisteae (Fabaceae), usually woody species (e.g. *Cytisus*, *Genista*, *Ulex*, etc.). Here it visits these flowers honestly for nectar, but roughly manipulates the petals with its two front pairs of legs and its mandibles in order to access the anthers. This can be seen in western and north-western Iberia, as well as in the Sistema Central such as at Segovia, Riofrío de Riaza, Embalse de Riofrío (27.vii.2021, Fig. 63C–F). In my experience, I have never observed *A. afzeliella* manipulating Fabaceae flowers like this. The relationship with woody Genisteae may explain the earlier emergence of the first generation of *A. ovatula* (peaking April compared to May for *A. afzeliella*; see typical emergence patterns in north-western Europe in Praz et al. 2022) due to the earlier flowering of woody Fabaceae relative to herbaceous Fabaceae. Consequently, *A. ovatula* is typically not encountered in open steppe habitats, whereas *A. afzeliella* typically avoids western parts of Iberia with a strong Atlantic influence.

Pollen use by bivoltine species

A widespread behaviour within *Andrena* is bivoltinism, i.e. species producing a spring and a summer generation. For several bivoltine species, their dietary niche is not yet clear. There is a lack of clarity over two species within *Aenandrena*. For the 15 pollen loads of *A. aeneiventris* (collected between 11th June and 25th July) and the 22 pollen loads of *A. hedikae* (collected between 21st May and 25th July), each load was comprised entirely of Apiaceae pollen. However, both species are bivoltine, and pollen loads from the spring generation must be analysed. Osytshnjuk et al. (2005) state that both species visit Brassicaceae in the spring generation, and Kocourek (1966) gives a

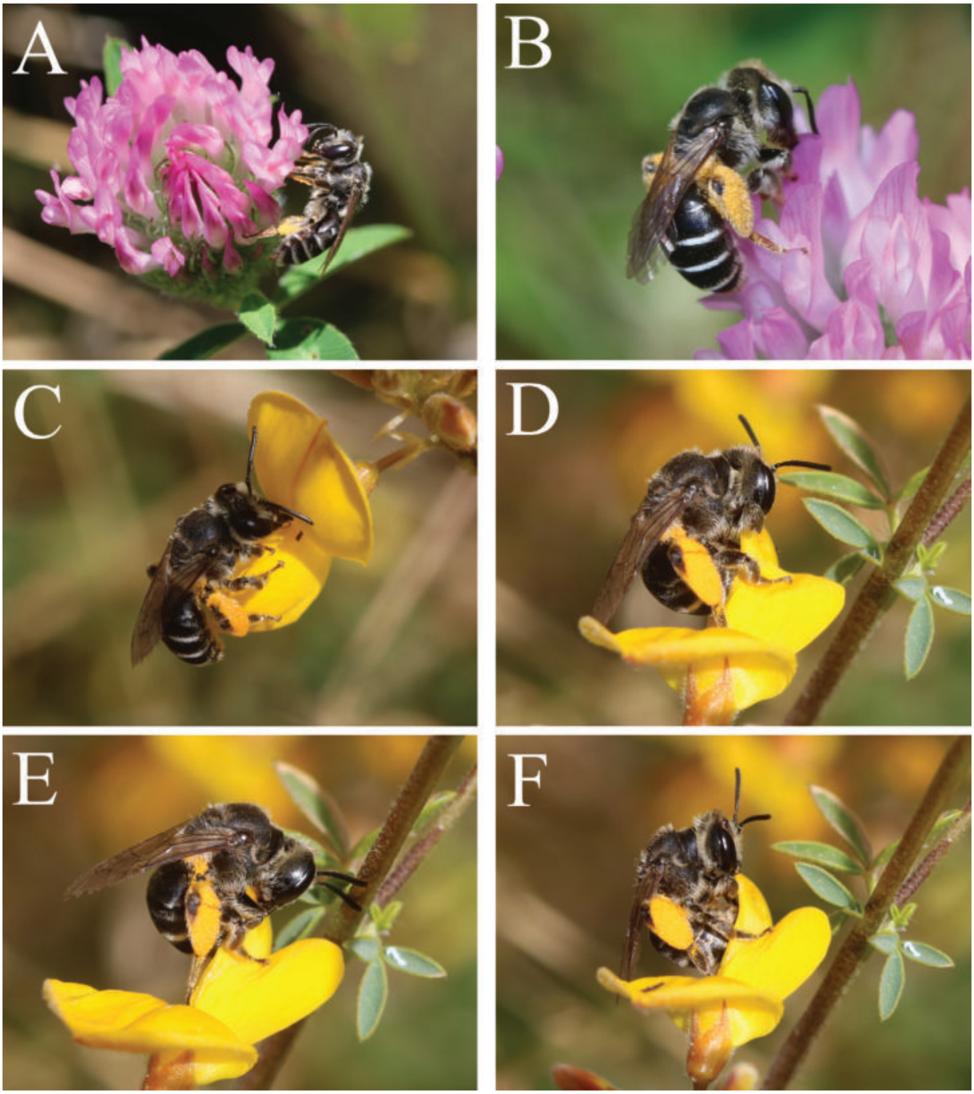

Figure 63. *Andrena* (*Taeniandrena*) *afzeliella* (Kirby, 1802) **A, B** foraging female at *Trifolium pratense* (Fabaceae); *Andrena* (*Taeniandrena*) *ovatula* (Kirby, 1802) **C–F** foraging female at Genistae spp. (Fabaceae).

list of several Brassicaceae species along with *Sedum* (Crassulaceae) and *Euphorbia* (Euphorbiaceae). I have personally never observed *A. aeneiventris* at flowers of Brassicaceae in the West Mediterranean despite extensively searching this botanical family during the Iberian spring for the large number of univoltine species that specialise on this family. However, in an Iberian context, both species are quite uncommonly observed and collected in their first generation, certainly compared to their abundance in the summer. More study is required, and neither species should be classified as oligolectic on Apiaceae until more pollen load data are available, ideally also from other parts of southern to south-central Europe. A similar problem is found within the subgenus *Brachyandrena* Pittioni, 1948. Very few pollen loads were available for analysis, but both *A. colletiformis* and *A. miegiella* Dours, 1873 were found to only collect Apiaceae pollen. Both species are also bivoltine. Osytshnjuk et al. (2005) state that *A. colletiformis* visits a variety of botanical families, but prefers the Apiaceae. In this dataset, pollen bearing-specimens of *A. colletiformis* were collected between 25th April and 20th July, thus encompassing both generations. More study is required to establish if pollen sources other than Apiaceae are utilised. Based on observations, they are almost exclusively found on Apiaceae and can be provisionally considered oligolectic on this family.

In contrast, *A. verticalis* provides an example of a bivoltine species that uses Apiaceae, but not exclusively. *Andrena verticalis* flies between March and August, and in this dataset collects 56.3% of its pollen from Brassicaceae (mostly in the spring) and 43.8% of its pollen from Apiaceae (mostly in the summer). However, the use of specific botanical families is not restricted to the two generations, and instead is based on local availability. Interestingly, no mixed pollen loads were detected in the 30 pollen loads examined here, each consisting only of a single botanical family. This recurring pattern of Apiaceae and Brassicaceae use within bivoltine species can be seen for *A. hypopolia*, which also displays mesolecty on these two families. Additional study is required across these aforementioned species to robustly test the limits of mesolecty on Apiaceae and Brassicaceae across two generations (*A. verticalis* and *A. hypopolia*), oligolecty on Apiaceae in both generations (possibly *A. colletiformis* and *A. miegiella*), and possible oligolecty in each generation but upon a different botanical family (potentially *A. aeneiventris* and *A. hedikae*).

Finally, it is necessary to discuss the case of *A. mucida* which appears to be differentially oligolectic in its spring and summer generation. The terminology surrounding pollen use in bees has been refined and categorised several times in recent years (Cane and Sipes 2006; Müller and Kuhlmann 2008; Kuhlmann and Timmermann 2011; Cane 2020), with debate over how broad or how narrow to make the existing categories. However, to my knowledge, no examples of bee species displaying different specialisation in different generations has been provided or discussed, much less this behaviour formally named. Kocourek (1966) noted the differential foraging behaviour of *A. mucida*, stating that the 1st generation visited *Salix* and *Muscari*, with the 2nd generation visiting *Scabiosa*. Unlike the case in some bivoltine *Andrena* species that may display differential levels of specialisation between generations but which cannot unambiguously be assigned to a specific generation morphologically (e.g. some *Micrandrena*), *A. mucida* displays simple tibial scopal hairs in the spring generation, and plumose tibial scopal hairs in the summer generation. Individuals can therefore be assigned to each generation with confidence (rather than based only on collection date), and when combined with pollen analysis the data confirm this differential pollen collection behaviour. Therefore, is *A. mucida* simply a polylectic species, or rather differentially oligolectic? Given the possibly unique nature of this behaviour, it would be beneficial to formally name this pattern of pollen collection *heterolecty*, in which a species is i) bivoltine, ii) oligolectic in both generations, and iii) each generation is oligolectic on different botanical families. This name will highlight this highly unusual behaviour, rather than have it hidden away under an all-encompassing 'polylecty'.

Summary for pollen use by Iberian *Andrena* species

For the 75 Iberian species (not including *A. rufiventris*) for which pollen data are presented, the majority are oligolectic or assessed as likely to be oligolectic. Excluding species for which insufficient data are available to allow confident classification (*A. aeneiventris*, *A. colletiformis*, *A. hedikae*, and *A. miegiella*), 49 species are classified as oligolectic, 21 as polylectic, and one (*A. mucida*) as heterolectic. This high proportion of oligolectic species, most of which have their pollen preferences demonstrated here for the first time, illustrates the degree to which the Iberian fauna i) hosts many specialised species and ii) has been chronically understudied with regard to the basic biology of its constituent bee species. Within the oligolectic species studied here, there is a clear preference for Brassicaceae, this family hosting 22 species, followed by Asteraceae (n=10), Resedaceae (n=6), Cistaceae (n=3), Geraniaceae (n=3), Apiaceae (n=2), and Crassulaceae, Fabaceae, and Plantaginaceae (n=1 each). The broader faunal trends shown by Iberian *Andrena* species will be examined in detail in a subsequent publication.

Identification key

The males of *A. cilissaeformis*, *A. erodiorum*, *A. foeniculae*, *A. juliae*, *A. macroptera*, *A.* aff *mica*, *A. ortizi*, *A. tenostra*, and *A. urdula* are currently unknown, so they are not included in the key; a level of caution must therefore be taken when working with morphologically similar species. The Spanish *A. allosa* Warncke, 1975 is unknown to me, so the relevant couplet is based on material from the Alps (see Praz et al. 2019).

Unfortunately, after consideration, I have also decided to exclude the male of *A. exigua* from the key because its confident determination is not clear to me. Existing literature (Gusenleitner and Schwarz 2002; Dardón et al. 2014) is light on detail, and my own examination of extremely limited material has not cemented the concept. Due to the nominal rarity of this taxon, no material was available for genetic study, further limiting the confidence with which the sexes can be associated. Confident sex association and determination of *A. exigua* males must remain an open question for students of the Iberian fauna.

For supplementary illustrations, please consult the works cited in the Methodology, particularly Schmid-Egger and Scheuchl (1997) for Euro-Siberian species, as well as my publications describing Iberian species. Moreover, in the near future, the ongoing ORBIT project (providing taxonomic resources for European bees, https://orbit-project.eu/) will provide images for all European *Andrena* species. Between this key and the images presented there, confident determination should be possible in the majority of cases.

The female and male keys are separated for convenience. For the female key, the following shortcuts can be used:

A. Posterior face of hind femur with latitudinal row of spines or teeth .... **go to 2**

B. Hind tibial spur clearly broadened, either at its base or submedially. Large to very large species, at least 12 mm in length .... **go to 25**

C. Hairs of the tibial scopae clearly plumose .... **go to 42**

D. Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate .... **go to 51**

E. Scutum and scutellum with squamous hairs .... **go to 55**

F. Viewed laterally, propodeal corbicula with internal surface (lateral faces of the propodeum) glabrous AND propodeal corbiculae complete (possessing both a dorsal and anterior fringe (subgenus *Simandrena*) .... **go to 64**

G. Fovea strongly constricted medially, strongly diverging from the inner margin of the compound eye dorsally (former subgenus *Hyperandrena*).............. **go to 75**

H. At least some tergal discs extensively red-marked................................ **go to 77**

I. Head, mesosoma, or tergal discs with metallic reflections (note, *A. nigroaenea* (Kirby) can have bronzy reflections on the terga; if the tibial scopa is composed at least partly of orange-red hairs, go to 205)...................................... **go to 84**

J. Small black species, body length under 8 mm, or if up to 10 mm then with lateral faces of the propodeum with clear pattern of raised star-shaped wrinkles (all members of the subgenera *Aciandrena*, *Graecandrena*, *Micrandrena*) ...... **go to 92**

K. Clypeus flattened over majority of its surface (subgenus *Taeniandrena*) ...**go to 139**

L. Fovea dorsally narrow, occupying at most ⅓ of space between lateral ocellus and compound eye, ventrally narrowing strongly (subgenus *Euandrena*)....... **go to 152**

M. Clypeus punctate, interspaces forming weakly raised longitudinal wrinkles (former subgenus *Zonandrena*).. **go to 163**

N. Dorsolateral surface of the propodeum reticulate, with large and shallow punctures, clearly contrasting the shagreened and shiny propodeal triangle, this lacking lateral carinae and becoming shinier on the declivity (subgenus *Hoplandrena*)....**go to 168**

O. Pronotum laterally keeled, angulate, keel runs up dorsally to an angled corner. .... **go to 174**

P. Large species (over 12 mm in length). Typically with abundant black, brown, and/or white pubescence. Clypeus strongly domed. Ocelloccipital distance long, at least 2 times the diameter of a lateral ocellus (subgenus *Melandrena partim*) ....**go to 206**

Q. Without this combination of characters; remaining species .... **go to 212**

Females

1 Posterior face of hind femur with latitudinal row of spines or teeth (Fig. 64A, B). Note, if there is also a developed latitudinal carina, then the spines can be difficult to see (subgenus *Lepidandrena*, these species with squamous hairs on the scutum and scutellum) **2**

– Posterior face of hind femur without latitudinal row of spines or teeth. A latitudinal carina may be present (e.g. *Andrena flavipes*) **24**

2 Mesonotum dorsally with short squamous hairs (Fig. 64C, D) **3**

– Mesonotum with longer hairs, these never squamous..... **9**

3 At least the disc of T2 red-marked **4**

– All terga dark **5**

4 Metasoma entirely red-marked; mesonotum with squamous hairs black. Widespread throughout Iberia, associated with *Asphodelus* (Asphodelaceae) ..... ***sardoa* Lepeletier**

– Metasoma with red markings typically restricted to T2–3; mesonotum with squamous hairs brown-grey. Restricted to the Pyrenees, associated with *Campanula* (Campanulaceae) ..... ***rufizona* Imhoff**

5 T1 comparatively sparsely punctate, large punctures separated by >1 puncture diameter, with scattered micropunctures between these large and relatively coarse punctures. Foveae with outer margin clearly defined, foveae depressed, separated from lateral ocellus by a distance subequal to its diameter (Fig. 64E) ..... ***leucolippa* Pérez**

– T1 finely and densely punctate, punctures separated at most by 1 puncture diameter, usually by 0.5 puncture diameters, without micropunctures. Foveae with outer margin poorly defined, foveae not clearly depressed, separated from lateral ocellus by a distance greater than its diameter (Fig. 64F) **6**

6 Galea shagreened and dull, clypeus also shagreened and dull with clear impunctate longitudinal midline. Hind tibiae orange. Associated with *Ornithogalum* (Asparagaceae) ..... ***baetica* Wood**

– Galea smooth and shiny, clypeus also at least partially shiny, without impunctate longitudinal midline. Hind tibiae dark. Associated with *Campanula* (Campanulaceae) **7**

7 Tarsal segment 5 of the hind leg elongate and strongly bent. Squamous hairs light brown. Larger, 13–14 mm ..... ***curvungula* Thomson**

– Tarsal segment 5 of the hind leg shorter, at most as long as the two preceding segments taken together, only weakly bent. Squamous hairs darker grey brown. Somewhat smaller, not larger than 12 mm **8**

8 Squamous hairs very thick, in fresh specimens the underlying scutal punctures are obscured. Midline of the scutum is only slightly impressed. Process of labrum markedly elongate with a clear apical emargination in the fore margin. Larger, 10–12 mm ..... ***pandellei* Pérez**

– Squamous hairs moderately thick, the underlying scutal punctures clearly visible. Midline of the scutum clearly impressed. Process of labrum regularly trapezoidal, not elongate, fore margin almost straight. Smaller, 8–10 mm ..... ***paucisquama* Noskiewicz**

9 Tibial scopae composed predominantly of simple hairs, at most with occasional and scattered plumose hairs (Fig. 64G) **10**

– Tibial scopae extensively composed of plumose hairs (Fig. 64H) **13**

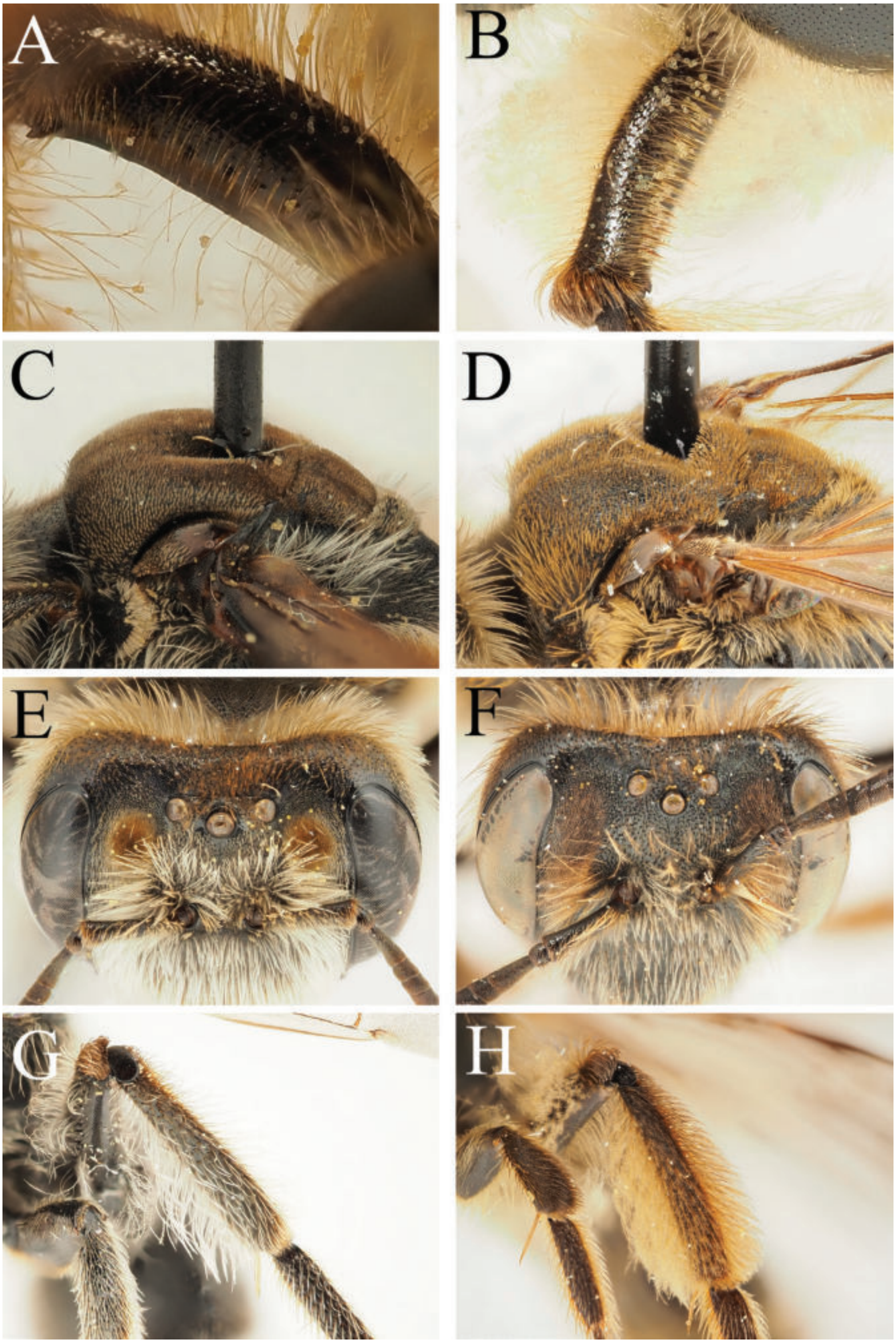

Figure 64. *Andrena* (*Chlorandrena*) *humilis* Imhoff, 1832, female **A** posterior face of hind femur; *Andrena* (*Rufandrena*) *orbitalis* Morawitz, 1871, female **B** posterior face of hind femur **H** tibial scopa, profile view; *Andrena* (*Lepidandrena*) *pandellei* Pérez, 1895, female **C** scutum, profile view; *Andrena* (*Chlorandrena*) *leucolippa* Pérez, 1895, female **D** scutum, profile view **E** foveae, dorsal view; *Andrena* (*Lepidandrena*) *curvungula* Thomson, 1870, female **F** foveae, dorsal view; *Andrena* (*Cryptandrena*) *ventricosa* Dours, 1873, female **G** tibial scopa, profile view.

10 Propodeal triangle poorly defined, without lateral carinae, smooth and with granular shagreen, more or less shiny over the majority of its area. Larger, 9–10 mm.. ***monilia* Warncke**

– Propodeal triangle shagreened and dull or with clearly raised carinae laterally and medially. Smaller, length never exceeding 8 mm **11**

11 Terga strongly and densely punctate, punctures separated by 0.5 puncture diameters, underlying surface smooth and shiny. Propodeal triangle clearly delineated laterally by strongly raised carinae .... ***ventricosa* Dours**

– Terga shagreened and matt, with obscure and shallow punctures. Propodeal triangle lacking lateral raised carinae, poorly defined.............................. **12**

12 Process of the labrum narrow, clearly produced into a narrow, apically pointed triangle. Head and mesosoma with black pubescence.................... .... ***panurgina* De Steffani**

– Process of the labrum broad, clearly at least three times broader than long. Head and mesosoma with brownish to greyish-white pubescence .... ***avara* Warncke aggregate** (potentially including multiple valid species)

13 Scutum and scutellum with clear longitudinal striations........***rhyssonota* Pérez**

– Scutum and scutellum without longitudinal striations **14**

14 Fovea with inner margin clearly dorsally diverging from the inner margin of the compound eye, curved towards the lateral ocellus (*livens*-group)........... **15**

– Fovea with inner margin not dorsally diverging from the inner margin of the compound eye, not noticeably curved towards the lateral ocellus **17**

15 Terga with weak but clear metallic green-blue reflections. Antennae usually ventrally dark, at most obscurely lightened dark brown. Process of the labrum trapezoidal, small, only lightly broader than long............***nigroolivacea* Dours**

– Terga dark, without any metallic reflections. Antennae usually extensively lightened orange ventrally. Process of the labrum broader, at least two times wider than long.. **16**

16 Discs of T2–3 at their bases consistently and densely punctate, punctures typically separated by 1 puncture diameter, at most by 2 puncture diameters. Distributed throughout Iberia .... ***livens* Pérez**

– Discs of T2–3 at their bases more sparsely punctate, punctures separated by more than 3 puncture diameters. Rare, known only from a single specimen captured near Madrid ....***agnata* Warncke**

17 Foveae strongly constricted ventrally, here narrower than the width of a flagellum (*taraxaci*-group).. **18**

– Foveae not strongly constricted ventrally, more or less as wide as dorsally, not narrower than the width of a flagellum **20**

18 Scutum medially with greatly reduced shagreenation, here more or less smooth and shiny. Facial pubescence relatively dark, with black to dark brown hairs along the inner margins of the compound eyes. Rare, southern and south-eastern Spain only .... ***curtivalvis* Morice**

– Scutum shagreened, uniformly dull across its entire surface. Facial pubescence bright, with at most scattered dark hairs. Throughout Iberia **19**

19 Depressions of terga, especially T3–4, extensively lightened orange-yellow, semi-transparent. Discs of T2–3 densely punctate, punctures with strongly raised rims .... ***senecionis* Pérez**

– Depressions of terga at most with apical rim narrowly lightened orange-yellow. Discs of terga weakly and relatively obscurely punctate, puncture rims weakly raised .... ***rhenana* Stöckhert**

20 Tergal margins entirely lightened whitish-yellow hyaline. Face (particularly vertex), scutum, and scutellum with subtle metallic blue-green reflections **21**

– Tergal margins never entirely lightened, at most narrowly lightened yellow hyaline. Face (particularly vertex), scutum, and scutellum dark, without metallic reflections **22**

21 Found in dry to steppic areas in central Spain. Scutum with clear punctures that are visible against the strong background shagreenation. Scutellum with shiny interspaces between punctures[3] .... ***elata* Warncke**

– Found in areas close to or on the coast in southern Portugal and Spain. Scutum with obscure punctures that disappear into the strong background shagreenation. Scutellum with interspaces shagreened[3] .... ***abrupta* Warncke**

22 T2–4 depressed at their base, marginal areas of T2–4 with apical white hair bands that obscure the underlying surface in fresh specimens. Posterior face of the hind femur with long spines .... ***orbitalis* Morawitz**

– T2–4 not depressed basally, apically with marginal areas with at most scattered orange-yellow hairs, these not forming distinct bands which obscure the underlying surface. Posterior face of the hind femur with short teeth **23**

23 T2 between the punctures weakly shagreened, comparatively shiny. Larger species, over 10 mm. Found in more temperate parts of Iberia, generally absent in hot Mediterranean habitats[4] .... ***humilis* Imhoff**

– T2 between the punctures strongly shagreened and dull. Smaller species, under 10 mm. Found in hotter parts of Iberia, the dominant taxon in Mediterranean habitats[4] .... ***cinerea* Brullé**

24 (1) Hind tibial spur clearly broadened, either at its base (Fig. 65A) or submedially (Fig. 65B). Large to very large species, at least 12 mm in length **25**

– Hind tibial spur not broadened at its base or submedially, more or less parallel-sided. Size variable **41**

25 Propodeum dorsolaterally with dense punctures, punctures separated by <1 puncture diameter (Fig. 65C). Propodeum rounded in profile view, without clearly separated horizontal and vertical parts (subgenus *Holandrena* Pérez)... **26**

– Propodeum dorsolaterally with raised reticulation or rugosity (Fig. 65D), without dense punctures or without punctures at all. Propodeum with separated horizontal and vertical parts **29**

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[3] These two species are challenging to separate in the female sex; geographical context cues and association with the more distinctive males should be used.

[4] These two species are challenging to separate in the female sex. Association with the more distinctive males should be made.

26 Vertex wide, ocelloccipital distance at least as wide as three times the diameter of a lateral ocellus.. ***variabilis* Smith**

– Vertex narrower, ocelloccipital distance never as wide as three times the diameter of a lateral ocellus.. **27**

27 Disc of T1 densely punctate, punctures typically separated by 1 puncture diameter. Scutellum dull between punctures. Tergal hair bands interrupted medially.. ***labialis* (Kirby)**

– Disc of T1 more sparsely punctate, punctures separated by greater than 1 puncture diameter, typically by 2 puncture diameters. Scutellum shiny between punctures. Tergal hair bands complete in fresh specimens............. **28**

28 Flying in the spring (April–May). Terminal fringe dark blackish-brown. Ocelloccipital distance narrower, 1 times the diameter of a lateral ocellus[5] .. .. ***flavilabris* Schenck**

– Flying in the summer (July–August). Terminal fringe light. Ocelloccipital distance wider, 1–1.5 times the diameter of a lateral ocellus[5] ... ***decipiens* Schenck**

29 Hind tibial spur broadened submedially. Propodeal triangle simply defined laterally by weak and obscurely raised carinae, internal surface without a dense network of strongly raised honeycomb-like rugosity. Terga often red-marked. Exclusively summer flying species, from May onwards............. **30**

– Hind tibial spur broadened at its base. Propodeal triangle clearly defined laterally by strongly raised carinae (Fig. 65D), internal surface with dense network of strongly raised honeycomb-like rugosity (though this can be weak in members of the subgenus *Suandrena* Warncke). Tergal only very rarely red-marked. Flying in the spring or summer **31**

30 Tibial scopa ventrally composed of long plumose hairs. Posterior face of the hind femora with clear latitudinal carina. Terga usually red marked, though an entirely melanic form can be found in south-eastern Spain (ssp. *nigricauda* Wood). Associated with scabious (former Dipsacaceae = Caprifoliaceae). Restricted to montane grasslands in northern and central Spain with isolated populations in the Sierra de Cazorla and Sierra Nevada.... ***hattorfiana* (Fabricius)**

– Tibial scopa simple or with at most occasional obscurely plumose hairs. Posterior face of the hind femora without a latitudinal carina. Terga never red-marked. Associated with yellow Cichorioideae (Asteraceae). Restricted to the Pyrenees and Cantabrian Mountains .... ***polita* Smith**

31 Terminal fringe dark medially and white laterally (Fig. 24D, F). Lateral faces of the propodeum with strongly pronounced network of coarse ridges and creases.. **32**

– Terminal fringe uniformly dark. Lateral faces of the propodeum without ridges, either unsculptured or at most with individually raised points which do not joint together to form a network **34**

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[5] These two species can be challenging to separate. Association with males should be made, along with phenological context.

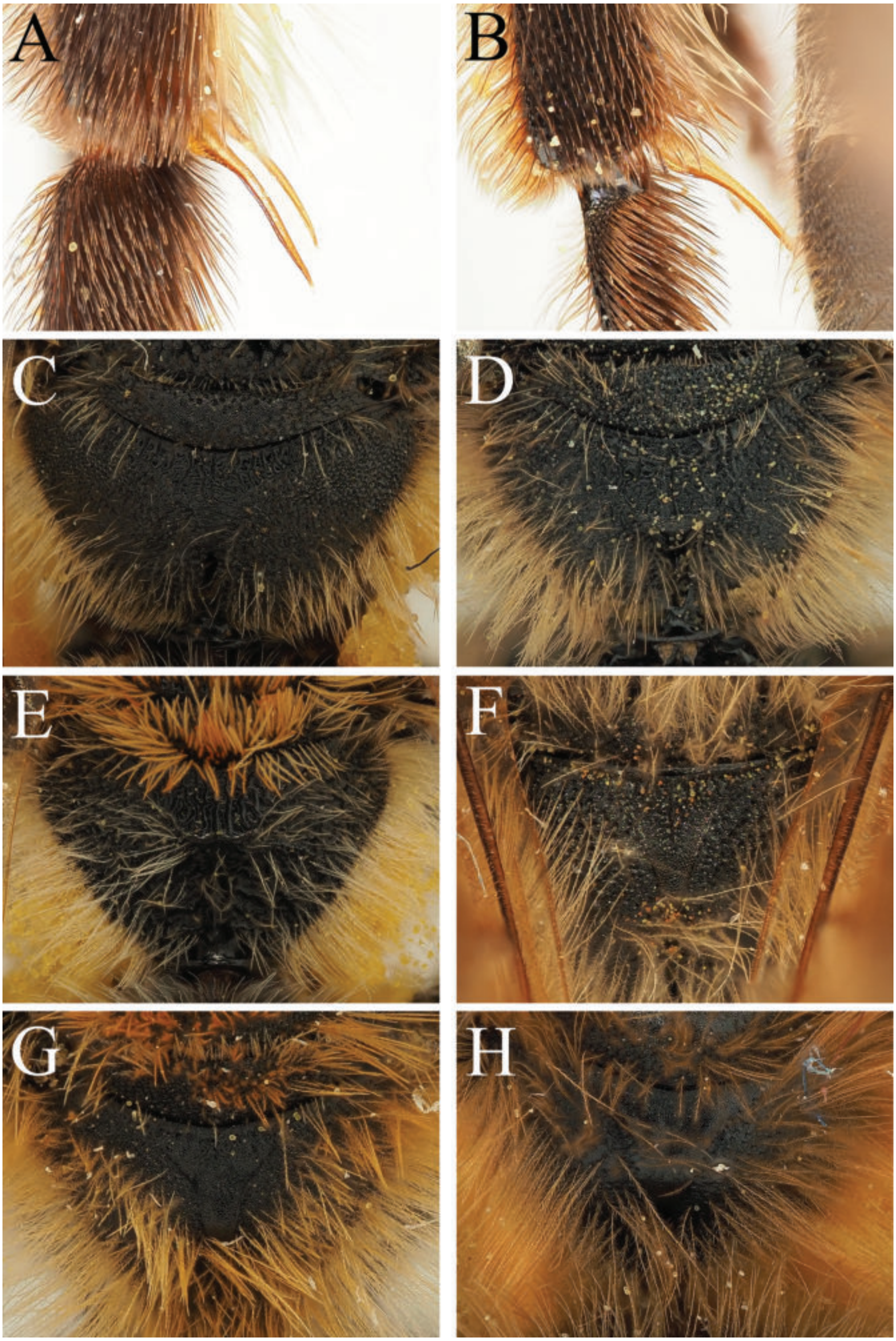

Figure 65. *Andrena* (*Plastandrena*) *bimaculata* (Kirby, 1802), female **A** hind tibial spurs, dorsal view **D** propodeum, dorsal view; *Andrena* (*Holandrena*) *labialis* (Kirby, 1802), female **B** hind tibial spurs, dorsal view **C** propodeum, dorsal view; *Andrena* (*Trachandrena*) *haemorrhoa* (Fabricius, 1781), female **E** propodeum, dorsal view; *Andrena* (*Melandrena*) *nigroaenea* (Kirby, 1802), female **F** propodeum, dorsal view; *Andrena* (*Andrena*) *helvola* (Linnaeus, 1758), female **G** propodeum, dorsal view; *Andrena* (*Hoplandrena*) *scotica* Perkins, 1916, female **H** propodeum, dorsal view.

32 Disc of T1 strongly and densely punctate, punctures separated by <1 puncture diameter .... ***asperrima* Pérez**

– Disc of T1 with sparse punctate, punctures on average separated by 2 puncture diameters **33**

33 Metasoma with metallic blue reflections. T4 laterally with thick white hair patches. Pygidial plate narrow, laterally with a shiny depressed marginal area .... ***agilissima* Scopoli**

– Metasoma black, without metallic blue reflections. T4 laterally with only loose white hair, not forming dense hair patches. Pygidial plate broad, flat, without a depressed and shiny marginal area .... ***afrensis* Warncke**

34 Terga with metallic blue-green reflections. Mesepisternum and dorsolateral faces of the propodeum more or less smooth, granularly shagreened, weakly and obscurely punctate (subgenus *Suandrena*) **35**

– Terga black or red-marked, but never with metallic reflections. Mesepisternum and dorsolateral faces of the propodeum with dense network of raised rugosity **37**

35 Propodeal triangle weakly defined, internal rugosity fine and obscure. Known only from Cádiz province, flying in December .... ***gades* Wood & Ortiz-Sánchez**

– Propodeal triangle strongly defined, with pronounced internal rugosity. More widespread across Iberia **36**

36 Process of the labrum triangular with clear apical point. Throughout Iberia[6] .... ***suerinensis* Friese**

– Process of the labrum broadly triangular with apical margin truncate. Confirmed males known only from central, eastern, and south-eastern Spain[6]... .... ***cyanomicans* Pérez**

37 Pronotum laterally with strong humeral angle. Terga with extremely fine punctation, punctures minute, separated by <0.5 puncture diameters......... .... ***fuscosa* Erichson**

– Pronotum laterally rounded, without humeral angle. Terga with much coarser punctation, punctures separated by >1 puncture diameter **38**

38 Pubescence of body predominantly black, tibial scopa predominantly composed of white hairs **39**

– Pubescence of body variable, but usually with extensive brown hairs on mesosoma; tibial scopa usually orange, never predominantly composed of white hairs **40**

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[6] These two species cannot be adequately separated in the female sex. Warncke's unpublished key gave this character, but I am not convinced that it is robust. Association must be made with the distinctive males.

39 Bivoltine (typically March–April and July–August). Common and widely distributed throughout Iberia[7] .... ***pilipes* Fabricius**

– Univoltine (typically May–June). Rare, restricted to mountainous parts of Iberia; known from the Pyrenees, the Sistema Central, Serra do Gerês, Sistema Ibérico, and Sierra de Cazorla[7] .... ***nigrospina* Thomson**

40 Depression of T1 sparsely punctate, punctures separated by more than 2 puncture diameters. Nominally univoltine, flying only in the spring[8] .... ***tibialis* (Kirby)**

– Depression of T1 densely punctate, punctures separated by 0.5 puncture diameters. Bivoltine, flying in the spring and the summer[8] .... ***bimaculata* (Kirby)**

41 (24) Hairs of the tibial scopae clearly plumose, with a majority of strongly branched hairs **42**

– Hairs of tibial scopae entirely simple, or with at most a mixture of simple and scattered and weakly branched hairs..**50**

42 Terga metallic blue, densely punctate, punctures separated by 1 puncture diameter ....***bellidis* Pérez**

– Terga variably coloured, but never metallic blue. Densely punctate or not **43**

43 Terga with discs extensively red-marked (some dark individual of *A. marginata* Fabricius with red markings restricted to the base of the tergal margins) **44**

– Terga dark, at most with depressions lightened, never with red markings at the base of the tergal depressions..**45**

44 Clypeus with fore margin slightly upturned. Foveae short, ventrally reaching only to the level of the antennal insertions. Tibial scopae uniformly yellowish...***pellucens* Pérez**

– Clypeus with fore margin straight, not upturned. Foveae long, ventrally extending beyond the level of the antennal insertions. Tibial scopae bicoloured, black-brown dorsally, brownish-white ventrally. Associated with scabious (former Dipsacaceae = Caprifoliaceae).............***marginata* Fabricius**

45 Tibial scopae with short hairs, at most half the length of the diameter of the hind tibia at its maximum apical width............ ***ranunculi* Schmiedeknecht**

– Tibial scopae with long hairs, clearly exceeding half the length of the diameter of the hind tibia at its maximal apical width.....................................**46**

46 Fovea narrow, dorsally occupying ⅓ of the space between the compound eye and the lateral ocellus, clearly narrowing ventrally to half its dorsal width.

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[7] These two taxa cannot be separated morphologically. Association must be made with males, or genetic barcodes generated.

[8] These two taxa are challenging to separate in the female sex due to extreme variation in colouration. Further genetic work is needed to clarify species boundaries in Iberia and more broadly. Association should be made with males.

Mid and hind basitarsi and hind tibiae lightened orange-yellow (subgenus *Chrysandrena* Hedicke) **47**

– Fovea broader, dorsally occupying at least ½ the space between the compound eye and the lateral ocellus, not narrowed ventrally. Basitarsi and hind tibiae dark.. **49**

47 Clypeus and scutellum strongly shagreened and matt ....***hesperia*** **Smith**

– Clypeus and scutellum at least partially shiny **48**

48 Disc of scutum shiny. Scutellum with uniformly light hairs. A2 as long as A3+4. Restricted to temperate areas in northern Portugal and Spain.......... ....***fulvago*** **(Christ)**

– Disc of scutum shagreened and dull. Scutellum with intermixed light and dark brown to black hairs. A2 as long as A3+4+5. Found in Mediterranean areas from southern Portugal to southern and eastern Spain ....***fertoni*** **Pérez**

49 Process of the labrum large, as long as broad, ventral surface covered with latitudinal wrinkles (Fig. 73D). Foveae dorsally poorly defined, not strongly impressed. Terminal fringe composed of simple dark hairs. Flying in the summer (June-August), associated with Dipsacaceae (=Caprifoliaceae) ....***mucida*** **Kriechbaumer** (*partim*, 2nd generation)

– Process of the labrum twice as broad as long, without wrinkles. Foveae dorsally strongly impressed and therefore well-defined. Terminal fringe composed of densely plumose orange hairs. Flying in the spring (April-May), Associated with yellow Cichorioideae (Asteraceae)...........***alluaudi*** **Benoist**

50 (41) Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate (Fig. 65E, c.f. Fig. 79A). Mesepisternum and dorsolateral parts of the propodeum with dense network of raised rugosity................**51**

– Propodeal triangle not strongly defined by lateral carinae with its internal surface rugose-areolate (Fig. 65F–H). Mesepisternum and dorsolateral parts of the propodeum with or without dense network of raised rugosity.. **54**

51 Forewing with two submarginal cells. Clypeus with longitudinal striations. .... ***lagopus*** **Latreille**

– Forewing with three submarginal cells. Clypeus without longitudinal striations **52**

52 Hind tibiae usually orange. Foveae clearly medially constricted. Terga without hair bands, T2 laterally without a pair of small foveae. Terminal fringe orange...***haemorrhoa*** **(Fabricius)**

– Hind tibiae always dark. Foveae lacking medial constriction. Terga in fresh specimens with apical white hair bands, T2 laterally with a pair of small foveae. Terminal fringe whitish-yellow **53**

53 Process of the labrum clearly deeply emarginate........***colletiformis*** **Morawitz**

– Process of the labrum triangular, anterior margin truncate, never emarginate.. ***miegiella*** **Dours**

54 (50) Scutum and scutellum with short squamous hairs (Figs 33C, D, 43A, 45C, 46B) **55**

– Scutum and scutellum without squamous hairs. If specimen shows longer semi-squamous hairs (e.g. *A. farinosa* Pérez, Fig. 45D), continue here **63**

55 Ocelloccipital distance at least three times the diameter of a lateral ocellus (Figs 33B, 43B). Large bees, exceeding 11 mm in length **56**

– Ocelloccipital distance less than two times the diameter of a lateral ocellus. Smaller bees, exceptionally reaching 11 mm in length............................ **60**

56 Dorsolateral faces of the propodeum clearly, densely, and deeply punctate, punctures separated by <0.5 puncture diameters, with shiny interspaces **57**

– Dorsolateral faces of the propodeum either impunctate, with dense network of raised rugosity, or with shallow and sparser punctures, punctures separated by 0.5–2 puncture diameters, interspaces dull **59**

57 Pubescence of scutum weakly squamous, anterior dorsolateral corners of scutum with pubescence longer, clearly exceeding width of antennae in length. Terga always predominantly red. Terga with clear apical hair bands. Punctation of T1 slightly spaced, punctures separated by 1–2 puncture diameters. Restricted to eastern and south-eastern Spain .... ***nilotica* Warncke**

– Pubescence of scutum short and strongly squamous, anterior dorsolateral corners of scutum with pubescence short, clearly shorter than width of antennae. Terga variable, red to black or any intermediate combination. Terga with or without clear apical hair bands. Punctation of T1 denser, punctures separated at most by 1 puncture diameter **58**

58 A3 exceeding A4+5 in length. Terga always extensively red-marked (central and south-eastern Spain).. ***parata* Warncke**

– A3 equalling A4+5 in length. Terga variable, from almost entirely black (Fig. 33D) to rarely entirely red-marked .... ***pruinosa* Erichson**

59 Scutal hairs orange-brown (Fig. 43A). Hind tibiae orange (Fig. 43C). Terga with obscure and narrow brownish-yellow hair bands (Fig. 43D). Terminal fringe orange.. ***limbata dusmeti* Warncke**

– Scutal hairs black and whitish-brown. Hind tibiae dark. Terga with clear and thick white apical hair bands. Terminal fringe dark brown .... ***lateralis* Morawitz**

60 T1 strongly and densely punctate, interspaces shiny (Fig. 46D). Mesepisternum evenly rounded ventrally... ***oviventris* Pérez**

– T1 weakly and obscurely punctate, underlying surface shagreened. Mesepisternum ventrally with an indentation anterior to the attachment point of the mid leg **61**

61 Clypeus without latitudinal ridges. T3–4 laterally with clear squamous hairs between the disc and marginal areas. Terga usually extensively red-marked. Basitarsi and hind tibiae orange .... ***hystrix* Schmiedeknecht**

– Clypeus with latitudinal ridges. T3–4 laterally without squamous hairs. Terga never red marked. Legs dark.. **62**

62 T2–3 laterally strongly shagreened, with obscure and scattered punctures... .... ***aeneiventris* Morawitz**

– T2–3 laterally finely shagreened, clearly and densely punctate, punctures separated by 0.5 puncture diameters .... ***hedikae* Jäger**

63 (54) Viewed laterally, propodeal corbicula with internal surface (lateral faces of the propodeum) glabrous AND propodeal corbiculae complete (possessing both a dorsal and anterior fringe) (Fig. 66A; subgenus *Simandrena*) **64**

– Propodeal corbiculae either incomplete (possessing only a dorsal fringe) AND/OR internal surface with hairs **74**

64 Tibial scopae bicoloured, dorsally dark and ventrally pale **65**

– Tibial scopae unicolourous, dorsally and ventrally light **68**

65 Fovea extremely broad, occupying entirety of space between the compound eye and the lateral ocellus (Fig. 66B). T1 extremely densely punctate, punctures separated by <0.5 puncture diameters, with shiny interspaces. Very rare, known only from one specimen Cádiz .... ***rhypara* Pérez**

– Fovea narrower, not occupying entirety of space between the compound eye and the lateral ocellus. T1 strongly shagreened, impunctate or with scattered punctures **66**

66 T2 impunctate. A2 longer than A3+4, almost as long as A3+4+5........ .... ***vetula* Lepeletier**

– T2 with fine and dense punctures, punctures separated by 0.5 puncture diameters. A2 as long as A3+4 .... **67**

67 Terga with thick white apical hair bands in fresh specimens (Fig. 27D). Foveae with outer margin straight, not deviating from the inner margins of the compound eyes .... ***cilissaeformis* Pérez**

– Terga with at most obscure narrow brownish hair bands. Foveae with outer margin constricted, clearly deviating from inner margins of the compound eyes submedially (Fig. 66C) .... ***antigana* Pérez**

68 Tibial scopae with short hairs, dorsally these hairs not greatly exceeding the width of a lateral ocellus. Metasoma with punctures on tergal discs dense medially, becoming sparse laterally **69**

– Tibial scopae with long hairs, very clearly greatly exceeding the width of a lateral ocellus. Metasoma with consistently dense punctures, not becoming sparser laterally **70**

69 Scutum medially strongly shagreened and dull (Fig. 66D). In fresh specimens, tergal hair bands short, not noticeably surpassing the apex of the tergal margins. Hind tibiae and basitarsi usually orange, but can be entirely dark. Restricted to temperate areas in northern Spain .... ***dorsata* (Kirby)**

– Scutum medially polished and shiny (Fig. 66E) or extensively but weakly shagreened with a silky shine. In fresh specimens, tergal hair bands long, clearly surpassing the apex of the tergal margins. Hind tibiae and basitarsi usually dark, occasionally lightened orange-brown. Common throughout Iberia .... ***propinqua* Schenck**

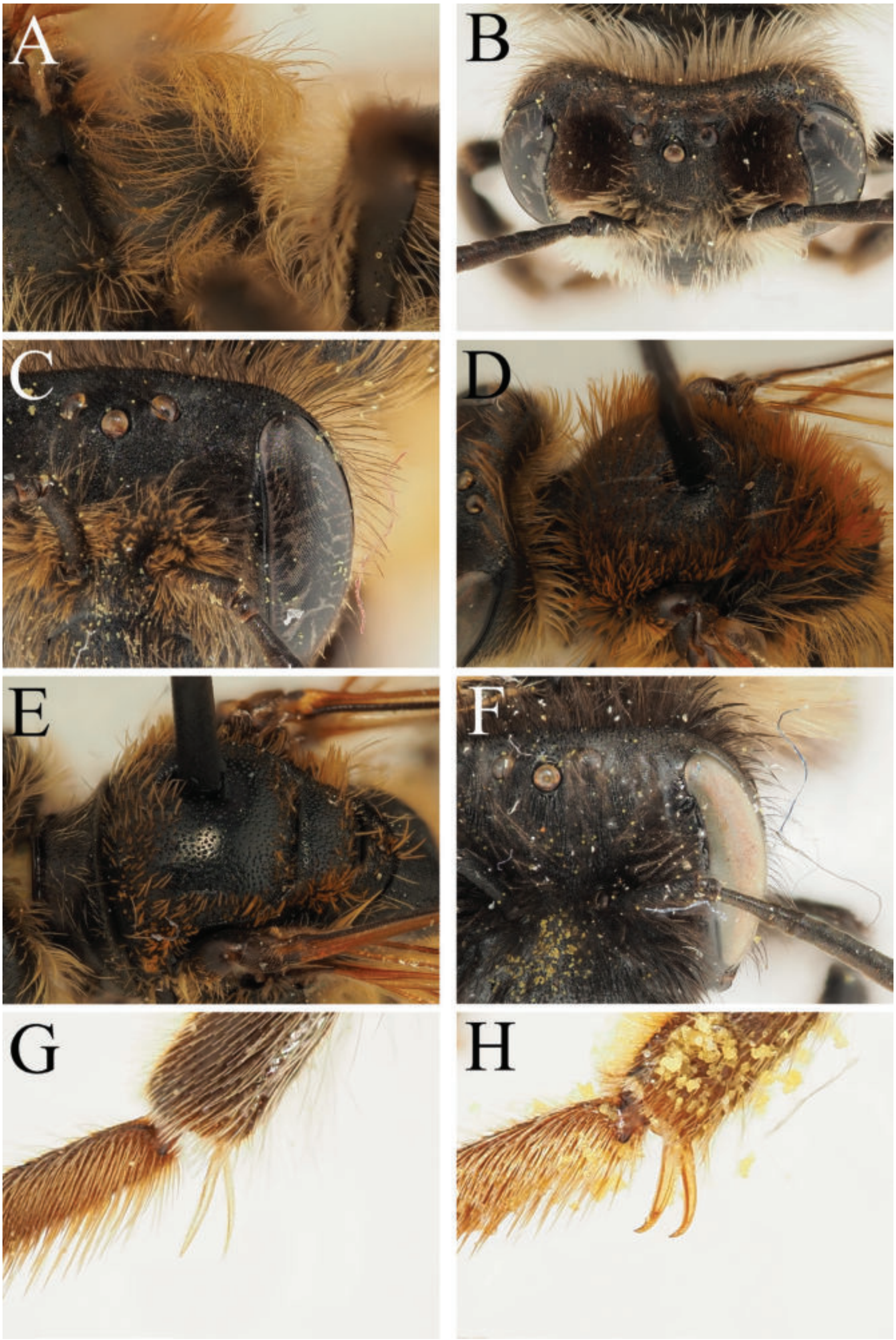

Figure 66. *Andrena* (*Simandrena*) *dorsata* (Kirby, 1802), female **A** propodeal corbicula, lateral view **D** scutum, dorsolateral view; *Andrena* (*Simandrena*) *rhypara* Pérez, 1903, female **B** foveae, dorsal view; *Andrena* (*Simandrena*) *antigana* Pérez, 1895, female **C** fovea, dorsofrontal view; *Andrena* (*Simandrena*) *propinqua* Schenck, 1853, female **E** scutum, dorsolateral view; *Andrena* (*Melandrena*) *bicolorata* (Rossi, 1790), female **F** fovea, dorsofrontal view; *Andrena* (*Notandrena*) *nigroviridula* Dours, 1873, female **G** hind tibial spurs, dorsal view; *Andrena* (*Notandrena*) *varuga* Warncke, 1975, female **H** hind tibial spurs, dorsal view.

70 Disc of T1 strongly and densely punctate, punctures separated by <1 puncture diameter **71**

– Disc of T1 finely and sparsely punctate, punctures separated by >1 puncture diameter **72**

71 Clypeus with pattern of raised latitudinal ridges .... ***combinata* (Christ)**

– Clypeus smooth in the middle, at most transversely wrinkled at the base, ventro-laterally with slight longitudinal wrinkles .... ***lepida* Schenck**

72 Head and mesosoma white-haired. Clypeus smooth and shiny between punctures. Restricted to areas close to the Pyrenees .... ***thomsonii* Ducke**

– Head and mesosoma with rich chestnut-brown hair. Clypeus shagreened and dull between punctures **73**

73 T2–4 with discs finely and densely punctate. Terminal fringe dark brown. Hind tibiae sometimes lightened orange. More widespread across Iberia[9] .... ***congruens* Schmiedeknecht**

– T2–4 with discs sparsely and obscurely punctate. Terminal fringe reddish-brown. Restricted to the Pyrenees and Cantabrian Mountains[9] .... ***confinis* Stöckhert**

74 (63) Fovea strongly constricted medially, strongly diverging from the inner margin of the compound eye dorsally (Fig. 66F; former subgenus *Hyperandrena* Pittioni) **75**

– Fovea not constricted medially, not strongly diverging from the inner margin of the compound eye **76**

75 Tibial scopae unicolourous black. Mesosoma entirely covered with light grey hairs .... ***bicolorata* (Rossi)**

– Tibial scopae dorsally black, ventrally orange-red. Mesosoma entirely covered with dark to light brown hairs .... ***florentina* Magretti**

76 (74) At least some tergal discs extensively red-marked (Fig. 41D) **77**

– Tergal discs never red-marked, at most with tergal margins lightened **83**

77 Small bees, never exceeding 9 mm in length. Fovea narrow, at most occupying ⅓ of space between the compound eye and the lateral ocellus **78**

– Large bees, greater than 11 mm in length. Fovea broader, occupying at least ½ the space between the compound eye and the lateral ocellus **80**

78 Propodeal triangle broad, laterally delineated with raised straight carinae, internal surface with fine network of raised rugae. Head and scutum without metallic reflections .... ***labiata* Fabricius**

– Propodeum narrow, poorly defined, lacking lateral carinae, internal surface at most with short and weak rugae basally, surface with fine granular shagreenation. Head and scutum with strong or weak metallic reflections **79**

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[9] These two species are challenging to separate, and there may be taxonomic complexity in Iberia. Further study is required.

79 Clypeus medially smooth and shiny between the punctures. Scutum anteriorly shagreened, medially becoming smooth and shiny, irregularly but clearly punctate, with strong greenish metallic reflections .... ***binominata* Smith**

– Clypeus medially completely shagreened and dull. Scutum shagreened and shallowly punctate, with weak bronzy metallic reflections .... ***leucophaea* Lepeletier**

80 Tibial scopae unicolourous light orange. Propodeal triangle clearly delineated laterally by fine carinae, internal surface with fine network of raised rugae. Clypeus densely and uniformly punctate, without a longitudinal impunctate midline.. ***schencki* Morawitz**

– Tibial scopae bicoloured, dorsally dark, ventrally light (Fig. 41A). Propodeal triangle poorly defined, lacking lateral carinae, internal surface more or less smooth, without network of rugae (Fig. 41C). Clypeus densely or sparsely punctate, with clear longitudinal impunctate midline............................**81**

81 Terga strongly and densely punctate, punctures separated by 1 puncture diameter. Compound eyes with inner margins diverging ventrally (Fig. 41B). Excluding impunctate midline, clypeus comparatively sparsely punctate, punctures separated by 1–2 puncture diameters .... ***florea* Fabricius**

– Terga shallowly and obscurely punctate, punctures separated by 2–3 puncture diameters. Compound eyes with internal margins more or less parallel. Excluding impunctate midline, clypeus comparatively densely punctate, punctures separated by 0.5–1 puncture diameters..................................**82**

82 T1–2 with long hair, equalling the length of the hair on the mesosoma[10] ... . ***trimmerana* (Kirby)** (*partim*, light form)

– T1–2 with shorter hair, never equalling the length of the mesosomal hair[10] .... ***rosae* Panzer** (*partim*, light form)

83 (76) Head, mesosoma, or tergal discs with metallic reflections (note, *A. nigroaenea* (Kirby) can have bronzy reflections on the terga; if the tibial scopae is composed of orange-red hairs or the tibial scopae is mainly dark with only the ventral hairs orange, go to 206) **84**

– Body without metallic reflections...**91**

84 Mesosoma with strongly contrasting pattern of black and white hairs; mesosoma anteriorly and posteriorly with white hairs, medially with a band of black hairs...**85**

– Mesosoma without strongly contrasting pattern of black and white hairs......**86**

85 Wings infuscate over their apical 2/3rds. Sterna laterally and apically with black hairs. A3 comparatively shorter, shorter than A4+5. Bivoltine (April–

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[10] Beware of abraded specimens when dealing with these two species.

May; July–August), restricted to mountains in northern Spain and the Pyrenees[11] .... ***barbareae* Panzer**

– Wings hyaline over the majority of their area, only slightly darkened apically. Sterna laterally and apically with white hairs. A3 comparatively longer, equalling A4+5. Univoltine (April–May), more widespread across northern Portugal and Spain[11] .... ***cineraria* (Linnaeus)**

86 Scutum uniformly densely shagreened and completely dull over its entire surface, extremely densely punctate, punctures shallow, flat, and confluent. Mesosoma and discs of T1–2 dorsally with long chestnut-brown hair......... .... ***doursana* Dufour**

– Scutum either at least partly shiny or less densely punctate, punctures clearly separated by at least 1 puncture diameter. Mesosoma and discs of T1–2 never with long chestnut-brown hair, either glabrous, with shorter hairs, or with hairs of a different colour **87**

87 Terga clearly punctate, punctures separated by up to 2 puncture diameters. **88**

– Terga obscurely and sparsely punctate, punctures separated by 4–5 puncture diameters **89**

88 Fovea broad, occupying 2/3rds of the space between the compound eye and a lateral ocellus. Tergal punctation comparatively sparse, punctures separated by 1–2 puncture diameters. Scutum medially becoming smooth and shiny between the punctures. Restricted to south-western Spain (Huelva, Sevilla) .... ***laurivora* Warncke**

– Fovea narrow, occupying less than ½ the space between the compound eye and a lateral ocellus. Tergal punctation dense, punctures separated by up to 1 puncture diameter. Scutum uniformly shagreened and dull. Restricted to the Pyrenees... ***viridescens* Viereck**

89 Larger species, 11–12 mm. Clypeus shagreened and dull over the majority of its surface. Fovea narrow, but uniformly wide along their length, not narrowing ventrally..***aerinifrons* Dours**

– Smaller species, under 9 mm. Clypeus shiny over the majority of its area. Foveae narrow, but also narrowing ventrally to approximately half of their dorsal width...**90**

90 Scutum with clear metallic green reflections. Hind tibial spurs straight (Fig. 66G)...***nigroviridula* Dours**

– Scutum dark, with at most weak and obscure metallic reflections. Hind tibial spurs strongly bent at their apexes (Fig. 66H) .... ***varuga* Warncke**

91 (83) Small black species without a keel laterally on the pronotum, body length under 8 mm, or if up to 10 mm then with lateral faces of the propodeum

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[11] These two species are challenging to separate morphologically.

with clear pattern of raised star-shaped wrinkles (all members of the subgenera *Aciandrena*, *Graecandrena*, *Micrandrena*)[12] **92**

– Species larger than 9 mm in length or with pronounced keel on the pronotum laterally **138**

92 Propodeal triangle smooth, not defined laterally by raised carinae, with internal surface lacking network of raised rugosity, at most with very short rugae at the base of the propodeal triangle (Fig. 67A) **93**

– Propodeal triangle either strongly defined by raised carinae, or with internal surface with network of raised rugosity covering at least the basal half (Fig. 67B; note, take care with *A. tenuistriata*, for which the lateral parts of the propodeal triangle present granular shagreen, Fig. 67C).................. **106**

93 Clypeus with clear raised longitudinal striations (Fig. 67D).................... **94**

– Clypeus without any striations... **96**

94 Clypeus flattened, medially slightly depressed, weakly concave. Process of the labrum short, twice as broad as long, forming a triangular point. A3 almost as long as A4+5+6. Central and eastern Spain only...................... ***fria* Warncke**

– Clypeus evenly arched. Process of the labrum narrower, as long as broad. A3 only slightly exceeding A4+5. More widespread **95**

95 Tibial scopa composed of unicolourous light hairs. T3 impunctate, with weak apical yellowish hair band, marginal area at most weakly depressed. Widespread across Iberia.. ***longibarbis* Pérez**

– Tibial scopa pale ventrally, dark dorsally. T3 with obscure punctures, with strong apical white hair band overlying the clearly depressed marginal area. Restricted to sandy and usually coastal habitats in southern Iberia .... ***orana* Warncke**

96 Foveae not ventrally narrowed, in their lower half at least half as wide as the distance from the inner margin of the compound eye (Fig. 67E) **97**

– Foveae ventrally narrowed, in their lower half as wide as the distance from the inner margin of the compound eye (Fig. 67F, G) **98**

97 T2–4 with narrow, widely interrupted hair bands. Wing venation brownish. Clypeus shagreened to smooth and shiny, densely punctate, punctures separated by 1 puncture diameter. Process of the labrum narrow and triangular with a pointed tip (Fig. 67E). Larger, 8 mm. Widespread across Iberia .... ***pandosa trigona* Warncke**

– T2–4 with complex wide and dense white hair bands. Wing venation light yellow. Clypeus uniformly shagreened, irregularly punctate, punctures separated by 1–3 puncture diameters. Process of the labrum with the apical margin truncate. Smaller, 6 mm. Rare, known only from central Spain .... ***montarca* Warncke**

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[12] Note, this couplet is not intended to include small examples of members of the subgenera *Leucandrena* Hedicke, 1933 and *Notandrena*. Therefore, small individuals with a clearly keeled pronotum should follow the alternative couplet.

98 Tergal discs clearly and regularly punctate, punctures separated by 1 puncture diameter, with punctures extending onto marginal areas .... ***fulica*** **Warncke**

– Terga either impunctate or obscurely punctate, but punctures never extending onto marginal areas **99**

99 Supraclypeal area covered with longitudinal striations (Fig. 67F) **100**

– Supraclypeal area without any striations (Fig. 67G) **105**

100 Longitudinal striations on the paraocular areas strong and pronounced, continuing ventrally to the lateral margins of the clypeus without becoming weaker. Clypeus flattened, with distinct longitudinal impression or furrow medially. Restricted to the extreme north-east of Spain .... ***impunctata*** **Pérez**

– Longitudinal striations on the paraocular areas ventrally extending to the lateral margins of the clypeus but here clearly weaker than their strength adjacent to the foveae. Clypeus either domed or if flattened then without longitudinal impression **101**

101 Clypeus strongly flattened, coarsely shagreened and dull over almost its entirely surface, apical margin narrowly and obscurely shiny; clypeus with shallow and obscure punctures that disappear into the underlying shagreen, punctures separated by 1–2 puncture diameters (Fig. 67F) .... ***verticalis*** **Pérez**

– Clypeus either domed, or if flattened then with a broad shiny apical margin (at least as broad at the width of a flagellum) and punctures that are clearly visible against the underlying shagreenation **102**

102 A3 exceeding the length of A4+5. Striations of supraclypeal area weakly continue onto clypeus basally and laterally, here shagreened with weakly raised striations. Clypeus shagreened basally and laterally, becoming smooth and shiny medially and apically, with narrow medial shagreened projection, shagreenation thus forming a weak trident shape. Known only from a few specimens from the extreme south of Spain, probably representing an undescribed species (Málaga, Sevilla) .... **aff *mica* Warncke**

– A3 at most equalling A4+5. Striations of supraclypeal area not continuing onto clypeus, entire clypeus free of even a hint of striations **103**

103 Clypeus with fine punctures, punctures separated by 1–3 puncture diameters. Underlying shagreenation weak basally. Process of the labrum slightly broader than long. Presence and distribution in Iberia unclear .... ***abjecta*** **Pérez**

– Clypeus with strong and coarse punctures, punctures separated by 0.5–2 puncture diameters. Underlying shagreenation strong and coarse basally. Process of the labrum narrow, slightly longer than broad **104**

104 Scutellum polished and shiny between punctures. Clypeus domed and somewhat flattened medially. Restricted to south-eastern Spain (Alicante, Almería, Granada, Murcia) .... ***tenostra*** **Warncke**

– Scutellum dull and shagreened. Clypeus largely flattened across its entire surface. More widespread across Iberia .... ***alma*** **Warncke**

105 Larger, 7–8 mm. T3–4 with discs obscurely punctate. Hind basitarsi lightened orange. Nervulus of the forewing interstitial to weakly antefurcal. Shagreenation of the clypeus becoming weaker at its apical margin .... ***nebularia*** **Warncke**

– Smaller, 4–5 mm. T3–4 with discs impunctate. Hind basitarsi dark. Nervulus of the forewing strongly antefurcal. Clypeus uniformly shagreened .... ***vacella*** **Warncke**

106 Lateral shoulders of T1 with a pair of strongly produced sharp ridges (Fig. 67H). Terga shiny with mixture of small and large punctures. Mesepisternum depressed above the insertion point of the mid legs. Rare, restricted to central Spain.. ***taxana*** **Warncke**

– Lateral shoulders of T1 never with clearly produced ridges, or if with ridges (*A. strohmella* Stöckhert) then terga never shiny and deeply punctate. Tergal punctation otherwise. Mesepisternum evenly rounded..........................**107**

107 Hind tibiae and basitarsi orange, tibial scopa composed of extremely short hairs. Restricted to the Pyrenees and the Cantabrian Mountains, flying July–August, associated with *Potentilla* (Rosaceae) .... ***tarsata*** **Nylander**

– Hind legs dark, tibial scopa with hairs normal, not extremely short **108**

108 Foveae long, dorsally extent reaching a line parallel to the hind margin of the lateral ocelli, foveae deeply impressed. Propodeal triangle not laterally delineated by carinae, internal surface weakly elevated, with irregular raised rugae that do not cover the entire area. Terga laterally with loose, white interrupted hair bands. Restricted to cooler areas in and around the Pyrenees and Cantabrian Mountains, flying July–August .... ***coitana*** **(Kirby)**

– Foveae shorter, not reaching level of the lateral ocelli dorsally, only weakly impressed. Propodeal triangle clearly delineated laterally by carinae, internal surface evenly and regularly covered by fine network of raised rugae. Terga with lateral hair bands or not **109**

109 Foveae either uniformly narrow or strongly narrowed ventrally, in their ventral half at most as wide as the distance to the inner margin of the compound eye..**110**

– Foveae not or only weakly narrowed ventrally, in their ventral half clearly wider than the distance to the inner margin of the compound eye........**115**

110 Clypeus with longitudinal striations (c.f. Fig. 67D) **111**

– Clypeus without striations **112**

111 Disc of T1 shagreened and dull. T2–4 with hair bands long, longer than the diameter of a flagellum. Scutum uniformly shagreened and dull. Restricted to the extreme north-east of Spain .... ***distinguenda*** **Schenck**

– Disc of T1 polished and shiny, contrasting the shagreened marginal area. T2–4 with short hair bands, shorter than the diameter of a flagellum. Scutum laterally shagreened, medially smooth and shiny. Widespread throughout Iberia... ***nitidula*** **Pérez**

112 T1 finely shagreened to polished and shiny. Mesonotum densely and strongly punctate **113**

– T1 strongly shagreened and dull. Mesonotum finely and sparsely punctate. **114**

113 Foveae uniformly narrow, dorsally narrower than the diameter of a flagellum. Disc of T1 with scattered punctures, separated by at least 2 puncture diameters .... ***fabrella* Pérez**

– Foveae dorsally broader than ventrally, dorsally as wide as the diameter of a flagellum. Disc of T1 more densely punctate, punctures separated by 0.5–1 puncture diameters .... ***nana* (Kirby)**

114 Foveae uniformly narrow, dorsally narrower than the diameter of a flagellum. Terga impunctate. Clypeus evenly domed, densely shagreened and dull. Associated with Cistaceae .... ***djelfensis* Pérez**

– Foveae dorsally broader than ventrally, dorsally as wide as the diameter of a flagellum. Terga obscurely punctate. Clypeus weakly three-faced, anterior margin shiny. Associated with Brassicaceae .... ***tenuistriata* Pérez**

115 Large species, 10 mm in length. Clypeus densely covered with latitudinal wrinkles. Lateral faces of the propodeum covered with pattern of raised star-shaped wrinkles .... ***ampla* Warncke**

– Most species smaller. Clypeus without latitudinal wrinkles and propodeum without pattern of raised star-shaped wrinkles **116**

116 Larger species, 8–9 mm. Discs of T1–3 extremely densely punctate, punctures almost confluent, separated by <0.5 puncture diameters. Clypeus densely punctate, punctures separated by 1 puncture diameter, interspaces with weakly raised ridges that form subtle pattern of longitudinal striations. Rare, known from eastern Spain (Jáen, Soria, Teruel) .... ***vaulogeri* Pérez**

– Smaller, usually shorter than 8 mm. Discs of T1–3 less densely punctate, punctures separated by >1 puncture diameter, or if punctures dense, then much smaller than 8 mm in length. Clypeus without pattern of longitudinal ridges or striations **117**

117 T3–4 with the marginal areas strongly depressed relative to the discs (Fig. 68A–E) 118

– T3–4 with the marginal areas only superficially depressed (Fig. 68F, G) **131**

118 T2–3 laterally without a gradulus **119**

– T2–3 laterally with gradulus present (c.f. Fig. 68F, G) **122**

119 Tergal discs and marginal areas completely smooth and shiny, without any shagreenation (Fig. 68B). Found in the Sistema Central to west and north-western Iberia. Associated with *Sedum* (Crassulaceae) .... ***omnilaevis* Wood**

– At least tergal discs shagreened **120**

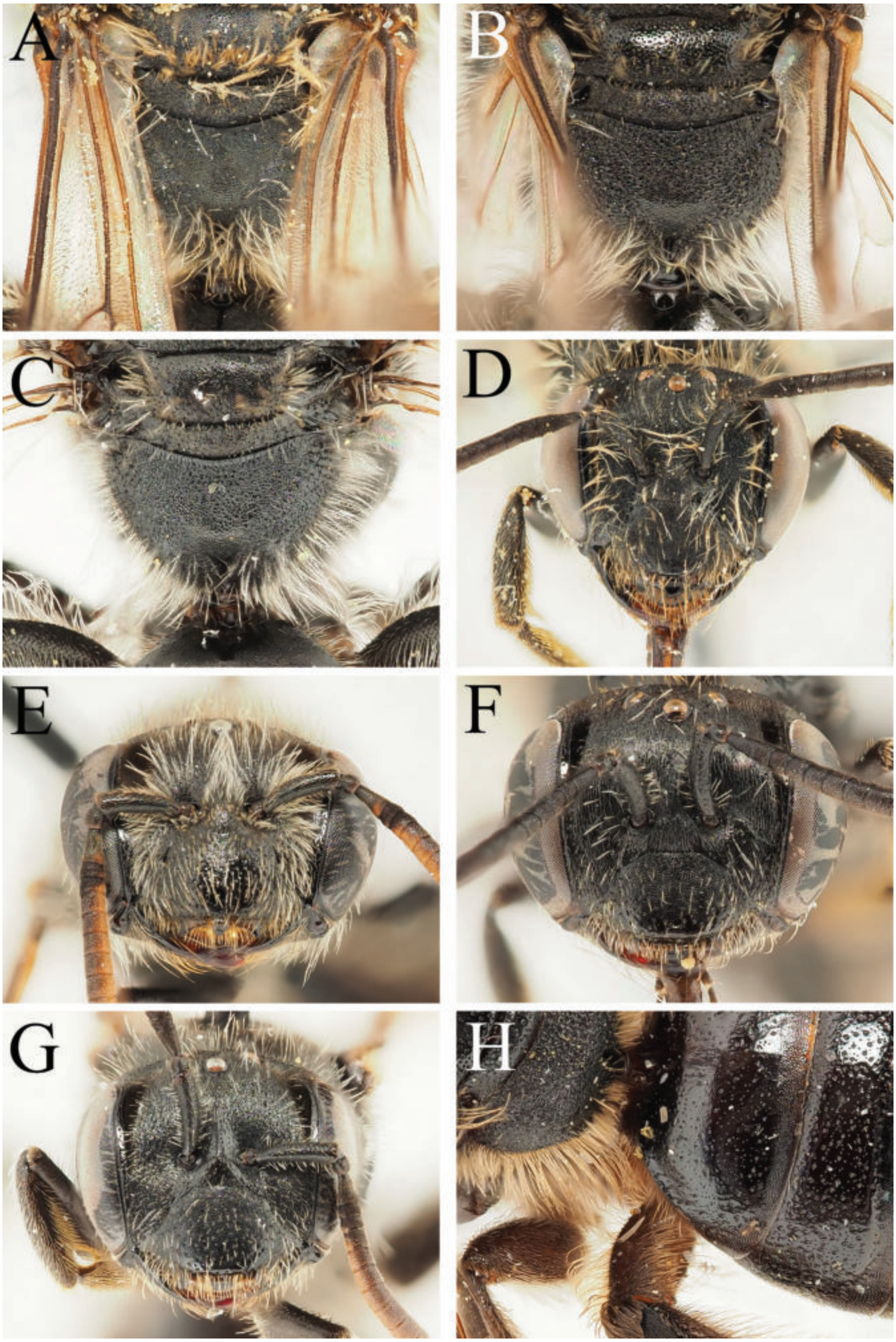

Figure 67. *Andrena* (*Micrandrena*) *longibarbis* Pérez, 1895, female **A** propodeum, dorsal view **D** clypeus, frontal view; *Andrena* (*Micrandrena*) *spreta* Pérez, 1895, female **B** propodeum, dorsal view; *Andrena* (*Micrandrena*) *tenuistriata* Pérez, 1895, female **C** propodeum, dorsal view; *Andrena* (*Micrandrena*) *pandosa trigona* Warncke, 1975, female **E** face, frontal view; *Andrena* (*Graecandrena*) *verticalis* Pérez, 1895, female **F** face, frontal view; *Andrena* (*Graecandrena*) *nebularia* Warncke, 1975, female **G** face, frontal view; *Andrena* (*Parandrenella*) *taxana* Warncke, 1975, female **H** T1, dorsal view.

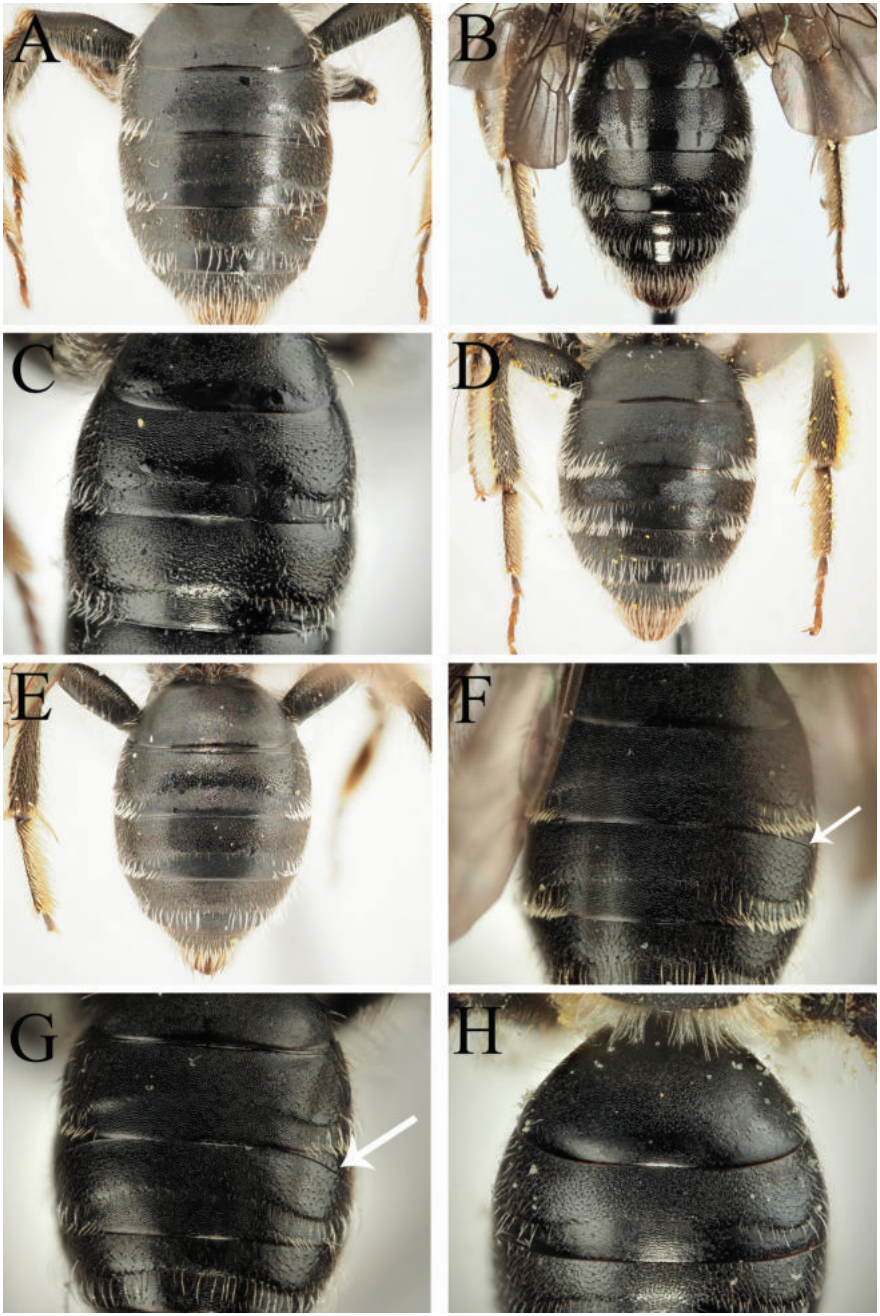

Figure 68. *Andrena* (*Micrandrena*) *spreta* Pérez, 1895, female **A** terga, dorsal view; *Andrena* (*Micrandrena*) *omnilaevis* Wood, 2020, female **B** terga, dorsal view; *Andrena* (*Micrandrena*) *anthrisci* Blüthgen, 1925, female **C** terga, dorsal view; *Andrena* (*Micrandrena*) *pauxilla* Stöckhert, 1935, female **D** terga, dorsal view; *Andrena* (*Micrandrena*) *bayona* Warncke 1975, female **E** terga, dorsal view; *Andrena* (*Micrandrena*) *minutula* (Kirby, 1802), female **F** terga, dorsal view (gradulus indicated by white arrow); *Andrena* (*Micrandrena*) *minutuloides* Perkins, 1914, female **G** terga, dorsal view (gradulus indicated by white arrow); *Andrena* (*Micrandrena*) *falsifica* Perkins, 1915, female **H** terga, dorsal view.

120 Terga with marginal areas not noticeably differentiated structurally from discs, strongly and densely shagreened and dull (Fig. 68D). Tergal discs essentially impunctate, with any obscure punctures disappearing into dense shagreenation. Scutum densely punctate, punctures separated by 0.5–1 puncture diameter .... ***pauxilla* Stöckhert**

– Terga with marginal areas noticeably shinier than discs, with weaker shagreenation. Tergal discs with clear punctures visible against the underlying shagreenation (Fig. 68C). Scutum less densely punctate, punctures separated by 1–2 puncture diameters.. **121**

121 Depressed tergal margins polished and shiny, clearly shinier than shagreened tergal discs. In dorsal view, lateral hairs at the base of the marginal area of T2 longer, erect, projecting at a 45° angle, breaking profile of metasoma laterally. Margin of T2 comparatively strongly depressed. Restricted to the Pyrenees and the Cantabrian Mountains .... ***semilaevis* Pérez**

– Depressed tergal margins shagreened, similar to and not strongly contrasting shagreened tergal discs (Fig. 68D). In dorsal view, lateral hairs at the base of the margin area of T2 shorter, flat, not projecting, almost parallel with lateral profile of metasoma. Margin of T2 comparatively weakly depressed. Slightly more widespread across central and northern Spain in mountainous areas.. ***anthrisci* Blüthgen**

122 Disc of T1 smooth and shiny, clearly punctate, punctures medially separated by 0.5–1 puncture diameter, not extending onto the broad impunctate marginal area. Rare, restricted to the Pyrenees and northern Spain .... ***floricola* Eversmann**

– Disc of T1 never smooth and shiny, always at least partially shagreened, punctate or not **123**

123 Gena entirely smooth and shiny, without any shagreenation. Scutum and scutellum polished and shiny. T2–3 with discs strongly and densely punctate, punctures separated by 1 puncture diameter (Fig. 68E). Restricted to dry and steppic habitats in central Iberia including northern Portugal .... ***bayona* Warncke**

– Gena shagreened and dull, at most with a narrow shiny strip along the outer margin of the compound eye. Scutum and scutellum variable, usually at least partially shagreened. T2–3 usually less densely and strongly punctate **124**

124 Head comparatively long, only slightly shorter than broad (Fig. 48B). Discs of T1–3 extremely densely punctate, punctures separated by 0.5–1 puncture diameters (Fig. 48D). Restricted to high-altitude on the Sierra Nevada .... ***ortizi* sp. nov.**

– Head shorter, clearly broader than long. T1–3 never so densely punctate, punctures when visible separated by at least 1 puncture diameter.......... **125**

125 Propodeal triangle poorly defined (Fig. 20E, F), lateral carinae disappearing medially, not extending from the base (metanotum) to the apex (vertical face of the propodeum). Tergal discs weakly to strongly shiny............... **126**

– Propodeal triangle well-defined, lateral carinae consistently strong from the base to the apex. Tergal discs weakly to strongly shagreened, never shiny............ **127**

126 Tergal discs entirely shiny, polished, and smooth (Fig. 20H). Scutum and scutellum extensively shiny, without shagreenation .... ***lecana* Warncke**

– Tergal discs at least partially shagreened, never entirely shiny (Fig. 20G). Scutum and scutellum with subtle shagreenation, not smooth and shiny.... .... ***niveata* Friese**

127 T1 laterally with slightly raised corners, visibly projecting and disrupting rounded profile when viewed dorsally. Clypeus slightly flattened centrally, with clear impunctate mid-line between large and well defined clypeal punctures. Terga 2–3 centrally impunctate, laterally with large punctures with raised margins (crater punctures). Restricted to areas close to the Pyrenees .... ***strohmella* Stöckhert**

– T1 laterally without such raised projections, in dorsal view evenly rounded. Clypeus with or without a clear impunctate mid-line. Terga punctation with or without lateral crater punctures. Distribution otherwise **128**

128 Clypeus weakly domed, sparsely punctate, punctures large, separated by 2–3 puncture diameters. T2–3 laterally with large hair-bearing punctures that contrast the underlying shagreenation and do not disappear into it .... ***icterina* Warncke**

– Clypeus more densely punctate, punctures separated by 1–2 puncture diameters. T2–3 laterally with at most obscure punctures **129**

129 Terga comparatively weakly shagreened and finely punctate, punctures relatively clearly visible against background shagreen, punctures extending onto tergal margins, most clearly visible on T1–3. Anterior ½ to ⅓ of clypeus usually polished and shiny. Probably univoltine (March-May). Central, eastern, and southern Spain, rare[13] .... ***exigua* Erichson**

– Terga comparatively strongly shagreened, obscurely punctate, punctures disappearing into underlying shagreenation (Fig. 68A). Tergal margins impunctate. Clypeus usually shagreened, without polished fore-margin[13] **130**

130 Scutum strongly and clearly punctate, punctures separated by 1–2 puncture diameters, underlying surface variable but always at least partially shiny. Bivoltine (March-July). Throughout Iberia, common[13] .... ***spreta* Pérez**

– Scutum obscurely punctate, punctures disappearing into the abundant underlying shagreen, scutum dull. Univoltine (April-May). Iberian distribution

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[13] These three species are challenging to separate without confidently identified reference material. Most specimens will be *A. spreta* Pérez which is by far the most commonly collected of the three.

unclear, but probably restricted to southern Spain (Cádiz, Málaga)[13] .... ***tiaretta*** **Warncke**

131 Disc of T1 clearly punctate, though sometimes finely and sometimes only punctate basally (Fig. 68H). Disc of T2 more strongly, clearly, and extensively punctate **132**

– Disc of T1 finely to strongly shagreened, at most obscurely punctate with punctures disappearing into the underlying surface sculpture (Fig. 67F, G). Disc of T2 with at most a few punctures laterally.................................**134**

132 Marginal area of T1 wide, strongly thickened, impunctate (Fig. 68H). Restricted to mountainous areas in northern Spain, associated with *Potentilla* (Rosaceae) .... ***falsifica*** **Perkins**

– Marginal area of T1 normal, not widened or thickened **133**

133 Disc of T1 strongly shagreened, predominantly punctured medially. Antennae ventrally at most lightened dark brown. Throughout Iberia, bivoltine .... ***alfkenella*** **Perkins**

– Disc of T1 finely shagreened, evenly and finely punctate over its entire area, with shiny interspaces. Antennae ventrally orange. Rare, restricted to northern Spain, univoltine (August–September)..................... ***nanula*** **Nylander**

134 Process of the labrum narrow, as long as broad. Scutum strongly shagreened and matt, densely punctate, punctures difficult to discern against the strong underlying sculpture. Clypeus sparsely punctate, with obscure and weak latitudinal striations .... ***simontornyella*** **Noskiewicz**

– Process of the labrum wider, broader than long. Scutum less strongly shagreened, with punctures of variable density that are clearly visible against the underlying sculpture. Clypeus variably punctate, but never with latitudinal striations **135**

135 Clypeus strongly flattened and sparsely punctate, punctures separated on average by more than 2 puncture diameters. Process of the labrum medially emarginate. Associated with *Ornithogalum* (Asparagaceae)......................... .... ***saxonica*** **Stöckhert**

– Clypeus domed, never strongly flattened, punctures dense or sparse. Process of the labrum truncate or apically rounded.. **136**

136 Clypeus sparsely and obscurely punctate, punctures separated by 2–3 puncture diameters or more. Scutum very sparsely and finely punctate, punctures small, separated by 2–3 puncture diameters, underlying surface shagreened and dull. Restricted to temperate areas close to the Pyrenees .... ***subopaca*** **Nylander**

– Clypeus clearly punctate, punctures separated by 1–2 puncture diameters. Scutum more densely punctate, punctures larger, separated by up to 2 puncture diameters, underlying surface dull to shiny. Throughout Iberia..................**137**

137 Scutellum shagreened, at most weakly shiny. Scutum more densely punctate, punctures separated by 1 puncture diameter, underlying surface shagreened and dull (1st generation) to weakly shiny (2nd generation). Terga with dense and narrow apical hair bands laterally, individual hairs touching

each other in fresh specimens (Fig. 68F). Foveae not noticeably narrowed ventrally... ***minutula* (Kirby)**

– Scutellum always polished and shiny. Scutum less densely punctate, punctures less regular, separated by 1–2 puncture diameters, underlying surface finely shagreened and weakly shiny (1st generation) to smooth and shiny (2nd generation). Terga with sparse apical hair bands, occasionally with some individual hairs touching each other (Fig. 68G; 1st generation), usually with all hairs individually separated (2nd generation). Foveae slightly but distinctively narrowed ventrally... ***minutuloides* Perkins**

138(91) Clypeus flattened over majority of its surface. Species strongly associated with Fabaceae (subgenus *Taeniandrena*)[14]... **139**

– Clypeus not noticeably flattened. Species not usually associated with Fabaceae **151**

138 Face and foveae black haired. Terminal fringe dark brown (Fig. 69A). Terga with weak and obscure punctures. Known only from central Portugal (Castelo Branco) and south-western Spain (Huelva, Cádiz). Univoltine (March–April) .... ***lusitania* Wood & Ortiz-Sánchez**

– Combination of characters otherwise; either face with pale hairs, terminal fringe light, or tergal densely punctate **140**

140 Terminal fringe composed of dark brown to brownish grey hairs. Hairs flanking the basitibial plate of the hind tibia also dark (Fig. 69B) **141**

– Terminal fringe and hairs flanking basitibial plate of hind tibia light, golden to yellow-orange (Fig. 69C–F) **143**

141 Discs of T2–4 strongly and densely punctate, punctures clearly visible against the underling shagreenation. Widespread throughout Iberia, most common in areas with an Atlantic climate and abundant Genisteae. Bivoltine (typically March–May; June–July) .... ***ovatula* (Kirby)**

– Discs of T2–4 obscurely and shallowly punctate, punctures disappearing into background shagreenation. Iberian distribution more restricted (see below) **142**

142 Scutum with punctures shallow and obscure, separated by >1 puncture diameter. T3 with apical hair band interrupted medially. Currently known only from the steppe of central Spain (Guadalajara, Salamanca, Segovia). Univoltine (May–June)... ***ovata* Schenck**

– Scutum with punctures dense and clear, separated by <1 puncture diameter. T3 with apical hair band complete in fresh specimens. Currently only confirmed from the coast of southern Spain (Málaga). Bivoltine (probably February–April; May–June) ....***poupillieri* Dours**

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[14] Females of this subgenus are highly challenging and in some cases impossible to identify. There are several outstanding taxonomic issues in this subgenus that require in-depth genetic study to resolve, and additional probably undescribed cryptic species are present. Do not expect to identify this group without consulting confidently determined reference material, and ideally barcoded specimens. Minimal characters are given here because of the ongoing lack of taxonomic clarity in this subgenus. See also the key of Praz et al. (2022).

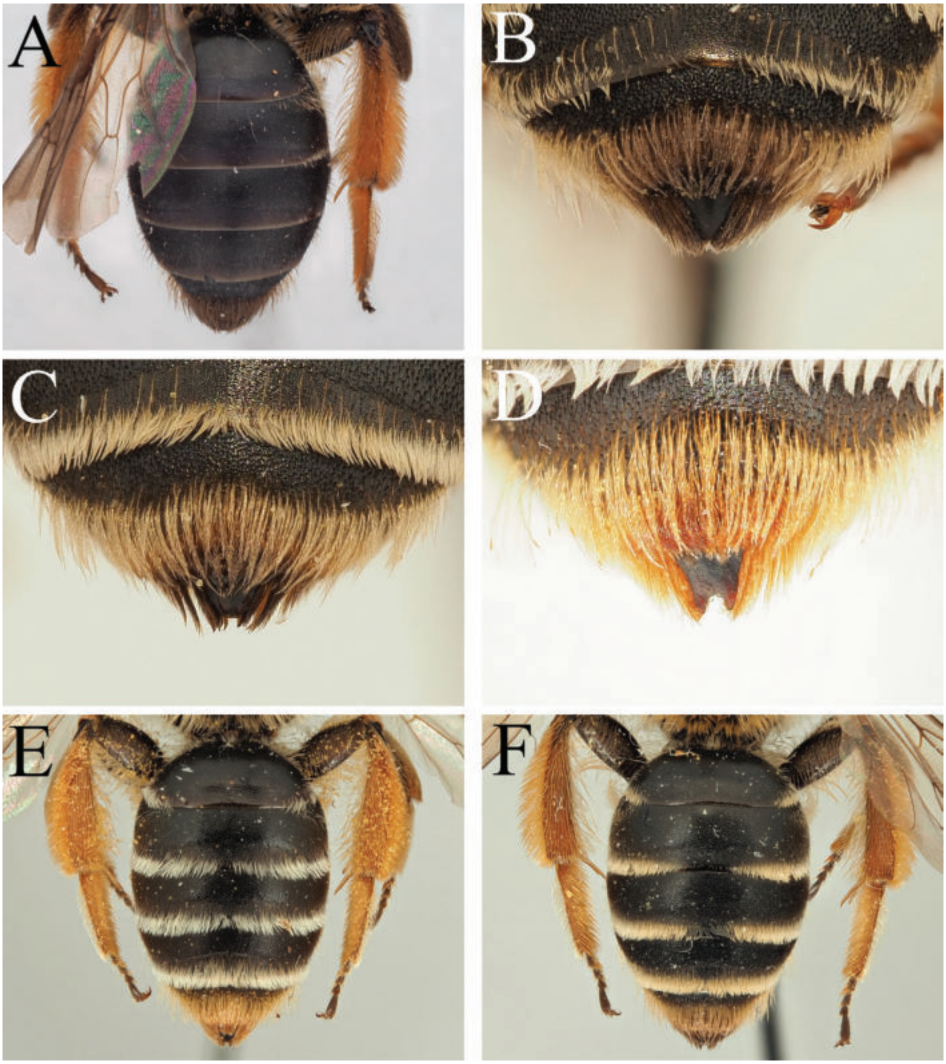

Figure 69. *Andrena* (*Taeniandrena*) *lusitania* Wood & Ortiz-Sánchez, 2022, female **A** terga, dorsal view; *Andrena* (*Taeniandrena*) *ovatula* (Kirby, 1802), female **B** terminal fringe; *Andrena* (*Taeniandrena*) *afzeliella* (Kirby, 1802), female **C** terminal fringe; *Andrena* (*Taeniandrena*) *lathyri* Alfken, 1900, female **D** pygidial plate, posterior view; *Andrena* (*Taeniandrena*) *gredana* Warncke, 1975, female **E** terga, dorsal view; *Andrena* (*Taeniandrena*) *benoisti* Wood & Praz, 2021, female **F** terga, dorsal view.

143 Pygidial plate apically with deep emargination medially (Fig. 69D). Clypeus medially with shallow but distinct longitudinal impression, surrounding surface with extremely shallow and obscure punctures. Terga impunctate. Restricted to northern Spain .... ***lathyri* Alfken**

– Pygidial plate apically rounded, never emarginate. Clypeus without medial impression, punctures usually clear. Terga with or without punctures **144**

144 Clypeus apically shiny. T2–4 apically with wide white hair bands that are complete in fresh specimens, these clearly exceeding the length of the marginal areas (Fig. 69E). Scutum laterally shagreened, becoming smooth and shiny medially. Restricted to the Sistema Central and northern and western Iberia .... ***gredana* Warncke**

– Clypeus uniformly dull. T2–4 with hair bands different, either shorter, broadly interrupted medially, or yellowish (Fig. 69F). Scutum uniformly dull or with circular shiny area medially **145**

145 Declivity of T1 medially strongly and densely punctate, punctures separated by <1 puncture diameter **146**

– Declivity of T1 with at most scattered punctures, never with dense patch of punctures medially **149**

146 T3 with interrupted apical hair band in fresh specimens. T2–4 with the apical hyaline part of the marginal areas narrow, not exceeding 3 times the diameter of a puncture from the tergal discs. Scutum uniformly dull. Restricted to northern Portugal and Spain with isolated populations at elevation in the Sistema Central and Sistema Ibérico ....
.... ***wilkella* (Kirby)**

– T3 with apical hair band complete in fresh specimens (Fig. 69F). T2–4 with the apical hyaline part of the marginal areas comparatively broad, exceeding 4 times the diameter of a puncture from the tergal discs. Scutum at least partly shiny **147**

147 Scutum shagreened laterally, medially with a circular area which is smooth and shiny; punctation here becoming weaker and sparser. Restricted to the Sistema Central to central and northern Portugal and north-western Spain (Zamora). Not known from the Cantabrian or Pyrenees Mountains ....
.... ***benoisti* Wood & Praz**

– Scutum more or less uniformly shagreened and punctate. Found across mountainous areas in eastern Spain (Sierra Nevada, Sierra de Cazorla, Sistema Ibérico) to the Pyrenees **148**

148 Restricted to the alpine zone of the Sierra Nevada (above 2000 m) ....
.... ***contracta* Wood**

– Found elsewhere .... ***intermedia* Thomson aggregate** (this likely represents a complex of an unknown number of species, potentially all of which are undescribed; the true *intermedia* may be absent from Spain)

149 Terga obscurely punctate, at least on the base of T2 with punctures disappearing into the underlying shagreenation. Univoltine (April–June) ...
.... ***russula* Lepeletier sensu lato** (including the distinct mitochondrial lineage from southern Portugal)

– Terga clearly punctate, at least on the base of T2 with punctures clearly visible against the underlying shagreenation **150**

150 Terga strongly shagreened, dull to weakly shiny. Scutellum shagreened and weakly shiny. Tergal hair bands yellowish. Larger, 11–12 mm. Restricted

to southern and south-eastern Spain (Almería, Granada, Málaga, Murcia, Valencia). Univoltine (April–June) .... ***levante* Wood & Praz**

– Terga less strongly shagreened, shiny comparatively more strongly. Scutellum medially almost without sculpture, brightly shiny. Tergal hair bands whitish. Smaller, 8–10 mm. Throughout Iberia. Bivoltine (typically May–June; July–August) .... ***afzeliella* (Kirby)**

151 (138) Fovea dorsally narrow, occupying at most ⅓ of space between lateral ocellus and compound eye, ventrally narrowing strongly (subgenus *Euandrena*) **152**

– Foveae either dorsally broader, or not strongly narrowing **162**

152 Head elongate, mouthparts extremely long, twice the length of the head (c.f. Fig. 89D). Process of the labrum triangular. Associated with *Lithodora* (Boraginaceae) .... ***solenopalpa* Benoist**

– Head and mouthparts shorter, mouthparts never twice the length of the head. Process of the labrum trapezoidal **153**

153 Clypeus densely and coarsely punctate with a raised longitudinal impunctate shiny line. Restricted to areas close to the Pyrenees. Associated with *Symphytum* (Boraginaceae) .... ***symphyti* Schmiedeknecht**

– Clypeus densely or weakly punctate, never with a raised longitudinal impunctate shiny line **154**

154 Pronotum with weak but distinct lateral keel. Clypeus medially with shallow longitudinal impression **155**

– Pronotum laterally rounded. Clypeus without longitudinal impression, in one species (*A. rufula* Schmiedeknecht) with hints of an impression caused by impunctate longitudinal midline **156**

155 T2 with marginal area long, occupying almost ½ the segment, strongly depressed and shiny (Fig. 70A). Facial pubescence light brown, with at most dark hairs laterally on the frons. Terminal fringe brown. Found in areas with a temperate Atlantic climate across central, north-western, and northern Iberia .... ***angustior* (Kirby)**

– T2 with marginal area shorter, not strongly depressed (Fig. 70B). Face with intermixed black hairs throughout, including on the vertex (Fig. 8C). Terminal fringe dark brown to black (Fig. 8D). Found in areas with a Mediterranean climate .... ***lavandulae* Pérez**

156 Tergal discs with extremely coarse and dense punctures, punctures separated by 0.5–1 puncture diameter. Tergal margins strongly depressed and essentially impunctate, margins of T2–4 overlain by sparse whitish hair bands that emerge from the apexes of the tergal discs and which do not obscure the underlying surface of the marginal areas (Fig. 70C). Known only from mountainous areas in north-western, central, and south-eastern Spain (Léon, Ávila, Jáen) .... ***fortipunctata* Wood**

– Tergal discs with normal punctures, not noticeably coarse, punctures separated on average by 1 puncture diameter. Tergal margins only weakly depressed, without long whitish hair bands, sometimes with obscure brownish lateral hair bands on the apexes of the marginal areas themselves **157**

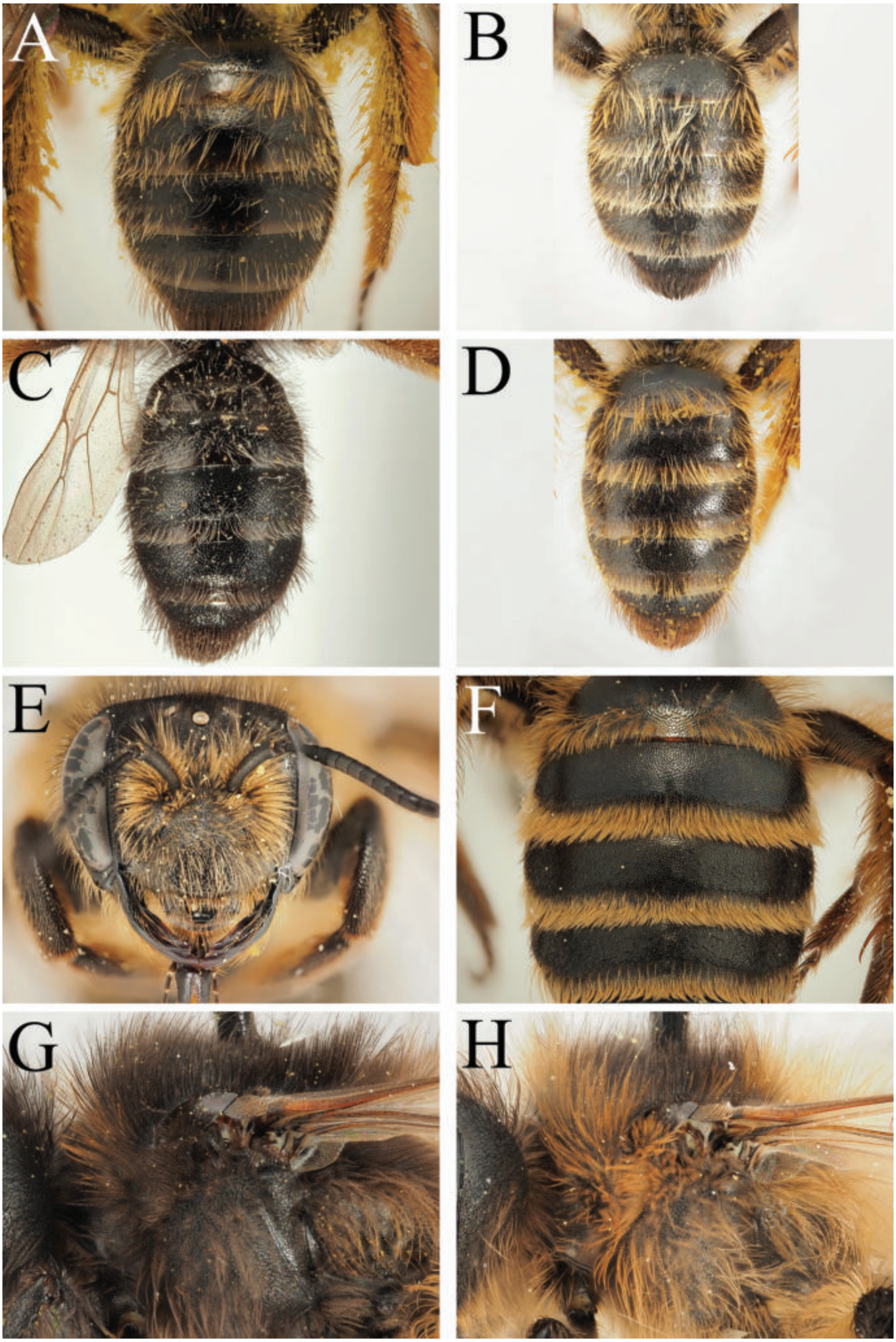

Figure 70. *Andrena* (*Euandrena*) *angustior* (Kirby, 1802), female **A** terga, dorsal view; *Andrena* (*Euandrena*) *lavandulae* Pérez, 1902, female **B** terga, dorsal view; *Andrena* (*Euandrena*) *fortipunctata* Wood, 2021, female **C** terga, dorsal view; *Andrena* (*Euandrena*) *granulosa* Pérez, 1902, female **D** terga, dorsal view; *Andrena* (*Melandrena*) *flavipes* Panzer, 1799, female **E** head, frontal view **F** terga, dorsal view; *Andrena* (*Melandrena*) *vulcana* Dours, 1873, female **G** mesosoma, profile view (dark form) **H** mesosoma, profile view (light form).

157 Apical margins of T1–4 extensively lightened yellow-hyaline, this lightened area clearly exceeding the diameter of a lateral ocellus (Fig. 70D). Associated with Cistaceae **158**

– Apical margins of T1–4 not extensively lightened yellow-hyaline, at most narrowly so, this lightened area not exceeding the diameter of a lateral ocellus **159**

158 Tergal margins comparatively more strongly depressed. Tergal discs on average more coarsely and densely punctate, punctures on the disc of T2 separated by 1.5–2 puncture diameters[15] .... ***granulosa* Pérez**

– Tergal margins comparatively more weakly depressed. Tergal discs on average less strongly and densely punctate, punctures on the disc of T2 separated by 3–4 puncture diameters[15] .... ***vulpecula* Kriechbaumer**

159 Facial pubescence predominantly light, with dark hairs restricted to the inner margins of the compound eyes. Mesepisternum entirely pale-haired. Restricted to temperate areas close to the Pyrenees .... ***rufula* Schmiedeknecht**

– Facial pubescence predominantly black, with occasional scattered light hairs (Fig. 48B). Mesepisternum with at least some black hairs (Fig. 48A), often with extensive dark pubescence **160**

160 Face long, majority of the clypeus passing below an imaginary line drawn between the ventral margins of the compound eyes. Clypeus comparatively sparsely punctate, punctures separated by an average of 1 puncture diameter, with impunctate longitudinal midline. Restricted to mountainous areas in northern and north-western Spain .... ***allosa* Warncke** (note, the Spanish taxon may be distinct from populations in Central Europe)

– Face short, only a small part of the clypeus falls below an imaginary line drawn between the ventral margins of the compound eyes. Clypeus comparatively densely punctate, punctures separated on average by 0.5–1 puncture diameter **161**

161 Clypeus extremely densely and coarsely punctate, punctures separated by 0.5 puncture diameters (Fig. 48B). Currently known only from the Sierra Nevada .... ***isolata* sp. nov.**

– Clypeus less densely punctate, punctures separated on average by 0.5–1 puncture diameters. Widespread across Iberia .... ***bicolor* Fabricius sensu lato** (two mitochondrial lineages are present in *A. bicolor*; to date, only the southern lineage has been found in Iberia)

162 (151) Clypeus punctate, interspaces forming weakly raised longitudinal wrinkles (Fig. 70E; former subgenus *Zonandrena*) **163**

– Clypeus without longitudinal wrinkles **167**

163 Face, mesepisternum, scutum anteriorly, and propodeum with abundant white hairs; scutum medially with contrasting short black pubescence.

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[15] These two species are very difficult to separate in the female sex. Association with males should be made where possible.

Marginal areas of T2–4 laterally with broad white hair patches that obscure the underlying surface. Restricted to steppic areas in central Spain............. ....***soror* Dours**

– Face with pubescence variable, either black or a mixture of black and brown; if entirely white, then mesosoma with extensive brown pubescence dorsally. Terga with complete apical hair bands that are never interrupted medially in fresh specimens or with hair bands reduced and essentially absent **164**

164 Facial pubescence white. Rare, restricted to the Pyrenees ....***gravida* Imhoff**

– Facial pubescence black or a mixture of black and brown; never pure white **165**

165 Posterior face of hind femur with a latitudinal carina. Facial pubescence never entirely black, usually a mixture of yellow, brown, and black hairs, sometimes whitish. Terga usually with strong apical hair bands (Fig. 70F; beware abraded specimens). The most common and widespread Iberian *Andrena* species..***flavipes* Panzer**

– Posterior face of hind femur rounded, without a latitudinal carina. Facial pubescence dark, often entirely black (Fig. 11C), usually predominantly black with at most some intermixed dark brown hairs. Terga with hair bands variable, sometimes weakly present, sometimes almost entirely absent (Figs 11F, 12D). Generally rare and found in southern Iberia **166**

166 Propodeal triangle with finely raised rugae covering entire surface. Pubescence variable, from almost entirely melanic (Fig. 70G, with only the tibial scopa remaining orange-red) to light, with extensive brown hairs on the mesosoma and terga (Fig. 70H). Foveae comparatively weakly constricted medially. Usually with complete tergal bands present[16] ....***vulcana* Dours**

– Propodeal triangle with finely raised rugae covering only basal half, apical parts with fine granular shagreenation. Pubescence variable, but never entirely melanic, mesonotum always with at least some brown hairs (Figs 11D, 12B). Foveae comparatively strongly constricted medially. Tergal bands usually greatly reduced[16] ....***discors* Erichson**

167 (162) Dorsolateral surface of the propodeum reticulate, with large and shallow punctures (can be small in *A. nuptialis* Pérez), clearly contrasting the shagreened and shiny propodeal triangle, this lacking lateral carinae and becoming shinier on the declivity (Fig. 65H, often entirely shagreened in *A. nuptialis*). Pronotum lacking lateral keel. Clypeus typically weakly to moderately domed, densely punctate (punctures separated by 1 puncture diameter, with more or less pronounded impunctate midline (subgenus *Hoplandrena*) **168**

– Without this combination of characters, pronotum keeled or not.........**173**

168 Hind tibiae and/or tarsi golden-orange **169**

– Both hind tibiae and tarsi dark, at most obscurely reddish-brown.........**170**

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[16] These two species are difficult to separate due to enormous colour variation.

169 Hind tibiae golden-orange. Clypeus medially with a clearly raised longitudinal impunctate area, this area smooth and shiny, strongly contrasting the remaining parts of the clypeus which are densely punctate. Northern and central Spain, in areas with deciduous forest. Associated with *Quercus* (Fagaceae) .... ***ferox* Smith**

– Hind tibiae dark. Clypeus with faint impunctate longitudinal line medially, but this is not raised and not shiny, therefore not strongly contrasting with the remaining parts of the clypeus which are regularly punctate. Rare, restricted to the Pyrenees .... ***bucephala* Stephens**

170 A3 clearly exceeding length of A4+5 .... ***nuptialis* Pérez**

– A3 not clearly exceeding length of A4+5, usually as long as or slightly shorter than A4+5..**171**

171 Metasomal terga with short hairs, most clearly seen in profile on T2–3 with hairs not exceeding width of a flagellum....... ***rosae* Panzer** (*partim*, dark form)

– Metasomal terga with extensive and abundant long hairs, most clearly seen in profile on T2–3 with hairs clearly exceeding width of a flagellum............**172**

172 Tibial scopa in fresh specimens usually dark dorsally and silver ventrally. Usually with light brown facial hair. Usually univoltine, flying April to mid-June, with potential sporadic emergence in August and September (not yet observed in Iberia). Rare, restricted to cooler parts of Iberia[17] ....***scotica* Perkins**

– Tibial scopa in fresh specimens dark dorsally and golden ventrally, but this can be ambiguous and fade to silver in older specimens or pinned material. Facial hair can be dark, particularly in the spring generation, the summer generation usually has lighter facial hair. Bivoltine, usually flying March–May and July–August, with phenology depending on local conditions. Common and widespread across Iberia[17] .... ***trimmerana* (Kirby)** (*partim*, dark form)

173 (167) Pronotum laterally keeled, angulate, keel runs up dorsally to an angled corner.. .... **174**

– Pronotum laterally rounded, without a keel **205**

174 Mesepisternum deeply and distinctly punctate, punctures separated by <1 puncture diameter, with weakly shiny interspaces. Ocelloccipital distance exceeding 3 times the diameter of a lateral ocellus. Terga extremely densely punctate, punctures separated by <0.5 puncture diameters, with shiny interspaces. No recent records, possibly extinct, restricted to central Spain......... ....***incisa* Eversmann**

– Without this combination of characters, mesepisternum usually impunctate or only obscurely punctate, ocelloccipital distance shorter, terga dull or less densely punctate **175**

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[17] These two species cannot be consistently morphologically separated with confidence. Association with males should be made. See discussion and notes in Wood et al. (2022c).

175 Fore margin of clypeus slightly upturned, forming wide] shape, dorsolateral surface of propodeum reticulate, impunctate, not strongly differentiated from the propodeal triangle, terga with dense apical hair bands on T2–4, fovea broad and occupying over ½ of the distance between the compound eye and the lateral ocellus, tibial scopae with hairs long and loose. Restricted to central, southern, and eastern Spain and associated with *Reseda* (Resedaceae) **176**

– Without this combination of characters **177**

176 Terminal fringe orange. Tibial scopae orange. Tergal discs with extremely fine shagreen, shiny, clearly and deeply punctate .... ***relata*** **Warncke**

– Terminal fringe dark brown medially and white laterally (Fig. 40D). Tibial scopae white (Fig. 40A). Tergal discs strongly shagreened, weakly shiny, obscurely and shallowly punctate (Fig. 40D) .... ***blanda*** **Pérez**

177 Pygidial plate flat to weakly convex, outer margin usually somewhat elevated, without clearly raised area medially (Fig. 71A; subgenus *Notandrena partim*)..**178**

– Pygidial plate with distinctly limited raised area medially (Fig. 71B)........**186**

178 Scutum with very dense and even punctation across the entire surface of the disc, punctures separated by much less than the diameter of a puncture, in some cases nearly touching (Fig. 57C). Underlying integument strongly shagreened and dull .... ***griseobalteata*** **Dours**

– Scutum with moderate and uneven punctation, punctures separated by 1–3 puncture diameters in some cases. If occasional punctures are close to touching, then this is not consistently replicated across the whole scutum, with other punctures being separated by a clear distance. Underlying integument variable, from shagreened to shiny **179**

179 Hind tibia and all tarsi completely orange. Restricted to areas close to the Pyrenees.. ***chrysosceles*** **(Kirby)**

– Hind tibia black, tarsi may be black or orange **180**

180 Larger species, body length 11–12 mm. T2–4 with thick white apical hair bands that obscure the underlying surface, only weakly interrupted medially on T2 .... ***langadensis albipila*** **Warncke**

– Smaller species, body length 7–10 mm. T2–4 usually with weaker hair bands **181**

181 Tibial scopa, when viewed in reverse profile (i.e. looking at the posterior face of the hind tibia) dorsally short and thick, hair length only 1–1.5 times the diameter of a lateral ocellus, clearly shorter than the ventral scopal hairs. Restricted to areas close to the Pyrenees .... ***pallitarsis*** **Pérez**

– Tibial scopa equally long dorsally and ventrally **182**

182 Terga very sparsely punctate, punctures of discs of T2–4 shallow, obscure, and separated by 3–4 puncture diameters. Clypeus comparatively flattened. Very rare, known only from southern Spain (Cádiz)................ ***microthorax*** **Pérez**

– Terga densely punctate, punctures on discs of T2–4 strong and deep, separated at most by 2 puncture diameters, usually by <2 puncture diameters. Clypeus comparatively domed **183**

Figure 71. *Andrena* (*Notandrena*) *griseobalteata* Dours, 1872, female **A** pygidial plate, posterior view; *Andrena* (*Leucandrena*) *leptopyga* Pérez, 1895, female **B** pygidial plate, posterior view; *Andrena* (*Notandrena*) *foeniculae* Wood, 2020, female **C** head, dorsal view; *Andrena* (*Notandrena*) *nitidiuscula* Schenck, 1853, female **D** head, dorsal view **E** scutum, dorsolateral view; *Andrena* (*Notandrena*) *fulvicornis* Schenck, 1861, female **F** scutum, dorsolateral view.

183 Vertex clearly elongate, the hind ocelli separated from the margin of the vertex by a distance greater than the diameter of a lateral ocellus (Fig. 71C). Genae enlarged so that the hind margin of the vertex forms a weak U-shape .... ***foeniculae* Wood**

– Vertex not elongate, the hind ocelli separated from the margin of the vertex by a distance clearly less than the diameter of a lateral ocellus (Fig. 71D). Hind margin of the vertex in comparison almost straight **184**

184 Central line in the front half of the scutum strongly impressed (Fig. 71E). Restricted to temperate habitats in northern Iberia. Hind basitarsi dark. Univoltine (July–August).. ***nitidiuscula* Schenck**

– Central line in the front half of the scutum only weakly and superficially impressed (Fig. 71F). Hind basitarsi dark to often entirely lightened orange. Not restricted to northern Iberia, and active in the spring or the summer.......... **185**

185 Disc of T1 densely punctate, punctures separated by 1 puncture diameter. Scutellum shagreened and dull. Hind basitarsi orange. Throughout Iberia. Bivoltine (March–August) .... ***fulvicornis* Schenck**

– Disc of T1 sparsely punctate, punctures separated by 2–3 puncture diameters. Scutellum polished and shiny. Restricted to strongly saline habitats in southern Iberia. Voltinism unclear, possibly bivoltine, recorded March–early June.. ***juliana* Wood**

186 Flying exclusively in the summer (July–September). Hind tibiae triangular, clearly much broader apically than basally, with short scopal hairs not greatly exceeding the diameter of a lateral ocellus (Fig. 72A). Terga with strong and broad apical tergal hair bands (Fig. 72B; subgenus *Cnemidandrena* Hedicke).. **187**

– Flying predominantly in the spring, some species extending into July. Hind tibiae normal, not greatly broader apically than basally, with long scopal hairs, clearly greatly exceeding the diameter of a lateral ocellus. Terga with or without clear apical hair bands **189**

187 Outer surface of the galea smooth and shiny. Associated with Ericaceae, found in Atlantic habitats across northern, central, and western Iberia........ .... ***fuscipes* (Kirby)**

– Outer surface of the galea shagreened and dull.................................... **188**

188 Mesosoma anteriorly and posteriorly with pale hairs, medially with abundant black hairs. Face with pale hairs. Associated with Asteraceae, restricted to northern Spain .... ***denticulata* (Kirby)**

– Mesosoma with pale to brown hairs, with at most occasional intermixed black hairs. Face black-haired. Polylectic, though often found on Asteraceae. Restricted to areas surrounding the Pyrenees and the Cantabrian Mountains with isolated populations in high mountains in southern Spain (particularly the Sierra Nevada) .... ***nigriceps* (Kirby, 1802)**

189 Process of the labrum either elongate (as long as or slightly longer than broad) or pointed triangular, never medially emarginate (Fig. 72C–H). Clypeus sometimes with transverse wrinkles (subgenus *Leucandrena*)............................ **190**

– Process of the labrum trapezoidal, always broader than long, usually medially emarginate, at least weakly. Clypeus never with transverse wrinkles (subgenus *Andrena* s. str.).. **197**

190 Fovea very wide, occupying the entirety of the space between the inner margin of compound eye and the lateral ocellus... **191**

– Fovea narrower, occupying between half and two-thirds of distance between the inner margin of compound eye and the lateral ocellus..................... **192**

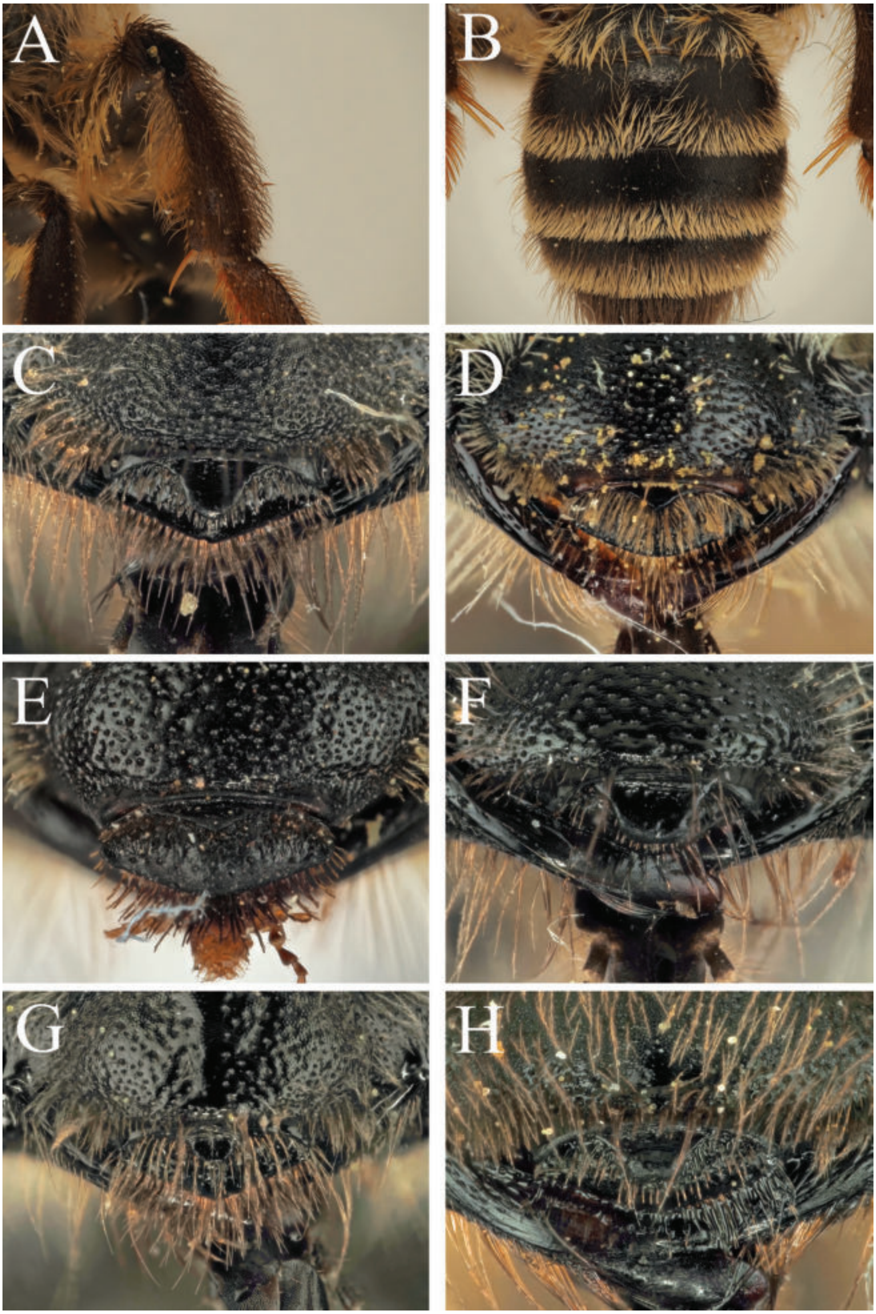

Figure 72. *Andrena* (*Cnemidandrena*) *denticulata* (Kirby, 1802), female **A** hind leg, profile view **B** terga, dorsal view; *Andrena* (*Leucandrena*) *barbilabris* (Kirby, 1802), female **C** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *tunetana* Schmiedeknecht, 1900, female **D** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *sericata* Imhoff, 1868, female **E** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *parviceps* Kriechbaumer, 1873, female **F** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *ventralis* Imhoff, 1832, female **G** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *leptopyga* Pérez, 1895, female **H** process of the labrum, frontal view.

191 Clypeus with network of fine, raised ridges that extend laterally across the disc, underlying surface shiny. Process of labrum short, broader than long, produced to a fine triangular point (Fig. 72D)...................... ***tunetana* Schmiedeknecht**

– Clypeus without any lateral ridges, underlying surface shagreened, dull. Process of labrum short and slightly broader than long, but clearly trapezoidal, apical margin slightly thickened and raised (Fig. 72H) ...... ***leptopyga* Pérez**

192 Scutum and scutellum shagreened, dull. Process of labrum as long as broad, evenly rounded apically (Fig. 72C) .... ***barbilabris* (Kirby)**

– At least some part of the scutum or scutellum shiny. Process of labrum either pointed triangular or apically truncate, not evenly rounded apically........... **193**

193 Process of labrum pointed triangular (Fig. 72E). Very rare, restricted to the Pyrenees.. ***sericata* Imhoff**

– Process of labrum apically truncate, not pointed (Fig. 72F, G) **194**

194 Terga clearly finely and densely punctured, punctures separated by 1–2 puncture diameters, visible against weakly shagreened integument. Restricted to mountainous areas of central and northern Spain .... ***argentata* Smith**

– Terga with punctures sparse and difficult to see, separated by 3–5 puncture diameters **195**

195 Process of labrum comparatively large, apex more rounded (Fig. 72F). Fovea, viewed dorsally, with dark brown hairs. Terminal fringe dark brown. Larger, 10–11 mm .... ***parviceps* Kriechbaumer**

– Process of labrum comparatively small, more clearly truncate (Fig. 72G). Fovea, viewed dorsally, with light brown hairs. Terminal fringe golden. Smaller, 7–9 mm **196**

196 Scutum shagreened laterally, but centrally shagreenation is absent, underlying surface therefore smooth and shiny. Lateral faces of the propodeum with clearly raised more or less parallel ridges. Scutum more strongly punctured, individual punctures larger and closer together, particularly anteriorly where they are separated by 1–2 puncture diameters .... ***dinizi* Warncke**

– Scutum shagreened, shagreenation weaker centrally but still clearly visible. Lateral faces of the propodeum with at most very small wrinkles. Scutum less strongly punctured, individual punctures normal and more scattered, separated by 1–3 puncture diameters .... ***ventralis* Imhoff**

197 Terga densely covered with long hairs, in fresh specimens these obscuring the underlying surface (Fig. 73A)...**198**

– Terga less thickly haired, sometimes with hair tufts on T1–2, but these not obscuring the underlying surface (Fig. 73B)..**199**

198 Hind tibiae orange. Terga predominantly black-haired, sometimes with light brown hairs on T1. Restricted to northern Spain, associated with *Salix* (Salicaceae) .... ***clarkella* (Kirby)**

– Hind tibiae dark. Terga 1–5 with extensive reddish-orange pubescence (Fig. 73A). With a patchy distribution from northern Portugal and Spain to the Pyrenees, with an isolated population in the Sierra de Cazorla (Jáen). Associated with various flowering trees and shrubs.............. ***fulva* (Müller)**

Figure 73. *Andrena* (*Andrena*) *fulva* (Müller, 1776), female **A** terga, dorsal view; *Andrena* (*Andrena*) *helvola* (Linnaeus, 1758), female **B** terga, dorsal view; *Andrena* (*?Euandrena*) *ramosa* Wood, 2022, female **C** propodeal corbicula, profile view; *Andrena* (*Didonia*) *mucida* Kriechbaumer, 1873, female **D** process of the labrum, ventral view; *Andrena* (*Avandrena*) *erodiorum* Wood & Ortiz-Sánchez, 2022, female **E** propodeum, dorsal view; *Andrena* (*Avandrena*) *melacana* Warncke, 1967, female **F** propodeum, dorsal view; *Andrena* (*Nobandrena*) *funerea* Warncke, 1975, female **G** propodeum, dorsal view; *Andrena* (*Truncandrena*) *ferrugineicrus* Dours, 1872, female **H** propodeum, dorsal view.

199 Marginal areas of T2–4 very wide, occupying ¾ of each segment ....***synadelpha* Perkins**

– Marginal areas of T2–4 never occupying more than ½ of each segment, usually covering only ⅓..**200**

200 Face with entirely pale hairs, at most with a few scattered dark hairs along the inner margin of the compound eye **201**

– Face with extensive black hairs, particularly around the antennal insertions and along the inner margin of the compound eye **203**

201 Terga sparsely haired, with at most weak hair tufts on T1–2. Terga finely shagreened and thus weakly shiny. Restricted to northern Spain. Flying later in the year (June–August), associated with shrubs, particularly *Rubus* (Rosaceae)..***fucata* Smith**

– Terga typically with long hairs, in fresh specimens with clear and dense hair tufts on T1–2. Abraded or older specimens may lack such hair tufts, in which case use the following characters: terga strongly shagreened, dull. Flying earlier in the year (March–May), associated with flowering trees... .... **202**

202 Basitarsi of hind tibiae parallel-sided, not converging apically. Restricted to the Pyrenees with an isolated population in the Sierra de Cazorla (Jáen). Associated with various flowering trees and shrubs ....***helvola* (Linnaeus)**

– Basitarsi of hind tibiae broader basally, narrower apically, therefore converging apically. Restricted to areas around the Pyrenees and the Cantabrian Mountains. Associated with *Salix* (Salicaceae) .... ***mitis* Schmiedeknecht**

203 Face entirely black haired, without any pale hairs. Terga basally (T1–2) with orange-brown hairs, apically (T3–4) with extensive and strongly contrasting black hairs. Associated with *Vaccinium* (Ericaceae) .... ***lapponica* Zetterstedt**

– Face with at least some pale hairs, particularly around the antennal insertions. Terga without extensive areas with black hairs, generally with mixture of predominantly yellowish to brownish hairs on T1–4. Species associated with *Salix* (Salicaceae)...**204**

204 Smaller, 10–11 mm. Clypeus predominantly shagreened and dull, with only the narrow longitudinal impunctate midline weakly shiny. Terminal fringe dark brown ....***praecox* (Scopoli)**

– Larger, 11–14 mm. Clypeus comparatively shinier, only laterally shagreened and dull, apico-medially broadly shiny around the comparatively broader longitudinal impunctate midline. Terminal fringe black............. ....***apicata* Smith**

205 (173) Large species (over 12 mm in length). With abundant black, brown, and/or white pubescence. Clypeus strongly domed. Ocelloccipital distance long, at least 2 times the diameter of a lateral ocellus (subgenus *Melandrena partim*) **206**

– Without this combination of characters; remaining species...................**212**

206 Tergal discs T1–3(4) with upstanding mixture of short pale whitish to light brown hairs extending over both disc and marginal areas. Tibial scopae orange-red, or bicoloured and dorsally dark, ventrally orange (dark form, active February-April). Terga sometimes with greasy-bronzy metallic reflections .... ***nigroaenea* (Kirby)**

– Tergal discs never with this sort of pubescence, sometimes with white to brownish pubescence in basolateral corners of tergal discs, never extending onto marginal areas. Tibial scopae entirely black or a combination of black and white, never orange-red. Terga dark, without metallic reflections.......................... **207**

207 Mesosoma with black and white hairs, never with brown hairs **208**

– Mesosoma with black, brown, and/or pale hairs, never with only black and white hairs **209**

208 T2–4 laterally with thick apical patches of white hairs, these strongly contrasting the black integument .... ***albopunctata* (Rossi)**

– T2–4 laterally without white hair patches, entirely dark......... ***morio* Brullé**

209 Tibial scopae bicoloured, black dorsally and white ventrally. Mesosoma dorsally with bright orange-brown pubescence, laterally with pale pubescence, never with black hairs on the mesepisternum. Univoltine, flying April-June. Restricted to temperate parts of northern Spain .... ***nitida* (Müller)**

– Tibial scopae entirely black. Mesosoma dorsally usually with the pubescence darker, laterally with pubescence never pale, usually with abundant black hairs, at most with pubescence of the mesepisternum brown **210**

210 Disc of T1 shagreened and barely punctate, punctures scattered and obscure against the underlying sculpture........................... ***assimilis* Radoszkowski**

– Disc of T1 polished and shiny, strongly punctate, punctures clearly visible against the underlying sculpture... **211**

211 Disc of T1 with punctures comparatively sparse, separated by 2 puncture diameters .... ***thoracica* (Kirby)**

– Disc of T1 with punctures dense, punctures separated by up to 1 puncture diameter, often separated by less .... ***limata* Smith**

212 (205) Propodeal corbicula complete, with both anterior and dorsal fringe, fringes composed of long, dense, and extremely plumose yellowish-brown hairs, these plumose hairs present also on the mesepisternum, the flocculus, and the femoral scopae (Fig. 73C), but hairs of the tibial scopae simple (see also illustrations in Wood et al. 2022). Known only from south-western Spain (Cádiz, Sevilla), flying in the very early spring (January–March) .... ***ramosa* Wood**

– Propodeal corbicula simple, composed of simple or weakly plumose hairs, but if plumose then these not extending onto the mesepisternum, flocculus, and femoral scopae **213**

213 Process of the labrum large, as long as broad, apically rounded, ventral surface covered with latitudinal wrinkles (Fig. 73D). Fovea narrow, occupying slightly less than half the space between the compound eye and the lateral

ocellus. Associated with *Muscari* (Asparagaceae).. ....***mucida* Kriechbaumer** (*partim*, 1st generation)

– Process of the labrum different, either wider than long, trapezoidal, or apically pointed, ventral surface never covered with latitudinal wrinkles. Foveae narrow or broad **214**

214 Head short and broad, at least 1.3 times wider than long. Fovea short and broad, only slightly longer than wide. Small bees, 8–10 mm, with long white pubescence in fresh specimens. Associated with *Erodium* (Geraniaceae) **215**

– Without this combination of characters, usually larger. Never associated with *Erodium* **217**

215 Propodeum and mesepisternum entirely microreticulate, without strong or weak raised network of reticulation (Fig. 73F). Mesepisternum laterally with extensive intermixed black and white hairs. Terga with sparse and short pubescence, T2–4 with only weak apical hair bands that do not obscure the underlying surface. Known from across southern Spain (Albacete, Cádiz, Granada, Málaga) .... ***melacana* Warncke**

– Propodeum and mesepisternum shiny or with granular microreticulation, overlain by strong or weak network of raised rugosity (Figs 47E, 73E). Mesepisternum predominantly pale-haired, at most with 30% of hairs black. Terga with long erect white hairs, forming dense apical hair bands on T2–4 which obscure the underlying surface (Fig. 47F). Known from either south-eastern (Albaceae) or south-western (Cádiz) Spain **216**

216 Propodeum (including propodeal triangle) and mesepisternum with strongly produced but fine interlinked network of raised rugosity (Fig. 73E). Facial foveae occupying ¾ of space between the compound eye and a lateral ocellus. Apical fringe of T5 and hairs flanking pygidial plate golden-brown. Known from south-eastern Spain (Albacete) .... ***erodiorum* Wood & Ortiz-Sánchez**

– Propodeum with fine granular shagreen, with weak network of raised rugosity, propodeal triangle slightly depressed, basal 2/3rds with raised longitudinal rugae (Fig. 47E). Facial foveae occupying ½ space between the compound eye and a lateral ocellus (Fig. 47C). Apical fringe of T5 and hairs flanking pygidial plate dark brown (Fig. 47F). Known from south-western Spain (Cádiz) ....***juliae* sp. nov.**

217 Terga shagreened and dull, impunctate or with obscure and scattered punctures (Figs 30D, 39D, 51C) **218**

– Terga polished and shiny, at most finely shagreened, clearly and densely punctate...**227**

218 Propodeal triangle with internal surface covered with fine network of raised reticulation **219**

– Propodeal triangle with internal surface smooth, entirely granularly shagreened, without raised reticulation (Fig. 73G, H)...............................**220**

219 Mid and hind basitarsi dark. Tergal discs in profile view with sparse and short dark hairs, apically with white hair bands. Throughout Iberia .... ***hypopolia* Schmiedeknecht**

– Mid and hind basitarsi orange (Fig. 39B). Tergal discs in profile view laterally with orange hair, apically with long yellowish hair bands (Fig. 39D). Restricted to high altitude sites (>1200 m) in the Pyrenees .... ***ranunculorum* Morawitz**

220 Propodeum with comparatively few hairs, these largely restricted laterally to the dorsal fringe of the propodeal corbicula, propodeum dorsally with sparse pubescence (Fig. 73G). Process of the labrum narrow, only slightly broader than long, more or less triangular with a rounded apex. Dorsolateral surfaces of the propodeum obscurely and shallowly punctate. T2–4 with narrow white apical hair bands. Terminal fringe bright orange. Restricted to central Spain .... ***funerea* Warncke**

– Propodeum covered with long abundant pubescence, no meaningful difference between hairs of the dorsal fringe of the propodeal corbicula and those on the dorsal surface of the propodeum (Fig. 73H). Process of the labrum usually trapezoidal, broader than long, with or without an emarginate front margin. If unclear, then dorsolateral surfaces of the propodeum clearly and coarsely punctate. T2–4 with or without hair bands. Terminal fringe darker, from light brown to dark brown or almost black (subgenus *Truncandrena*) **221**

221 T2–4 with clear apical hair bands **222**

– Terga without apical hair bands, hairs may be present on the tergal discs **224**

222 Fovea relatively narrow, occupying ½ the space between the compound eye and the lateral ocellus. Process of the labrum triangular, slightly truncate. Smaller, not exceeding 10 mm in length. Associated with Brassicaceae........ .... ***medeninensis donata* Warncke**

– Fovea broad, occupying ¾ of space between the compound eye and the lateral ocellus. Process of the labrum trapezoidal with a strong emargination medially. Larger, exceeding 12 mm in length. Associated with *Cistus* (Cistaceae) **223**

223 Scopa bicoloured, black dorsally and orange ventrally (Fig. 51D). Face longer, clypeus ventrally projecting well below a line drawn between the lower margins of the compound eyes (Fig. 51B). Larger, 15–16 mm. Known only from southern Spain (Málaga) .... ***ghisbaini* sp. nov.**

– Scopa unicolourous orange (Fig. 30B). Smaller, 12–13 mm. Face shorter, clypeus only slightly projecting below a line drawn between the lower margins of the compound eyes (Fig. 30C). Throughout Iberia .... ***villipes* Pérez**

224 Mid and hind basitarsi entirely lightened orange.................................. **225**

– Mid and hind basitarsi dark, at most obscurely dark reddish................. **226**

225 Mesepisternum laterally with abundant dark hairs. Base of discs of T2–4 strongly depressed (depressed relative to the apical margin of the preceding tergum, often with a physical space between them), this depression therefore laterally exaggerating the gradulus along its inner margin. Tergal margins (and sometimes sides of terga when viewed laterally) sometimes lightened reddish, contrasting the dark discs. Rare, known only from southern Spain (Alicante, Cádiz) .... ***minapalumboi* Gribodo**

– Mesepisternum laterally with entirely pale hairs. Base of T2–4 not noticeably depressed, therefore gradulus not particularly noticeable. Tergal margins always dark. Common throughout Iberia ....***ferrugineicrus* Dours**

226 Discs of T2–4 with abundant and extensive pale pubescence, in fresh specimens this pubescence forming distinct patches laterally. Marginal areas broad, on T3–4 occupying $^{2}/_{5}$ of the length of the segment. Clypeus shagreened and dull, with a narrow impunctate longitudinal mid line, only slightly shiny at extreme apex. Throughout Iberia.................................. ***nigropilosa* Warncke**

– Discs of T2–4 with at most scattered and fine hairs, never forming patches. Marginal areas narrow, on T3–4 occupying at most 1/5th of the length of the segment. Clypeus less extensively shagreened and dull, becoming smooth and shiny in its apical half, with broader impunctate longitudinal mid line. Rare, known only from southern Spain (Córdoba) .... ***varia* Pérez**

227 Terga without apical hair bands, or with obscure hair bands that are widely interrupted medially even in fresh specimens (Fig. 74A, B). Tibial scopae bicoloured, dark dorsally and white ventrally. Terminal fringe dark brown to black, with some white hairs laterally..**228**

– Terga with clear apical hair bands, these complete at least on T3–4 (Fig. 74C, E, F). Tibial scopae unicolourous white or golden-orange. Terminal fringe light, reddish-brown to golden..**229**

228 Terga with widely interrupted apical hair bands, often abraded and absent. Terga coarsely and densely punctate, tergal margins strongly depressed, with punctures at most half the size of those on the tergal discs (Fig. 74A). Rare, restricted to southern Iberia .... ***macroptera* Warncke**

– Terga without apical hair bands. Terga extremely finely punctate, no major difference in the size of the punctures on the weakly depressed marginal areas compared to the discs (Fig. 74B). More widespread across southern, central, and eastern Iberia .... ***corax* Warncke**

229 Scutum sparsely punctate, punctures separated by 1–2 puncture diameters, laterally shagreened and dull, shagreenation weakening medially and on the scutellum, here shiny. Process of the labrum short and triangular (Fig. 74D)... ***urdula* Warncke**

– Scutum and scutellum densely punctate, punctures separated by up to 1 puncture diameter, underlying surface uniformly finely shagreened and weakly shiny. Process of the labrum trapezoidal, margin truncate to weakly emarginate... **230**

230 Tergal discs extensively covered with extremely short hairs, forming a velvety pubescence in addition to denser and longer hairs on tergal margins, almost obscuring the underlying surface in fresh specimens (Fig. 74E). Mesosoma dorsally with whitish-brown pubescence. Tibial scopae white. Terminal fringe whitish-orange overlain by white hairs. Associated with small-flowered Fabaceae (*Lotus*) ....***farinosa* Pérez**

– Tergal discs with scattered short orange hairs, not forming a velvety pubescence (Fig. 74F). Mesosoma dorsally with rich orange-brown pubescence. Tibial scopae and terminal fringe uniformly orange. Associated with *Reseda* (Resedaceae) ....***murana* Warncke**

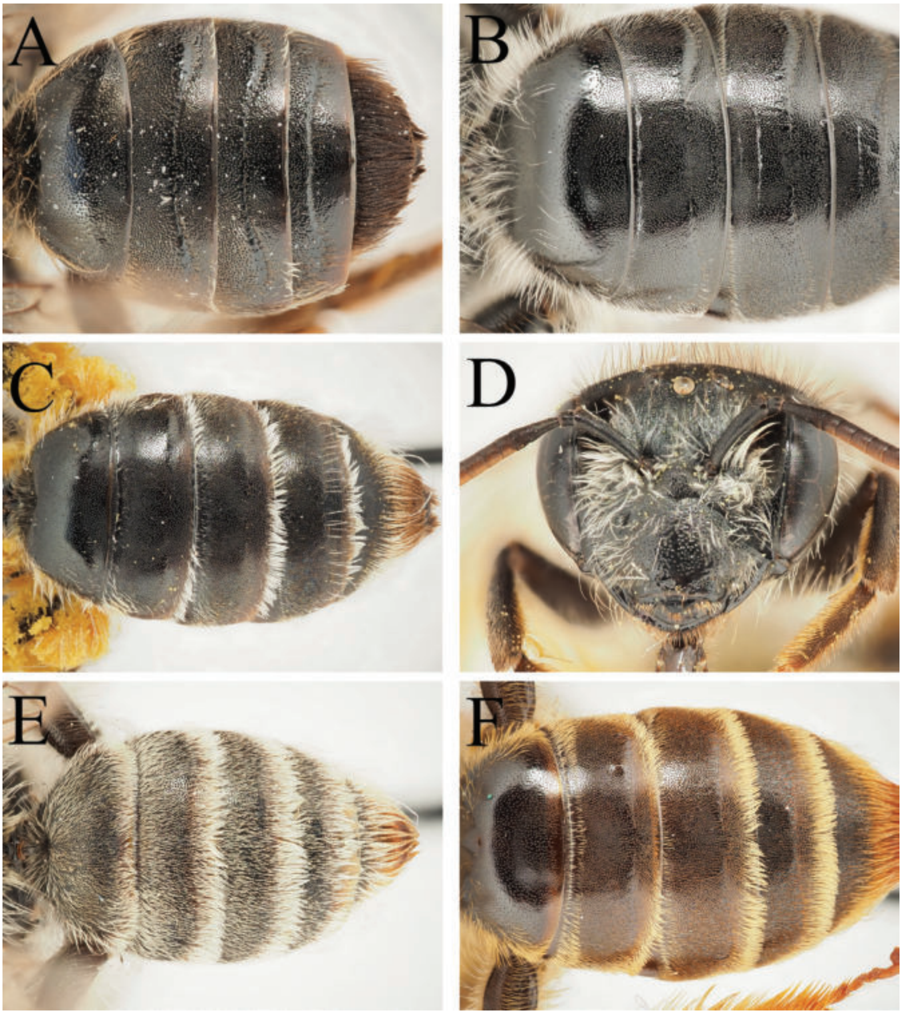

Figure 74. *Andrena* (incertae sedis) *macroptera* Warncke, 1974, female **A** terga, dorsal view; *Andrena* (incertae sedis) *corax* Warncke, 1975, female **B** terga, dorsal view; *Andrena* (incertae sedis) *urdula* Warncke, 1965, female **C** terga, dorsal view **D** face, frontal view; *Andrena* (*Ovandrena*) *farinosa* Pérez, 1895, female **E** terga, dorsal view; *Andrena* (incertae sedis) *murana* Warncke, 1975, female **F** terga, dorsal view.

For the male key, the following shortcuts can be used:

A. Clypeus at least partly yellow-marked .... **go to 2**
B. Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate .... **go to 52**
C. Genital capsule distinctive, with clear 90° emargination in the outer parts of the gonostyli. The most common *Andrena* species in Iberia .... **go to *Andrena flavipes* Panzer**
D. Process of the labrum thickened and expanded, anteriorly projecting beyond the fore margin of the clypeus. Pronotum with strong humeral angle. Active in the summer (mid-June to September) (subgenus *Cnemidandrena* and remaining *Margandrena*) .... **go to 68**
E. Fore margin of clypeus upturned AND gena conspicuously broadened, wider than the width of the compound eye AND pronotum with a conspicuous humeral angle (remaining *Notandrena*) .... **go to 72**
F. Small species, body length of 5–7 mm (exceptionally 8 mm), terga always dark (remaining *Aciandrena*, *Aenandrena partim*, *Avandrena*, *Cordandrena*, *Cryptandrena partim*, *Graecandrena*, and almost all *Micrandrena*) .... **go to 77**
G. Mesepisternum and/or dorsolateral parts of the propodeum conspicuously punctate AND ocelloccipital distance at least 3 times the diameter of a lateral ocellus (*incisa*-group, *Pruinosandrena*) .... **go to 122**
H. Clypeus flattened over majority of its surface (subgenus *Taeniandrena*) .... **go to 127**
I. At least some tergal discs red-marked .... **go to 140**
J. Tergal discs with metallic blue reflections .... **go to 145**
K. Mandibles elongate, sickle-like, strongly crossing apically. Pronotum with strong humeral angle. Gena often expanded, broader than the width of a compound eye .... **go to 148**
L. Measured along ventral margin, A3 twice as long as A4.................... **go to 168**
M. Measured along ventral margin, A3 shorter than or as long as A4 .... **go to 194**
N. Remaining species; measured along ventral margin, A3 slightly longer than A4 .... **go to 215**

Males

1 Clypeus at least partly yellow-marked (Figs 44D, 75A–F); marking may be reduced to small marking medially or apically... **2**
– Clypeus entirely dark, never with yellow markings................................ **51**
2 Clypeus and lower paraocular areas with yellow markings; paraocular markings may be reduced to small spots (Fig. 75A–C).................................... **3**
– Yellow facial markings restricted to the clypeus, paraocular areas entirely dark (Figs 44D, 75D–F) **15**
3 Propodeum almost entirely declivous, without clearly differentiated horizontal and vertical parts. Propodeum with dorsolateral parts adjacent to

the propodeal triangle densely and deeply punctate, punctures separated by <0.5 puncture diameters (c.f. Fig. 65C) **4**

– Propodeum with clearly differentiated horizontal and vertical parts. Propodeum with or without punctures, but never with punctures separated by <0.5 puncture diameters **6**

4 Ocelloccipital distance 2.5–3 times the diameter of a lateral ocellus. Tergal discs occasionally red-marked .... ***variabilis* Smith**

– Ocelloccipital distance <2 times the diameter of a lateral ocellus. Tergal discs always dark **5**

5 S5 apically with extremely dense and pronounced latitudinal tuft of yellowish hairs. Terga with apical hair bands broadly interrupted. Typically flying earlier, May-June... ***labialis* (Kirby)**

– S5 apically without dense latitudinal hair tuft, at most with scattered hairs. Terga typically with clear and uninterrupted apical hair bands, though beware abraded specimens. Typically flying later, July-August......... ***decipiens* Schenck**

6 Discs of T2–3 entirely and conspicuously red-marked **7**

– Discs of T2–3 dark, at most with the apical margins lightened **8**

7 Large species, 11–13 mm. Mandibles long, sickle-like, crossing in their apical third (Fig. 74A). Head short, clearly broader than long. Genital capsule with gonostyli broad, weakly converging apically (Fig. 75G).......***schencki* Morawitz**

– Smaller species, never exceeding 9 mm. Mandibles normal, not strongly crossing apically. Head more or less round. Genital capsule with gonostyli apically narrow, strongly converging subapically (Fig. 75H)....................... .... ***labiata* Fabricius**

8 Paraocular areas with markings narrow, running up the inner margin of the compound eye, clearly dorsally exceeding the antennal insertions (Fig. 75C). S8 with a ventrally projecting spine at each lateral margin ....***orbitalis* Morawitz**

– Paraocular areas with markings more or less rectangular or quadrangular, never narrow and running up the inner margin of the compound eye (Fig. 75B); typically not exceeding the antennal insertions dorsally........... **9**

9 Fore margin of the clypeus clearly and strongly upturned. Pronotum with strong carinate humeral angle. Head broad, clearly broader than long........ **10**

– Fore margin of the clypeus normal, not upturned. Pronotum without a strong humeral angle. Head variable, but not strongly broadened........... **13**

10 Scutum strongly and densely punctate, punctures separated by 0.5–1 puncture diameter, underlying surface shagreened. A5 long, clearly exceeding the length of A4; A4 at most 0.6 times as long as A5. Larger, 9–10 mm .... ***griseobalteata* Dours**

– Scutum either strongly shagreened and obscurely punctate, or with shiny interspaces, never strongly punctured and shagreened. A5 short, not noticeably longer than A4, both segments quadrate or subquadrate. Smaller, 8–9 mm.. **11**

11 Gena posteriorly rounded, without carina. All tarsi and the apex of the hind tibia lightened orange. Scutum strongly shagreened and obscurely punctate. Flying April-June .... ***chrysosceles* (Kirby)**

– Gena posteriorly with clear carina. Scutum with surface shiny between punctures..**12**

12 Hind tarsi dark. Genital capsule with penis valves comparatively narrow. Associated with saline soils in southern Iberia. Flying March-June ....***juliana* Wood** (*partim*, with yellow markings on lower paraocular areas)

– Hind tarsi lightened orange. Genital capsule with penis valves broad, occupying the majority of the space between the gonostyli. Restricted to the Pyrenees. Flying July-August..***pallitarsis* Pérez**

13 Terga clearly and finely shagreened, dull to weakly shiny, with small and weak punctures. Facial markings yellow. Ocelloccipital distance short, equalling the diameter of a lateral ocellus. Restricted to central Spain.........***funerea* Warncke**

– Terga smooth and shiny between strongly pronounced punctures. Facial markings white. Ocelloccipital distance larger, at least 2 times the diameter of a lateral ocellus **14**

14 Larger, exceeding 10 mm in length. Mandibles basally with white markings. Body with abundant white pubescence, with dense hairs on the clypeus and ventrally on the gena that can obscure the underlying surface in fresh individuals. Widespread across all of Iberia. Flying April–July.............***leucolippa* Pérez**

– Small species, 7–8 mm. Mandibles dark, without basal white markings (Fig. 75B). Body with reduced pubescence, never with dense hairs that obscure the underlying surface. Rare, restricted to cool temperate habitats in and around the Pyrenees and Cantabrian Mountains. Flying July–August .. ..***coitana* (Kirby)**

15 Discs of T2–3 clearly and extensively red-marked **16**

– Tergal discs dark, at most with the apical margins lightened **18**

16 Clypeus with yellow marking small, occupying only a small proportion of the clypeus medially, without internal black markings (Fig. 75F). Flying early in the year, March-May; widespread throughout Iberia. Associated with *Asphodelus* (Asphodelaceae)...................................***sardoa* Lepeletier**

– Clypeus almost entirely pale, with two small black markings. Flying later in the year, from late May to August; restricted to temperate habitats across Spain, including mountains in eastern and south-eastern Spain Associated with scabious (former Dipsacaceae = Caprifoliaceae) **17**

17 Pronotum with strong humeral angle. Fore margin of the clypeus laterally produced into two small but distinctly projecting points (Fig. 76A). Smaller, 7–9 mm. Restricted to areas in and around the Pyrenees.........***marginata* Fabricius**

– Pronotum rounded. Fore margin of the clypeus normal, without lateral projections. Larger, 14–16 mm. Restricted to montane grasslands in northern and central Spain with isolated populations in the Sierra de Cazorla and Sierra Nevada........................ ***hattorfiana* (Fabricius)** (*partim*, light form)

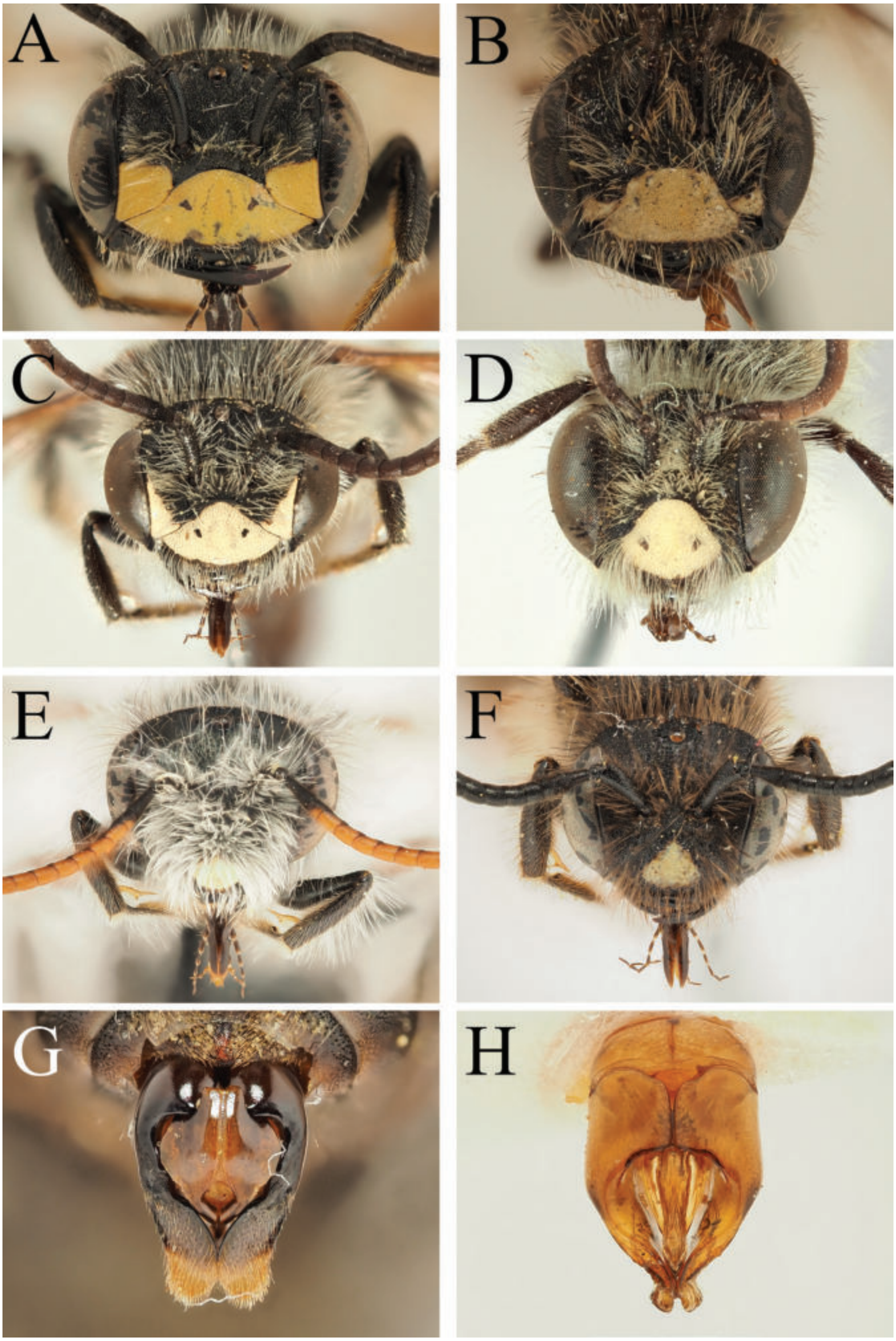

Figure 75. *Andrena* (*Opandrena*) *schencki* Morawitz, 1866, male **A** face, frontal view **G** genital capsule, dorsal view; *Andrena* (*Oreomelissa*) *coitana* (Kirby, 1802), male **B** face, frontal view; *Andrena* (*Rufandrena*) *orbitalis* Morawitz, 1871, male **C** face, frontal view; *Andrena* (*Orandrena*) *monilia* Warncke, 1975, male **D** face, frontal view; *Andrena* (*Truncandrena*) *doursana* Dufour, 1853, male **E** face, frontal view; *Andrena* (*Lepidandrena*) *sardoa* Lepeletier, 1841, male **F** face, frontal view; *Andrena* (*Poecilandrena*) *labiata* Fabricius, 1781, male **H** genital capsule, dorsal view.

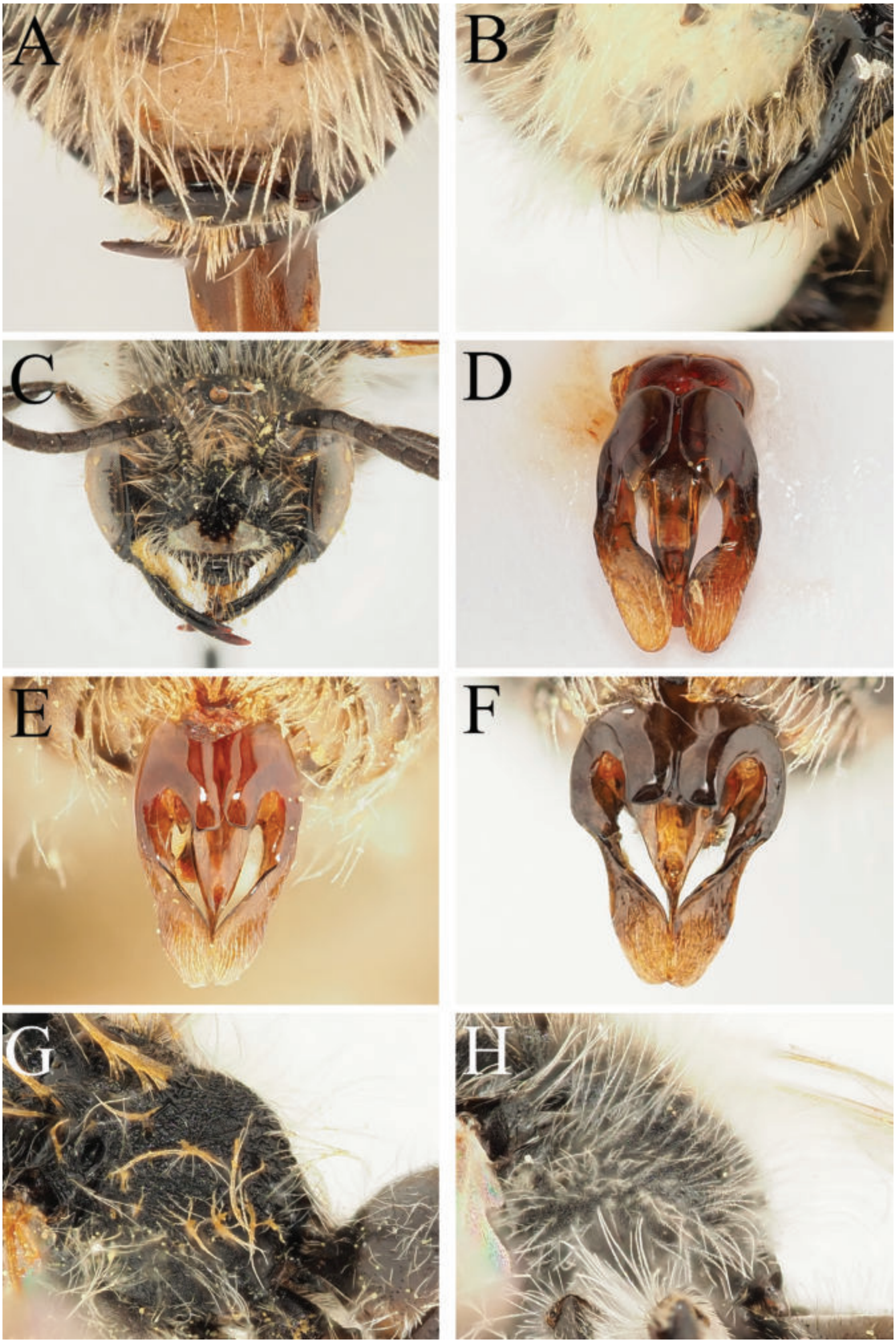

Figure 76. *Andrena* (*Margandrena*) *marginata* Fabricius, 1776, male **A** apex of clypeus, frontal view; *Andrena* (*Holandrena*) *flavilabris* Schenck, 1874, male **B** apex of clypeus, frontolateral view; *Andrena* (*Leucandrena*) *dinizi* Warncke, 1975, male **C** face, frontal view **F** genital capsule, dorsal view **G** propodeum, profile view; *Andrena* (*Leucandrena*) *tunetana* Schmiedeknecht, 1900, male **D** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *sericata* Imhoff, 1868, male **E** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *ventralis* Imhoff, 1832, male **H** propodeum, profile view.

18 Head, mesosoma, and/or metasoma with metallic green or blue reflections **19**

– Body lacking metallic reflections..**24**

19 Yellow marking of clypeus very small, reduced to a narrow latitudinal strip at the fore margin of the clypeus (Fig. 75E) .... ***doursana* Dufour**

– Yellow or white marking of the clypeus always larger, covering the majority or the entirety of the clypeus (with exception of pair of small black dots) **20**

20 Discs of T2–4 clearly and densely punctate with strong punctures, punctures separated by ≤1 puncture diameter...**21**

– Tergal discs with weaker and more scattered punctures, punctures either fine or separated by >1 puncture diameter **22**

21 Pronotum rounded. Tergal margins not strongly depressed, more or less at the same level as the tergal discs. Gena normal, as wide as the width of the compound eye. Restricted to high elevation sites in the Pyrenees .... ***viridescens* Viereck**

– Pronotum laterally carinate. Tergal margins strongly depressed, clearly lower than the level of the tergal discs. Gena broadened, clearly broader than the width of the compound eye. Found in central and southern Iberia... ***bellidis* Pérez**

22 Larger, 8–10 mm. Scutum laterally shagreened, medially with a large more or less circular smooth and shiny area, this almost impunctate................... ....***aerinifrons* Dours**

– Smaller, 6–7 mm. Scutum uniformly shagreened and punctate, without a smooth and shiny area **23**

23 Inner hind tibial spurs strongly bent at their apexes. Body with subdued metallic reflections, almost without reflections................ ***varuga* Warncke**

– Inner hind tibial spurs straight, parallel-sided. Body with clear metallic reflections ....***nigroviridula* Dours**

24 Fore margin of the clypeus upturned (Fig. 76B). Pronotum with a strong humeral angle **25**

– Fore margin of the clypeus normal, not upturned. Pronotum with or without a humeral angle **28**

25 Propodeum almost entirely declivous, without clearly differentiated horizontal and vertical parts. Propodeum with dorsolateral parts adjacent to the propodeal triangle densely and deeply punctate, punctures separated by <0.5 puncture diameters ....***flavilabris* Schenck**

– Propodeum with clearly differentiated horizontal and vertical parts. Propodeum at most obscurely punctate...**26**

26 Larger, 10 mm. Scutum and scutellum shagreened, without shiny areas .... ***langadensis albipila* Warncke**

– Smaller, 6–7 mm. Scutum and scutellum at least medially with smooth and shiny areas **27**

27 Gena posteriorly carinate. Surface of gena predominantly smooth and shiny. Associated with saline soils in southern Iberia ....***juliana*** **Wood** (*partim*, with yellow markings restricted to the clypeus)

– Gena posteriorly rounded, without carina. Surface of gena microreticulate and dull. Very rate, recorded only from the Cádiz region, habitat preference unknown ....***microthorax*** **Pérez**

28 Mandibles elongate, sickle-like, strongly crossing in their apical third (Fig. 76C) AND pronotum with strong humeral angle AND gena broadened, clearly broader than the width of the compound eye, usually produced into a 90° angulation posteroventrally (yellow-faced *Leucandrena*) **29**

– Without this combination of characters; mandibles either shorter, pronotum laterally rounded, or gena not exceeding width of head **32**

29 Ocelloccipital distance short, <0.5 times the diameter of a lateral ocellus. Genital capsule with gonocoxal teeth apically strongly diverging, apexes pointed (Fig. 76D). Found in hot or Mediterranean areas in central and southern Iberia with Brassicaceae.................... ***tunetana*** **Schmiedeknecht**

– Ocelloccipital distance long, 1–2 times the diameter of a lateral ocellus. Genital capsule with gonocoxal teeth not strongly diverging, apexes truncate (Fig. 76E, F). Found in temperate areas in central and northern Iberia with *Salix* (Salicaceae)...**30**

30 Typically larger, 9–10 mm. Genital capsule more elongate, gonocoxal teeth with apexes comparatively narrow, gonostyli not noticeably constricted medially (Fig. 76E). Very rare, restricted to the Pyrenees ....***sericata*** **Imhoff**

– Typically smaller, 7–9 mm. Genital capsule more compact, gonocoxal teeth with apexes comparatively broad, gonostyli strongly constricted medially (Fig. 76F). More widespread across central and northern Iberia.............**31**

31 Lateral faces of the propodeum with a fine network of raised rugosity on top of the underlying granular microreticulation (Fig. 76G). Scutum with strong and obvious punctures, medially becoming smooth and shiny... ***dinizi*** **Warncke**

– Lateral faces of the propodeum with regular granular microreticulation (Fig. 76H). Scutum obscurely punctate, uniformly microreticulate and dull..***ventralis*** **Imhoff**

32 Small species, length not exceeding 8 mm...**33**

– Larger species, at least 9 mm in length...**38**

33 Propodeal triangle with smooth granular microreticulation, without raised rugosity. Very small species, usually not exceeding 6 mm (yellow-faced *Aciandrena*)...**34**

– Propodeal triangle with at least some raised rugosity, never with uniformly smooth microreticulation. Usually a little larger, 6–8 mm.......................**35**

34 Terga regularly and clearly punctate, punctures extending onto depressed tergal margins. Throughout Iberia..***fulica* Warncke** (*partim*, light form with yellow clypeus)

– Terga obscurely punctate, punctures disappearing into underlying microreticulation, tergal margins more or less impunctate. Restricted to central and eastern Spain...***vacella* Warncke**

35 Hind basitarsi entirely lightened orange. Frons with contrasting black and white pubescence, black on the frons and gena posteriorly, intermixing with white around the antennal insertions, becoming white on the clypeus and on the gena ventrally. Restricted to *Potentilla*-rich (Rosaceae) cool habitats in the Pyrenees. Flying July-August................................ ***tarsata* Nylander**

– Hind basitarsi dark. Face with uniformly bright white or yellowish pubescence. Not restricted to the Pyrenees, usually flying earlier in the year **36**

36 Tergal discs covered with upstanding whitish pubescence, this forming dense apical hair bands on tergal margins in fresh individuals. Scutum anteriorly shagreened, becoming smooth and shiny posteriorly. Antennae ventrally strongly and extensively lightened orange. Restricted to south-western Spain (Huelva, Sevilla), flying March-April...***laurivora* Warncke**

– Tergal discs never with upstanding pubescence; white apical hair bands can be present on tergal margins. Scutum with uniform sculpture, consistently shiny across its surface. Antennae typically dark ventrally **37**

37 Disc of T1 with scattered punctures, punctures separated by 1–3 puncture diameters, strongly contrasting punctation of the discs of T2–4, here punctures separated by 0.5 puncture diameters. Clypeus yellow-marked across its entire surface with the exception of two small black marks. Genital capsule compact, with pronounced gonocoxal teeth and small and spatulate gonostyli (Fig. 77A). Restricted to central Spain .... ***taxana* Warncke**

– All tergal discs uniformly punctate, punctures separated by 0.5 puncture diameters. Clypeal marking often reduced in size, not covering entire surface. Genital capsule elongate, with weakly pronounced gonocoxal teeth, gonostyli apically produced into triangular wedges (Fig. 77B)... ***ventricosa* Dours** (*partim*, light form)

38 Mid and hind basitarsi entirely lightened orange (Fig. 44B)....................**39**

– Mid and hind basitarsi dark...**41**

39 Ocelloccipital distance 3 times the diameter of a lateral ocellus. Terga very finely shagreened, more or less smooth and shiny. Tergal discs regularly and deeply punctate, punctures separated by 1–2 puncture diameters, punctures becoming smaller and continuing onto tergal margins. Genital capsule, see Fig. 44H...***limbata dusmeti* Warncke**

– Ocelloccipital distance <2 times the diameter of a lateral ocellus. Terga strongly shagreened, at most weakly shiny, tergal discs with small and obscure punctures that disappear into the underlying structure, tergal margins more or less impunctate..**40**

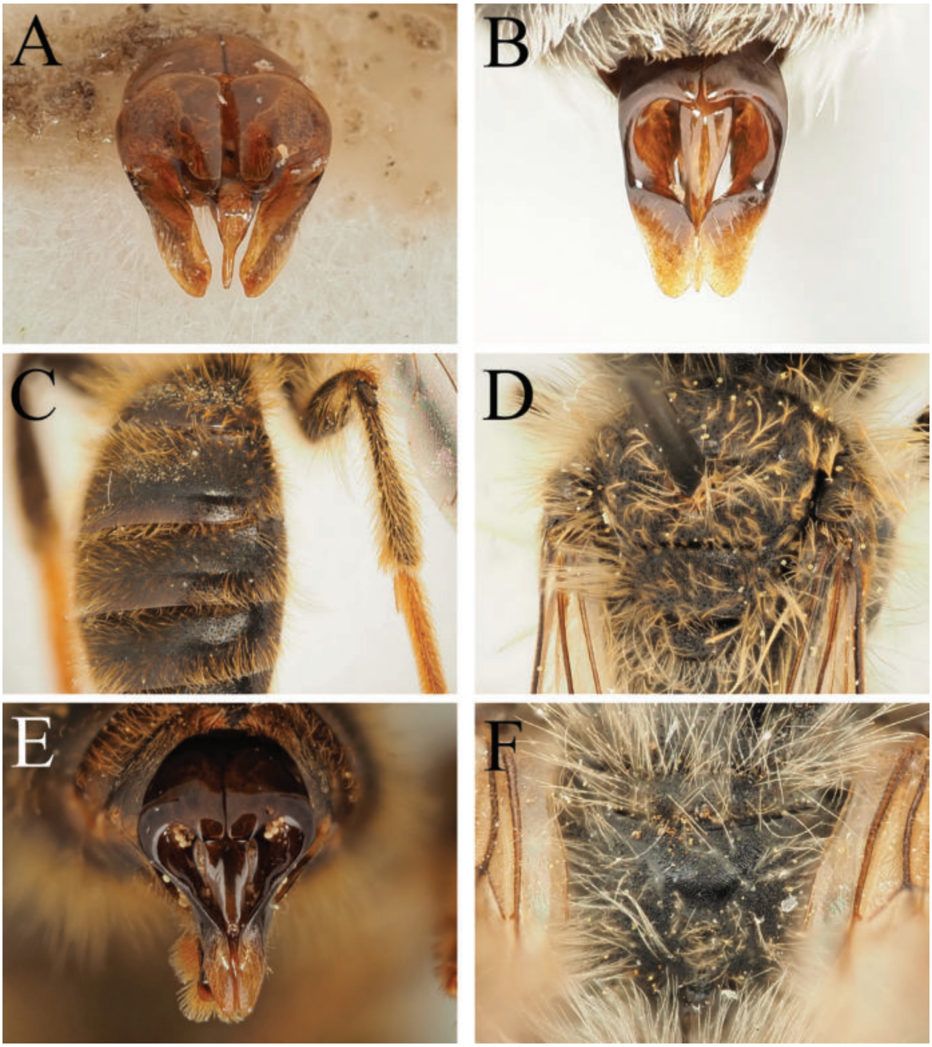

Figure 77. *Andrena* (*Parandrenella*) *taxana* Warncke, 1975, male **A** genital capsule, dorsal view; *Andrena* (*Cryptandrena*) *ventricosa* Dours, 1873, male **B** genital capsule, dorsal view; *Andrena* (*Truncandrena*) *minapalumboi* Gribodo, 1894, male **C** terga, dorsolateral view; *Andrena* (*Chlorandrena*) *rhyssonota* Pérez, 1895, male **D** scutum and scutellum, dorsal view; *Andrena* (*Charitandrena*) *hattorfiana* (Fabricius, 1775), male **E** genital capsule, dorsal view; *Andrena* (*Orandrena*) *monilia* Warncke, 1975, male **F** propodeum, dorsal view.

40 T2–5 laterally with extremely strong gradulus emerging from under the preceding terga, tergal margins of T1–4 elevated, not in contact with basal parts of T2–5 (Fig. 77C). Entire body with bright orange pubescence. Rare, known only from southern Spain (Alicante, Cádiz) .... ***minapalumboi* Gribodo**

– T2–5 laterally with very weak gradulus, margins of T1–4 not elevated, in contact with basal parts of T2–5. Body with paler pubescence, white hairs on face, gena ventrally, and mesepisternum, with light brown hairs dorsally. Common throughout Iberia .... ***ferrugineicrus* Dours**

41 Scutum and scutellum with dense network of raised longitudinal striations, most obvious on the scutellum (Fig. 77D). Tergal margins and tergal bases strongly depressed, giving individual tergal segments a domed appearance when viewed in profile .... ***rhyssonota* Pérez**

– Scutum and scutellum without longitudinal striations. Tergal margins depressed or not, but not in combination with tergal bases depressed.........**42**

42 Large species, 14–16 mm. Genital capsule distinctive, elongate with projecting and apically truncate gonocoxal teeth (Fig. 77E). Pubescence variable, from light brown to almost entirely black (ssp. *nigricauda* Wood). Restricted to montane grasslands in northern and central Spain with isolated populations in the Sierra de Cazorla and Sierra Nevada ....
....***hattorfiana* (Fabricius)** (*partim*, dark form)

– Smaller, sometimes reaching 14 mm, but usually 9–12 mm. Genital capsule different; if elongate, then gonocoxal teeth pointed, not truncate. Pubescence predominantly bright, never almost entirely black.........................**43**

43 Face with strongly contrasting black and white pubescence; clypeus medially with white hairs, inner margins of the compound eyes and area around antennal insertions and frons with abundant black hairs.........................**44**

– Face with bright pubescence, at most with occasional scattered dark hairs, never strongly contrasting light pubescence **46**

44 A3 short, only slightly longer than A4. A4 rectangular, only slightly longer than broad, clearly shorter than A5. Antennal segments slightly bulging ventrally. Rare, known only from southern Spain (Córdoba)............ ***varia* Pérez**

– A3 long, clearly longer than A4. A4 rectangular, clearly longer than broad, slightly shorter than A5. Antennal segments parallel-sided, without ventral bulges **45**

45 Genital capsule with apical flattened part elongate, longer than broad, appearing triangular (Fig. 51D, E). Inner margin of these flattened areas strongly and acutely raised, slightly reflexed. Larger, 13–14 mm. Known only from southern Spain (Málaga)................................***ghisbaini* sp. nov.**

– Genital capsule with apical flattened part rounded, as long as broad (Fig. 51F). Inner margin of these flattened areas less strongly raised and not reflexed. Smaller, 10–11 mm. Throughout Iberia.................. ***villipes* Pérez**

46 Propodeal triangle broad, internal surface with very fine granular reticulation, laterally and posteriorly weakly shiny, contrasting the dorsolateral parts of the propodeum (Fig. 77F). Face in frontal view with compound eyes large, almost bulbous, separated by a distance only not greatly exceeding the diameter of an individual compound eye (Fig. 75D). Genital capsule elongate (Fig. 78A). Restricted to hot steppe in central Spain..***monilia* Warncke**

– Propodeal triangle with clearer structure of raised reticulation or rugosity, without weakly shiny margins. Face in frontal view with compound eyes normal, separated by a distance much greater than the diameter of an individual compound eye (Fig. 78B). Genital capsule otherwise **47**

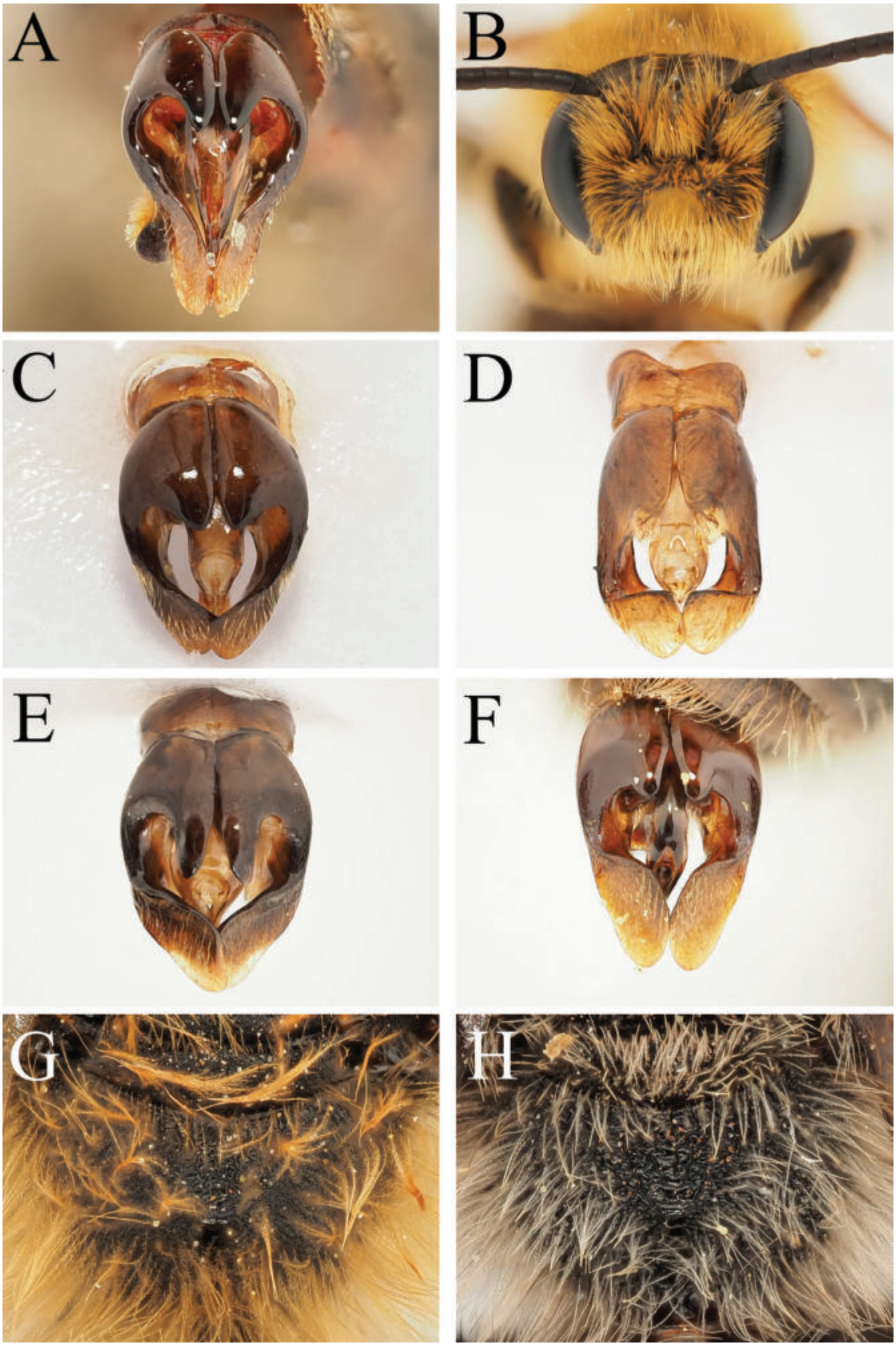

Figure 78. *Andrena* (*Orandrena*) *monilia* Warncke, 1975, male **A** genital capsule, dorsal view; *Andrena* (incertae sedis) *murana* Warncke, 1975, male **B** face, frontal view **D** genital capsule, dorsal view; *Andrena* (incertae sedis) *relata* Warncke, 1975, male **C** genital capsule, dorsal view; *Andrena* (*Chlorandrena*) *humilis* Imhoff, 1832, male **E** genital capsule, dorsal view; *Andrena* (*Truncandrena*) *nigropilosa* Warncke, 1967, male **F** genital capsule, dorsal view; *Andrena* (*Suandrena*) *suerinensis* Friese, 1884, male **G** propodeum, dorsal view; *Andrena* (*Plastandrena*) *pilipes* Fabricius, 1781, male **H** propodeum, dorsal view.

47 Terga finely shagreened, more or less smooth and shiny, regularly and deeply punctate, punctures separated by 1–2 puncture diameters, punctures extending onto the tergal margins. A3 comparatively short, only slightly exceeding length of A4. Nervulus antefurcal **48**

– Tergal shagreened to microreticulate, dull to weakly shiny, obscurely or clearly punctate, but marginal areas impunctate. A3 comparatively long, clearly exceeding length of A4. Nervulus interstitial to weakly postfurcal **49**

48 Genital capsule simple, with small gonocoxal teeth, gonostyli spatulate and more or less parallel-sided (Fig. 78C) .... ***relata* Warncke**

– Genital capsule complex, with inner margins progressively diverging, forming 90° inner angle. Gonostyli apically strongly flattened and broadened, more or less triangular shovel-like (Fig. 78D) .... ***murana* Warncke**

49 Disc of T1 with large ‘crater punctures’, punctures with distinctly raised margins. Terga shagreened and weakly shiny. Genital capsule with long, strongly produced gonocoxal teeth (Fig. 78E) ....***humilis* Imhoff**

– Disc of T1 with small hair-bearing punctures, without raised, crater-like rims. Terga microreticulate and dull. Genital capsule with only weakly produced gonocoxal teeth **50**

50 A3 very long, slightly exceeding the length of A4+5. A4 very short, broader than long. Genital capsule relatively compact, with flattened apical part clearly longer than broad ....***medeninensis donata* Warncke**

– A3 comparatively shorter, at most equalling the length of A4+5. A4 longer, slightly longer than broad. Genital capsule relatively elongate, with flattened apical part only slightly longer than broad (Fig. 78F)...................... .... ***nigropilosa* Warncke**

51 (1) Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate (Figs 78G, H, 79A) **52**

– Propodeal triangle not strongly defined by lateral carinae with its internal surface rugose-areolate **66**

52 Forewing with two submarginal cells. Clypeus with longitudinal striations. .... ***lagopus* Latreille**

– Forewing with three submarginal cells. Clypeus without longitudinal striations **53**

53 Small species, 6–7 mm. Clypeus, scutum, and terga extremely densely and deeply punctate with small punctures, punctures almost confluent. Each side of T2 laterally with a small but deep and clearly defined fovea (Fig. 79B, C; subgenus *Brachyandrena*) **54**

– Larger species, at least 8 mm in length, usually >10 mm. Body never so densely punctate, punctures always a little separated, never confluent. T2 with fovea obscure **55**

54 T2 laterally with foveae narrow and relatively elongate (Fig. 79B). Common and widespread across Iberia[18] .... ***colletiformis* Morawitz**

– T2 laterally with foveae shorter and relatively broad (Fig. 79C). Rare, encountered predominantly in southern Spain (Cádiz, Málaga)[18] .... ***miegiella* Dours**

55 Pronotum laterally with strong humeral angle with well-developed carina. Fore margin of clypeus weakly upturned .... ***fuscosa* Erichson**

– Pronotum laterally rounded. Fore margin of clypeus normal, not upturned **56**

56 Hind basitarsi and majority of hind tibiae lightened orange. Body with integument uniformly dark. Pubescence bright, face and mesepisternum with light brown hairs, scutum and T6 with bright orange hairs. A3 clearly shorter than A4 .... ***haemorrhoa* (Fabricius)**

– Without this combination of characters; either hind legs dark, body with darker pubescence, or A3 clearly longer than A4 .... **57**

57 Terga with metallic reflections and at most superficial punctures AND genital capsule distinctive, with strongly produced gonocoxal teeth and gonostyli strongly reflexed, with long plumose hairs present on their outer margin (subgenus *Suandrena*) **58**

– Terga without metallic reflections OR if with metallic reflections, then genital capsule otherwise, either lacking pronounced gonocoxal teeth or without plumose hairs on the outer margin of the gonostyli OR terga clearly and abundantly punctate (subgenus *Plastandrena*) **60**

58 Genital capsule with penis valves grossly inflated, occupying entirety of space between the gonostyli, laterally produced into bulbous projections (Fig. 79D). Known only from Cádiz province, flying in December............ .... ***gades* Wood & Ortiz-Sánchez**

– Genital capsule with penis valves narrower, essentially parallel-sided, not occupying entirety of space between the gonostyli, without lateral projections... **59**

59 A3 ventrally rounded, lacking any kind of triangular point (Fig. 79E). Genital capsule less elongate, gonocoxal teeth relatively short (Fig. 79F). Confirmed males known only from eastern and southern Spain. Bivoltine, flying February-April and September-October .... ***cyanomicans* Pérez**

– A3 ventrally produced into triangular point (Fig. 79G). Genital capsule more elongate, with long and strongly produced gonocoxal teeth (Fig. 79H). Widespread across Iberia. Univoltine, flying March-May....... .... ***suerinensis* Friese**

60 Genital capsule with gonocoxae apically rounded (Fig. 80A, B) **61**

– Genital capsule with clearly produced gonocoxal teeth (Fig. 80C–G) **62**

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[18] These two species are very difficult to separate in the male sex. Association with females should be made, as well as taking account of their known distributions.

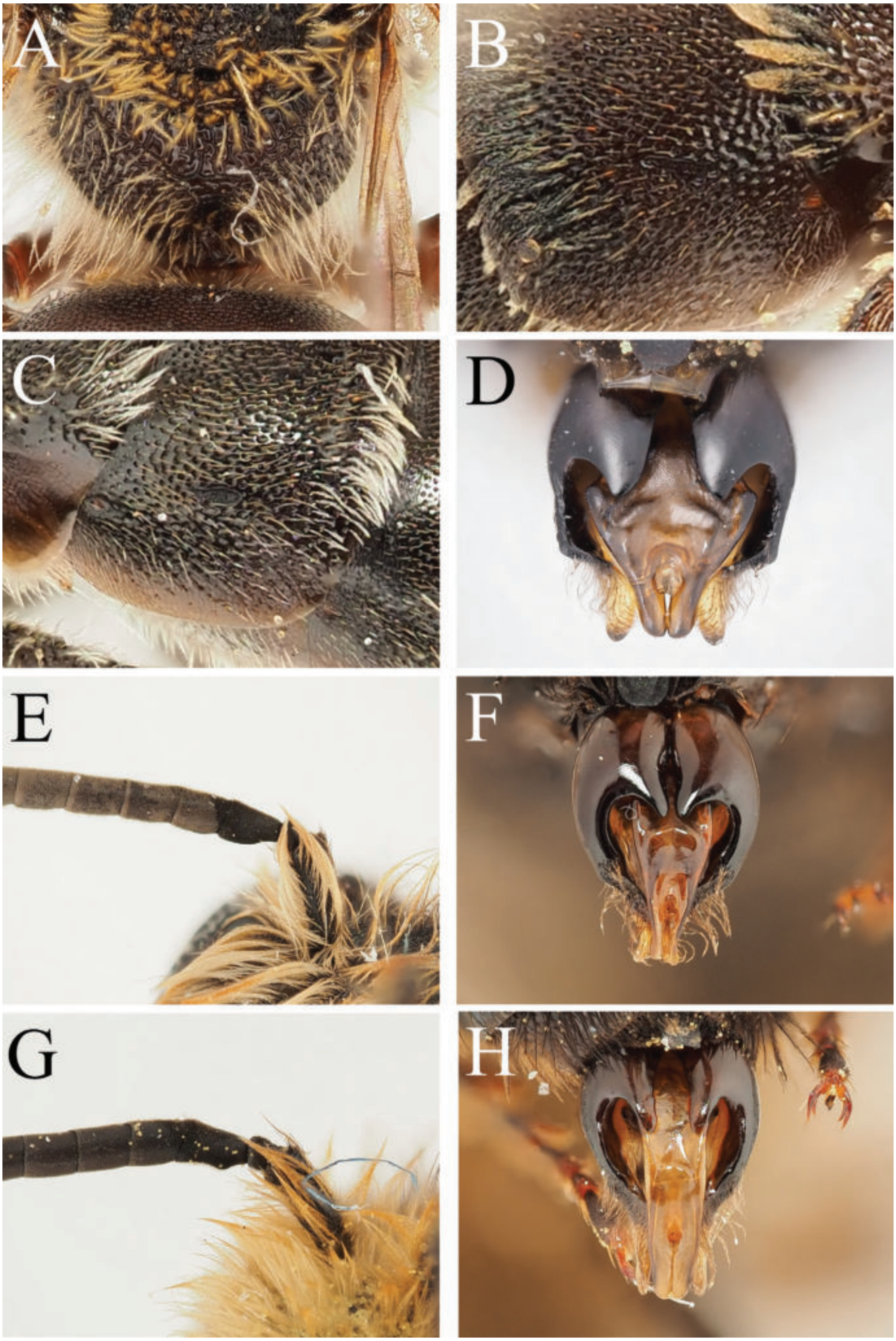

Figure 79. *Andrena* (*Brachyandrena*) *colletiformis* Morawitz, 1873, male **A** propodeum, dorsal view **B** T2, profile view; *Andrena* (*Brachyandrena*) *miegiella* Dours, 1873, male **C** T2, profile view; *Andrena* (*Suandrena*) *gades* Wood & Ortiz-Sánchez, 2022, male **D** genital capsule, dorsal view; *Andrena* (*Suandrena*) *cyanomicans* Pérez, 1895, male **E** antennae, frontal view **F** genital capsule, dorsal view; *Andrena* (*Suandrena*) *suerinensis* Friese, 1884, male **G** antennae, frontal view **H** genital capsule, dorsal view.

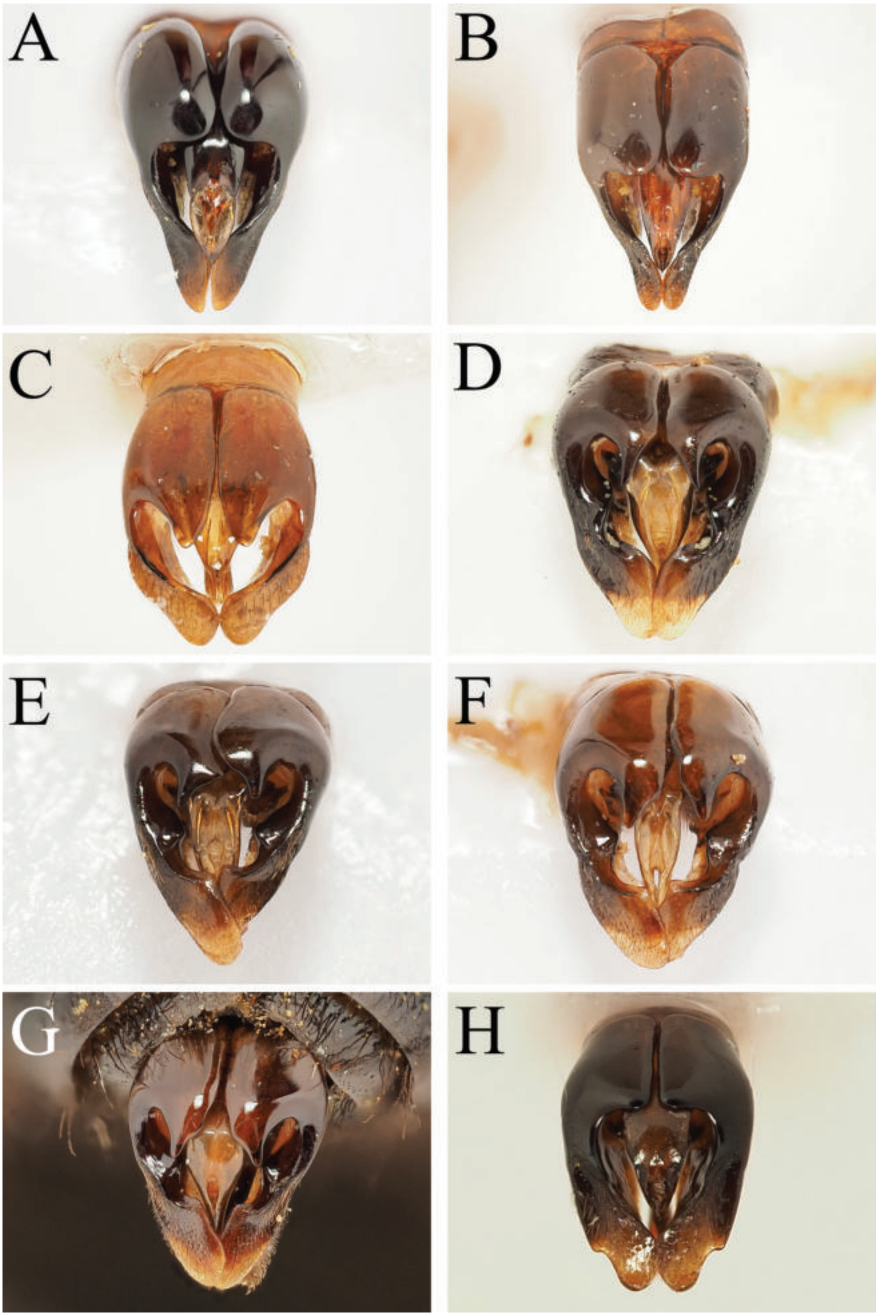

Figure 80. *Andrena* (*Plastandrena*) *agilissima* (Scopoli, 1770), male **A** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *afrensis* Warncke, 1967, male **B** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *asperrima* Pérez, 1895, male **C** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *tibialis* (Kirby, 1802), male **D** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *bimaculata* (Kirby, 1802), male **E** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *pilipes* Fabricius, 1781, male **F** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *nigrospina* Thomson, 1872, male **G** genital capsule, dorsal view; *Andrena* (*Melandrena*) *flavipes* Panzer, 1799, male **H** genital capsule, dorsal view.

61 Terga with metallic blue reflections. Genital capsule with penis valves medially with and oval hyaline expansion, this breaking the profile of the penis valves themselves (Fig. 80A). Gonostyli with inner margin raised .... ***agilissima* (Scopoli)**

– Terga dark, without metallic blue reflections. Genital capsule penis valves uniformly converging apically (Fig. 80B). Gonostyli with inner margin not raised .... ***afrensis* Warncke**

62 Terga usually extremely densely punctate, punctures almost confluent. Terga with weak metallic blue hints. Genital capsule, see Fig. 80C, see also Fig. 25D .... ***asperrima* Pérez**

– Terga never so densely punctate, punctures never confluent, always separated by at least 0.5 puncture diameters. Terga never with metallic blue reflections. Genital capsule otherwise **63**

63 Mesosoma with brown pubescence dorsally and laterally, at most with occasional black hairs **64**

– Mesosoma with grey and black pubescence, always with at least some black hairs laterally on the mesepisternum **65**

64 Genital capsule with penis valves basally broad (Fig. 80D). Nominally univoltine, flying only in the spring .... ***tibialis* (Kirby)**

– Genital capsule with penis valves basally narrow (Fig. 80E). Bivoltine, flying in the spring and the summer .... ***bimaculata* (Kirby)**

65 Penis valves basally narrow, apical spatulate parts of gonostyli comparatively narrow (Fig. 80F). Bivoltine (typically March–April and July–August). Common and widely distributed throughout Iberia .... ***pilipes* Fabricius**

– Penis valves basally broad, apical spatulate parts of gonostyli comparatively broad (Fig. 80G). Univoltine (typically May–June). Rare, restricted to mountainous parts of Iberia; known from the Pyrenees, the Sistema Central, Serra do Gerês, Sistema Ibérico, and Sierra de Cazorla .... ***nigrospina* Thomson**

66 (51) Genital capsule distinctive, with more or less 90° emargination in the outer parts of the gonostyli (Fig. 80H). The most common *Andrena* species in Iberia .... ***flavipes* Panzer**

– Genital capsule otherwise **67**

67 Process of the labrum thickened and expanded, anteriorly projecting beyond the fore margin of the clypeus. Pronotum with strong humeral angle. Active in the summer (mid-June to September) (subgenus *Cnemidandrena* and remaining *Margandrena*) **68**

– Without this combination of characters **71**

68 T2–3 extensively red-marked. Clypeus with apical corners produced into distinct anteriorly projecting knobs (c.f. Fig. 76A). Restricted to north-eastern Spain in Mediterranean habitats .... ***pellucens* Pérez**

– Terga dark, without red markings. Clypeus without apically projecting knobs **69**

69 Outer surface of the galea smooth and shiny. Associated with Ericaceae, found in Atlantic habitats across northern, central, and western Iberia........ .... ***fuscipes* (Kirby)**

– Outer surface of the galea shagreened and dull..**70**

70 Gena posteriorly produced into a strong winged carina. Scutum with abundant black hairs. Associated with Asteraceae, restricted to northern Spain... .... ***denticulata* (Kirby)**

– Gena posteriorly rounded. Scutum at most with occasional black hairs, usually entirely brown-haired. Polylectic, though often found on Asteraceae. Restricted to areas surrounding the Pyrenees with isolated populations in high mountains in southern Spain (particularly the Sierra Nevada)............ .... ***nigriceps* (Kirby, 1802)**

71 (67) Fore margin of clypeus upturned AND gena conspicuously broadened, wider than the width of the compound eye AND pronotum with a conspicuous humeral angle (remaining *Notandrena*) **72**

– Without this exact combination of characters. (Note, male members of the *Ovandrena* are very similar, but the gena is as broad as the width of the compound eye, not broader. They can be found at couplet 168; *Andrena blanda* is also similar, but the gena is only slightly wider than the width of the compound eye. It should be diagnosed by its genital capsule, go to couplet 184)...**76**

72 Mandibles long, sickle-shaped, strongly crossing apically. A3 long, exceeding length of A4+5. Clypeus covered with dense plumose hairs than obscure the underlying surface in fresh specimens. Clypeus sometimes with weak metallic reflections..**73**

– Mandibles normal, not sickle-shaped, not strongly crossing apically. A3 short, slightly shorter than A4+5. Clypeus without plumose hairs that obscure the underlying surface. Clypeus dark, without metallic reflections.....................**75**

73 Terga uniformly dark, at most with marginal areas lightened dark brown. A3 comparatively short, only moderately exceeding length of A4+5. Discs of T2–4 clearly and regularly punctate, punctures separated by 2 puncture diameters, underlying surface shagreened and weakly shiny .... ***ranunculi* Schmiedeknecht**

– Terga red-marked, with at least marginal areas and lateral parts of T2–3 lightened red. A3 comparatively long, almost equalling or equalling length of A4+5+6. Terga shagreened, obscurely punctate, punctures disappearing into background sculpture **74**

74 Clypeus polished and shiny, with scattered punctures. Mesonotum with shiny areas medially. A3 equalling A4+5+6 .... ***binominata* Smith**

– Clypeus uniformly shagreened and dull. Scutum uniformly shagreened and dull. A3 slightly shorter than A4+5+6...................... ***leucophaea* Lepeletier**

75 Terga with marginal areas of T2–4 puncture-free. A3 shorter than A4+5, never twice as long as A4. Basitarsi usually dark, sometimes apically lightened

orange. Restricted to cooler parts of northern and western Iberia; univoltine, flying on July-August .... ***nitidiuscula* Schenck**

– Terga with punctures of discs of T2–4 extending onto marginal areas. A3 almost as long as A4+5, typically twice as long as A4. Basitarsi usually entirely lightened orange. Widespread across Iberia; bivoltine, flying in April-May and July-August .... ***fulvicornis* Schenck**

76 (71) Small species, body length of 5–7 mm, terga always dark, legs always dark (remaining *Aciandrena*, *Aenandrena partim*, *Avandrena*, *Cordandrena partim*, *Cryptandrena partim*, *Graecandrena*, and almost all *Micrandrena*)..**77**

– Larger species, at least 8 mm in length. Terga lightened red in some species, either on the discs or the margins. Hind tarsi or basitarsi lightened orange in some species **121**

77 All tergal discs uniformly punctate, punctures separated by 0.5 puncture diameters, underlying surface weakly shiny. Genital capsule elongate, with weakly pronounced gonocoxal teeth, gonostyli apically produced into triangular wedges (Fig. 77B) .... ***ventricosa* Dours** (*partim*, dark form)

– Genital capsule otherwise; tergal punctation variable **78**

78 A3 much shorter than A4, at most ½ the length (Fig. 81A, C). Terga often with weak metallic bronzy reflections (Fig. 81D) **79**

– A3 as long as A4 or longer. Terga without metallic reflections **81**

79 A3 extremely short relative to A4, at most 1/5 the length (Fig. 81A). Terga dark. Genital capsule distinctive, with extremely narrow parallel-sided penis valves (Fig. 81B). Rare, known from eastern Spain (Jáen, Soria, Teruel).................................. ***vaulogeri* Pérez** (*partim*, small individuals)

– A3 not so short, around ½ the length of A4 (Fig. 81C). Terga with metallic bronzy reflections. Genital capsule otherwise **80**

80 T3–4 laterally almost impunctate, any obscure punctures disappear into the background sculpture .... ***aeneiventris* Morawitz**

– T3–4 laterally with abundant clear punctures, these distinct against the background structure (Fig. 81D) .... ***hedikae* Jäger**

81 A3 long, equalling or exceeding length of A4+5. Face with abundant dark pubescence, sometimes intermixed with white hairs. Propodeal triangle narrow, with fine granular shagreenation over the majority of its area, sometimes with short, fine, and raised rugae basally (Fig. 82A). Scutum shagreened, dull to weakly shiny, with obscure scattered punctures. Metasoma with obscure and scattered hair-bearing punctures, punctures separated by 3–4 puncture diameters. Active in the early spring (March-April), associated with *Erodium* (Geraniaceae; subgenus *Avandrena*) **82**

– Without this combination of characters..**84**

82 Genital capsule relatively compact, gonostyli apically flattened, more or less triangular shovel-like, more or less as broad as long (Fig. 82B). Tergal discs

Figure 81. *Andrena* (*Cordandrena*) *vaulogeri* Pérez, 1895, male **A** antennae, frontal view **B** genital capsule, dorsal view; *Andrena* (*Aenandrena*) *hedikae* Jäger, 1934, male **C** antennae, frontal view **D** terga, posterolateral view.

very finely shagreened, almost smooth and shiny. Known from southern Spain (Albacete, Cádiz, Granada, Málaga) .... ***melacana* Warncke**

– Genital capsule elongate, gonostyli with apical flattened part much longer than broad (Fig. 82C, D). Tergal discs more strongly shagreened, at most weakly shiny **83**

83 Viewed ventrally, process of S8 narrow, more or less the same width as the basal stem part (Fig. 82E). Smaller, 6–7 mm[19] ....***panurgina* De Steffani**

– Viewed ventrally, process of S8 large, clearly broader than the basal stem part (Fig. 82F). Slightly larger, 7–8 mm[19].. ...... ***avara* Warncke aggregate** (potentially including multiple valid species)

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[19] Because of taxonomic complexity and variation in the shape of the genital capsule within *A. avara* (e.g. the capsule pictured here in Fig. 82D is *A. avara liturata* Warncke, 1975 that has apically truncate gonocoxal teeth), it is best to use only the form of S8 to separate *A. panurgina* from the *A. avara* complex.

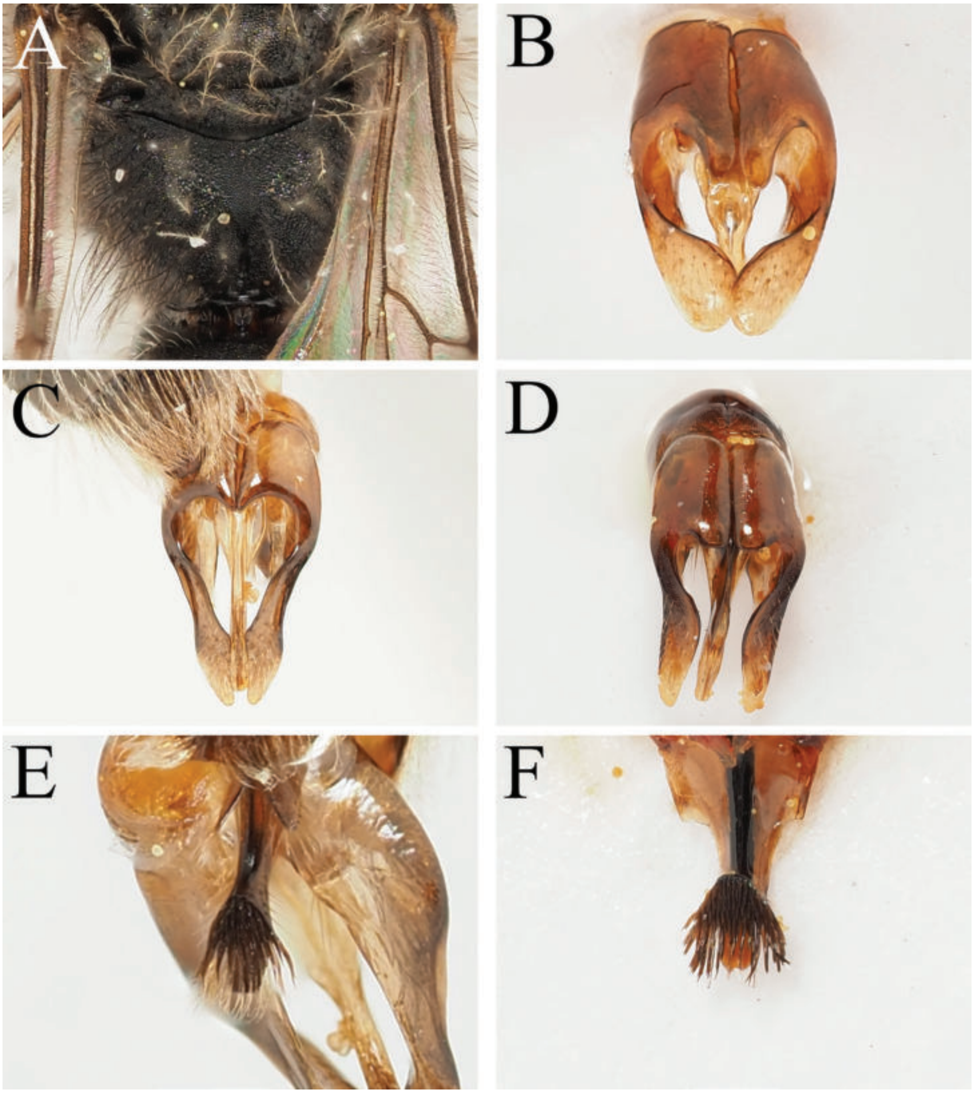

Figure 82. *Andrena* (*Avandrena*) *panurgina* De Steffani, 1889, male **A** propodeal triangle **C** genital capsule, dorsal view **E** S8, ventral view; *Andrena* (*Avandrena*) *melacana* Warncke, 1967, male **B** genital capsule, dorsal view; *Andrena* (*Avandrena*) *avara liturata* Warncke, 1975, male **D** genital capsule, dorsal view **F** S8, ventral view.

84 Propodeal triangle smooth, not defined laterally by raised carinae, with internal surface lacking network of raised rugosity, at most with very short rugae at the base of the propodeal triangle (Fig. 52D)............................**85**

– Propodeal triangle either strongly defined by raised carinae, or with internal surface with network of raised rugosity covering at least the basal half (specifically, take care with *A. tenuistriata*, for which the lateral parts of the propodeal triangle present granular shagreen) **95**

85 Clypeus with clear longitudinal striations covering the entire surface. Restricted to sandy and usually coastal habitats in southern Iberia.......... ***orana* Warncke**

– Clypeus without striations, or with at most obscure striations at the base of the clypeus, never covering the entire surface **86**

86 Clypeus weakly but distinctly domed, basally densely punctate, punctures separated by 0.5 puncture diameters, punctures becoming sparse apically, here separated by 2–3 puncture diameters; underlying surface smooth and shiny (Fig. 83A). Fore margin of the clypeus forming a very wide and gentle emargination, process of the labrum narrow, slightly longer than wide. Genital capsule, see Fig. 83B........................... ***pandosa trigona* Warncke**

– Without this combination of characters, clypeus usually flattened and/or shagreened and dull, or genital capsule otherwise...................................**87**

87 Terga strongly and clearly punctate, tergal margins strongly depressed, with punctures continuing onto marginal areas; underlying surface finely shagreened and weakly shiny. Very small species, not exceeding 6 mm............ ....***fulica* Warncke** (*partim*, dark form with black clypeus)

– Terga either impunctate (Fig. 52E) or obscurely punctate, without clear punctures extending onto the tergal margins..**88**

88 Clypeus flattened, shagreened in basal half, finely shagreened in apical half, the two half therefore contrasting; surface with obscure and scattered punctures. Genital capsule elongate, with long and sharply pointed penis valves (Fig. 83C)..***verticalis* Pérez**

– Clypeus flattened or domed, but without this combination of characters. Genital capsule otherwise **89**

89 Genital capsule unusual, gonocoxae with inner margins forming obtuse angle, without gonocoxal teeth, gonostyli flattened with square truncate apexes (Fig. 83D, E) **90**

– Genital capsule otherwise **91**

90 Genital capsule with gonostyli comparatively narrow, apically narrower than the basal width of the penis valves; penis valves occupying comparatively little of the space between the gonostyli (Fig. 83D). Restricted to the extreme north-east of Spain..***impunctata* Pérez**

– Genital capsule with gonostyli comparatively broad, apically as broad as the basal width of the penis valves; penis valves occupying majority of space between the gonostyli (Fig. 83E). Restricted to central, southern, and eastern Spain, not known from the north-east.. ***nebularia* Warncke**

91 Tergal margins extensively lightened hyaline-yellow, T2–4 with dense and thick complete apical hair bands that occupy and slightly exceed the entire length of the margin, obscuring the underlying surface in fresh individuals. Small species, not exceeding 6 mm. Rare, known only from central Spain ....***montarca* Warncke**

– Tergal margins with weaker apical hair bands, tergal margins not so extensively lightened yellow. If in doubt, species exceeding 6 mm in length, or with clypeus flattened **92**

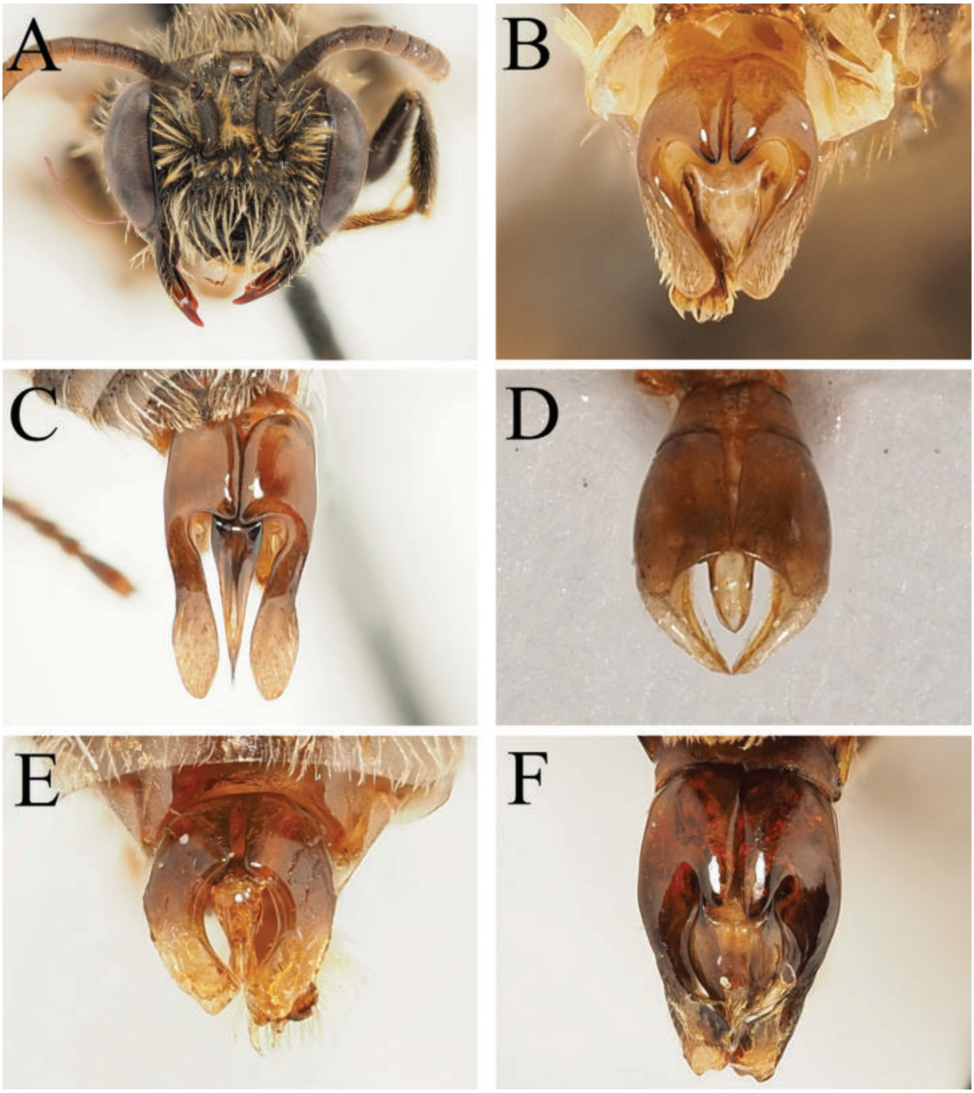

Figure 83. *Andrena* (*Micrandrena*) *pandosa trigona* Warncke, 1975, male **A** face, frontal view **B** genital capsule, dorsal view; *Andrena* (*Graecandrena*) *verticalis* Pérez, 1895, male **C** genital capsule, dorsal view; *Andrena* (*Graecandrena*) *impunctata* Pérez, 1895, male **D** genital capsule, dorsal view; *Andrena* (*Graecandrena*) *nebularia* Warncke, 1975, male **E** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *longibarbis* Pérez, 1895, male **F** genital capsule, dorsal view.

92 Genital capsule with penis valves basally strongly swollen, blister-like, gonocoxae with well-developed gonocoxal teeth (Fig. 83F)............................**93**

– Genital capsule with penis valves normal, not noticeably broadened (Fig. 52F)..**94**

93 A3 shorter than A4+5. Clypeus flattened, with slight metallic green-purple hints medially. Terga essentially impunctate. Widespread across Iberia .... ***longibarbis* Pérez**

– A3 slightly longer than A4+5. Clypeus flattened, almost with slight longitudinal concavity medially, uniformly black. Terga obscurely punctate. Central and eastern Spain only........ ***fria* Warncke**

94 Gena broad, clearly broader than the width of a compound eye (Fig. 52B, C). Scutum with obscure and shallow but large, hair-bearing punctures, punctures separated by 2–3 puncture diameters. Pronotum with strong humeral angle. Widespread across western and southern Iberia........ ***alma* Warncke**

– Gena normal, equalling the width of a compound eye. Scutum extremely obscurely punctate, punctures disappearing into background structure. Pronotum rounded. Presence and distribution in Iberia unclear........ ***abjecta* Pérez**

95 Genital capsule distinctive, with strongly reflexed gonostyli (Fig. 84A) .... ***djelfensis* Pérez**

– Genital capsule otherwise **96**

96 Genital capsule with penis valves clearly and strongly broadened basally, clearly bulbous in appearance (Fig. 84B–D)........ **97**

– Genital capsule with penis valves not strongly broadened basally **100**

97 Marginal area of T1 wide, strongly thickened, impunctate. Scutum with scattered punctures, punctures separated by 1–3 puncture diameters. Genital capsule with gonocoxal teeth weakly produced (Fig. 84B) Restricted to mountainous areas in northern Spain, associated with *Potentilla* (Rosaceae) .... ***falsifica* Perkins**

– Marginal area of T1 not strongly thickened, flat or slightly depressed. Genital capsule with gonocoxal teeth truncate (Fig. 84C, D). Scutum densely punctate, punctures separated by 0.5–1 puncture diameter........ **98**

98 Clypeus flattened, with slight longitudinal impression medially. Inner margin of the gonostyli upturned, diverging dorsally from outer margin, forming a slight but visible ‘kink’ (Fig. 84C). Associated with *Ornithogalum* (Asparagaceae) .... ***saxonica* Stöckhert**

– Clypeus less strongly flattened. Inner margin of the gonostyli parallel with the outer margin, without a visible ‘kink’ (Fig. 84D). Associated with a wider variety of flowering plants **99**

99 Restricted to areas close to the Pyrenees. A4 slightly longer than A6. Broadened penis valves comparatively longer[20] .... ***strohmella* Stöckhert**

– Found in mountainous areas across southern and central Spain and northern Portugal. A4 as long as A6. Broadened penis valves comparatively shorter[20] .... ***icterina* Warncke**

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[20] These two species are very difficult to separate morphologically; geographic context should be used.

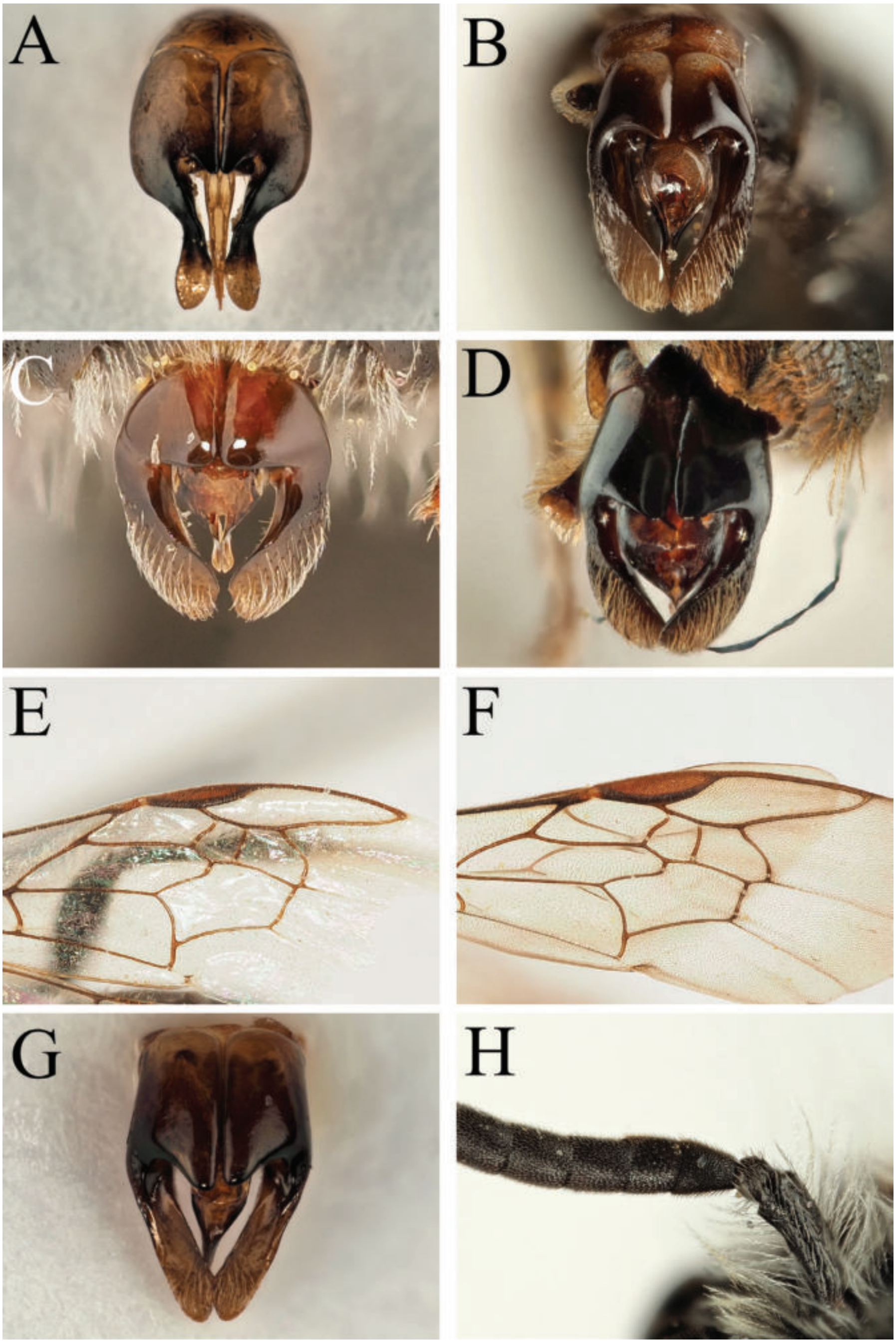

Figure 84. *Andrena* (*Micrandrena*) *djelfensis* Pérez, 1895, male **A** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *falsifica* Perkins, 1915, male **B** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *saxonica* Stöckhert, 1935, male **C** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *icterina* Warncke, 1974, male **D** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *nana* (Kirby, 1802), male **E** forewing, dorsal view **F** *Andrena* (*Micrandrena*) *fabrella* Pérez, 1903, male **F** forewing, dorsal view **G** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *semilaevis* Pérez, 1903, male **H** antennae, frontal view.

100 Genital capsule with outer margins of the gonostyli concave. Clypeus strongly shagreened and dull.......................... ***simontornyella*** **Noskiewicz**

– Genital capsule with outer margins of the gonostyli essentially parallel with the inner margin..**101**

101 Clypeus flattened, basally with obscure but distinct longitudinal striations, these covering the basal quarter of the clypeus and are channelled laterally along its margins..**102**

– Clypeus typically domed, without longitudinal striations basally..........**103**

102 Facial pubescence predominantly black. Scutum shagreened with faint and weak greasy metallic reflections. Tergal discs shagreened, weakly shiny. Tergal margins distinctly depressed. Widespread throughout Iberia..... ***nitidula*** **Pérez**

– Facial pubescence predominantly pale, with scattered black hairs laterally. Scutum more strongly shagreened, matt. Tergal discs with strong microreticulation, dull. Tergal margins weakly depressed. Restricted to the extreme north-east of Spain.. ***distinguenda*** **Schenck**

103 Genital capsule elongate with penis valves converging apically to form a tapering point (Fig. 20A, B). Propodeum with propodeal triangle broad, laterally poorly defined with lateral carinae becoming shorter and weaker posteriorly..**104**

– Genital capsule and propodeal triangle otherwise.................................**105**

104 Genital capsule with the inner margins of the gonostyli only weakly produced towards the penis valves; apical spatulate part of the gonostyli comparatively elongate (Fig. 20A). Tergal discs typically more shagreened and dull, punctures disappearing somewhat into underlying sculpture .... ***niveata*** **Friese**

– Genital capsule with the inner margins of the gonostyli strongly produced towards the penis valves; apical spatulate part of the gonostyli comparatively short (Fig. 20B). Tergal discs typically smooth and shiny, punctures clearly visible .... ***lecana*** **Warncke**

105 Tergal discs, at least on T1, smooth and shiny, at most with very fine shagreenation..**106**

– Tergal discs shagreened or microreticulate, not strongly shiny, most dull and matt..**113**

106 Forewing with first submarginal cross vein separated from the stigma by three times its own width (Fig. 84E)..**107**

– Forewing with first submarginal cross vein separated from the stigma by more or less its own width (Fig. 84F)..**108**

107 Clypeus medially shagreened. Stigma dark brown. Sterna shagreened with the exception of the marginal zones. Common and widespread across Iberia.. ***nana*** **(Kirby)**

– Clypeus medially shiny. Stigma bright, yellowish to reddish. Sternal discs shiny. Very rare, restricted to the Pyrenees.................***floricola*** **Eversmann**

108 Scutum densely shagreened, with large shallow ‘crater-punctures’. In fresh specimens, T1–5 with broad white apical hair bands that exceed the length

of the marginal areas. S2–5 with distinct white apical hair bands. Restricted to mountainous areas of central and northern Spain .... ***argentata* Smith** (*partim*, small individuals)

– Scutum shiny or obscurely shiny, never densely shagreened, with normal punctures without raised rims. Terga and sterna without clear and dense complete hair bands **109**

109 Dorsal part of gena completely smooth and shiny, without any microsculpture. Discs of T2–4 very densely punctate, punctures separated by 0.5 puncture diameters. Restricted to dry and steppic habitats in central Iberia including northern Portugal... ***bayona* Warncke**

– Gena uniformly shagreened, never with extensive smooth and shiny areas. Discs of T2–4 less densely punctate, punctures separated by at least 1 puncture diameter **110**

110 Antennae extensively lightened orange ventrally. T1 with very fine and scattered punctation. Rare, restricted to northern Spain, univoltine (August–September) .... ***nanula* Nylander**

– Antennae dark ventrally. T1 with clearer and denser punctation, punctures separated by 1–2 puncture diameters **111**

111 Terga with punctation clearly extending onto the depressed marginal areas. Genital capsule, see Fig. 84G. Associated with Cistaceae .... ***fabrella* Pérez**

– Terga with marginal areas essentially impunctate, at most with occasional puncture. Genital capsule otherwise.. **112**

112 Marginal areas of T2–4 strongly depressed, mirror-smooth, without a single puncture. A4 as long as broad, equalling A3 in length. Found in the Sistema Central to west and north-western Iberia. Associated with *Sedum* (Crassulaceae).. ***omnilaevis* Wood**

– Marginal areas of T2–4 comparatively weakly depressed, smooth and shiny, but with occasional punctures. A4 subquadrate, broader than long, shorter than A3 in length. Widespread in Iberia .... ***alfkenella* Perkins**

113 A4 quadrate, as wide as long (Fig. 84H). Tergal margins strongly depressed and polished, mirror-smooth, impunctate. Restricted to the Pyrenees and Cantabrian Mountains.. ***semilaevis* Pérez**

– A4 subquadrate, broader than long. Tergal margins depressed or not......... **114**

114 Propodeal triangle laterally poorly defined, without clear carinae, internal surface with raised rugosity covering only central part in the form of a triangle, lateral parts therefore with granular shagreenation (Fig. 85A). Facial hair predominantly black. Clypeus usually smooth and shiny in its apical half. Terga essentially impunctate, regularly shagreened and dull, tergal margins weakly depressed. Univoltine (February–April) .... ***tenuistriata* Pérez**

– Without this exact combination of characters **115**

115 Scutum strongly shagreened and dull, very obscurely punctate, punctures separated by 2–4 puncture diameters, underlying surface matt; punctures often disappear into background sculpture..**116**

– Scutum less strongly shagreened to shiny, with at least some punctures clearly visible against the background sculpture; punctures separated by 1–2 puncture diameters **117**

116 Tergal discs finely shagreened and weakly shiny, with scattered punctures that are nevertheless distinct against the background sculpture, punctures separated by 1–3 puncture diameters. Tergal margins with finer shagreen, impunctate, thus contrasting the tergal discs. Restricted to temperate areas close to the Pyrenees ....***subopaca* Nylander**

– Tergal discs strongly shagreened and dull, with extremely obscure punctures that are hard to distinguish against the background sculpture, separated by 2–4 puncture diameters. Tergal margins with equally strong shagreen, not strongly contrasting the tergal discs. Iberian distribution unclear, but probably restricted to southern Spain (Cádiz, Málaga) ....***tiaretta* Warncke**

117 T1–3 with discs strongly and coarsely punctate, punctures clearly visible against the background sculpture (Fig. 85B). Tergal margins strongly depressed, finely shagreened, more or less shiny, thus strongly contrasting the tergal discs. Restricted to central and northern Spain, typically at altitude in mountainous areas ....***anthrisci* Blüthgen**

– T1–3 without strong and coarse punctures, at most with occasional punctures that typically disappear into the background sculpture. Tergal margins depressed or not, but not noticeably more finely sculptured or more brightly shiny than the tergal discs **118**

118 T2–4 with tergal margins strongly depressed **119**

– T2–4 with tergal margins at most weakly depressed.............................**120**

119 Scutum with scattered punctures, punctures separated by 1–3 puncture diameters. Mesopleuron finely microreticulate, punctate, punctures separated by >1 puncture diameter. Throughout Iberia, common[21].......................***spreta* Pérez**

– Scutum with denser punctures, punctures separated by 1–2 puncture diameters. Mesopleuron more coarsely microreticulate, punctate, punctures separated by <1 puncture diameter. Exact Iberian distribution unclear, but currently known only from eastern Spain, typically in mountainous areas[21]...***pauxilla* Stöckhert**

120 Scutum densely punctate, punctures typically separated by 1 puncture diameter. Scutum and scutellum shagreened and dull (1st generation) to weakly shiny (2nd generation). Genital capsule, see Fig. 85C..........***minutula* (Kirby)**

– Scutum more sparsely and irregularly punctate, punctures separated by 1–3 puncture diameters. Scutum and scutellum finely shagreened and weakly

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[21] The differentiation between these two species in Iberia in the male sex is not completely clear due to lack of available Iberian male material. Association with females should be made.

shiny (1st generation) to polished and shiny (2nd generation). Genital capsule, see Fig. 85D... ***minutuloides* Perkins**

121 (76) Mesepisternum and/or dorsolateral parts of the propodeum conspicuously punctate AND ocelloccipital distance at least 3 times the diameter of a lateral ocellus (*incisa*-group, *Pruinosandrena*) **122**

– Mesepisternum either impunctate or ocelloccipital distance of less than 3 times the diameter of a lateral ocellus..**126**

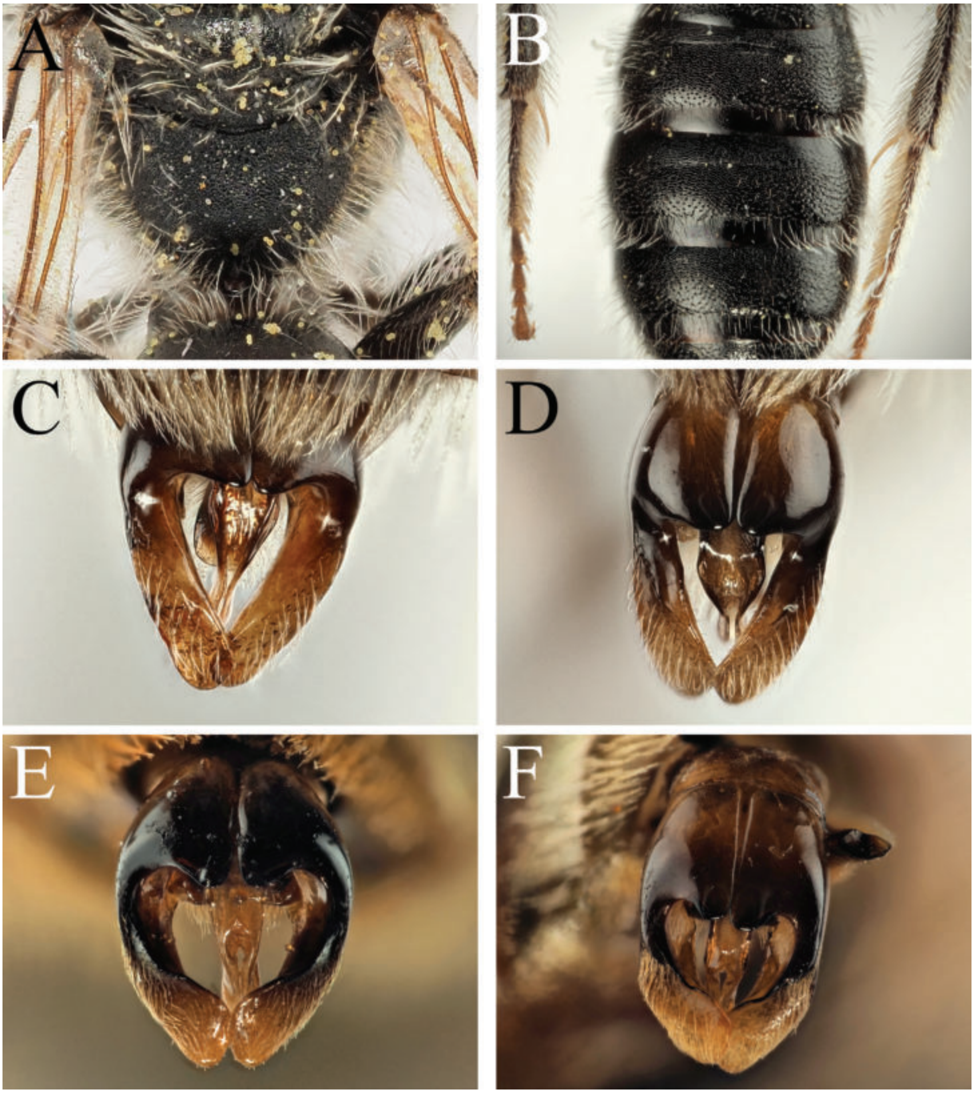

Figure 85. *Andrena* (*Micrandrena*) *tenuistriata* Pérez, 1895, male **A** propodeum, dorsal view; *Andrena* (*Micrandrena*) *anthrisci* Blüthgen, 1925, male **B** terga, dorsal view; *Andrena* (*Micrandrena*) *minutula* (Kirby, 1802), male **C** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *minutuloides* Perkins, 1914, male **D** genital capsule, dorsal view; *Andrena* (*Pruinosandrena*) *nilotica* Warncke, 1975, male **E** genital capsule, dorsal view **F** *Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835, male **F** genital capsule, dorsal view.

122 Dorsolateral parts of the propodeum impunctate, with dense network of raised rugosity..**123**

– Dorsolateral parts of the propodeum regularly punctate, without a dense network of raised rugosity..**124**

123 Face and mesosoma with a mixture of black and white pubescence. T2–4 laterally with widely separated patches of dense white pubescence on their apical margins that obscure the underlying surface. Terminal fringe black... .... ***lateralis* Morawitz**

– Face and mesosoma with light brown pubescence. T2–4 laterally without patches of white pubescence, at most with obscure whitish hair bands. Terminal fringe light brown..***incisa* Eversmann**

124 A3 exceeding A4+5 in length...***parata* Warncke**

– A3 not exceeding A4+5...**125**

125 Genital capsule without clear kink in the inner margins of the gonostyli (Fig. 85E). Scutum less densely punctate, punctures separated by 0.5 puncture diameters, with shiny interspaces, predominantly shiny...................... .... ***nilotica* Warncke**

– Genital capsule with clear kink in the inner margins of the gonostyli (Fig. 85F). Scutum more densely punctate, punctures almost confluent, predominantly dull...***pruinosa* Erichson**

126 (121) Clypeus flattened over majority of its surface (subgenus *Taeniandrena*)[22] **127**

– Clypeus not noticeably flattened..**139**

127 Genital capsule with pronounced gonocoxal teeth, these clearly projecting anteriorly for a distance greater than the diameter of an antenna (Fig. 86A, B) **128**

– Genital capsule with at most weakly projecting gonocoxal teeth (Fig. 86C–F)..**129**

128 Penis valves more or less parallel-sided (Fig. 86A). Gonostyli basally (before flattened apical parts) with dense network of longitudinal striations on their dorsal surface. Known only from central Portugal (Castelo Branco) and south-western Spain (Huelva, Cádiz). Flying early in the season (March–April).. ***lusitania* Wood & Ortiz-Sánchez**

– Penis valves very broad basally, occupying almost entire space between gonostyli (Fig. 86B). Gonostyli without longitudinal striations on their dorsal surface. Restricted to northern Spain. Flying slightly later (April–June) .... ***lathyri* Alfken**

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[22] Males of this subgenus are highly challenging and in some cases impossible to identify. There are several outstanding taxonomic issues in this subgenus that require in-depth genetic study to resolve, and additional probably undescribed cryptic species are present. Do not expect to identify this group without consulting confidently determined reference material, and ideally barcoded specimens. Minimal characters are given here because of the ongoing lack of taxonomic clarity in this subgenus.

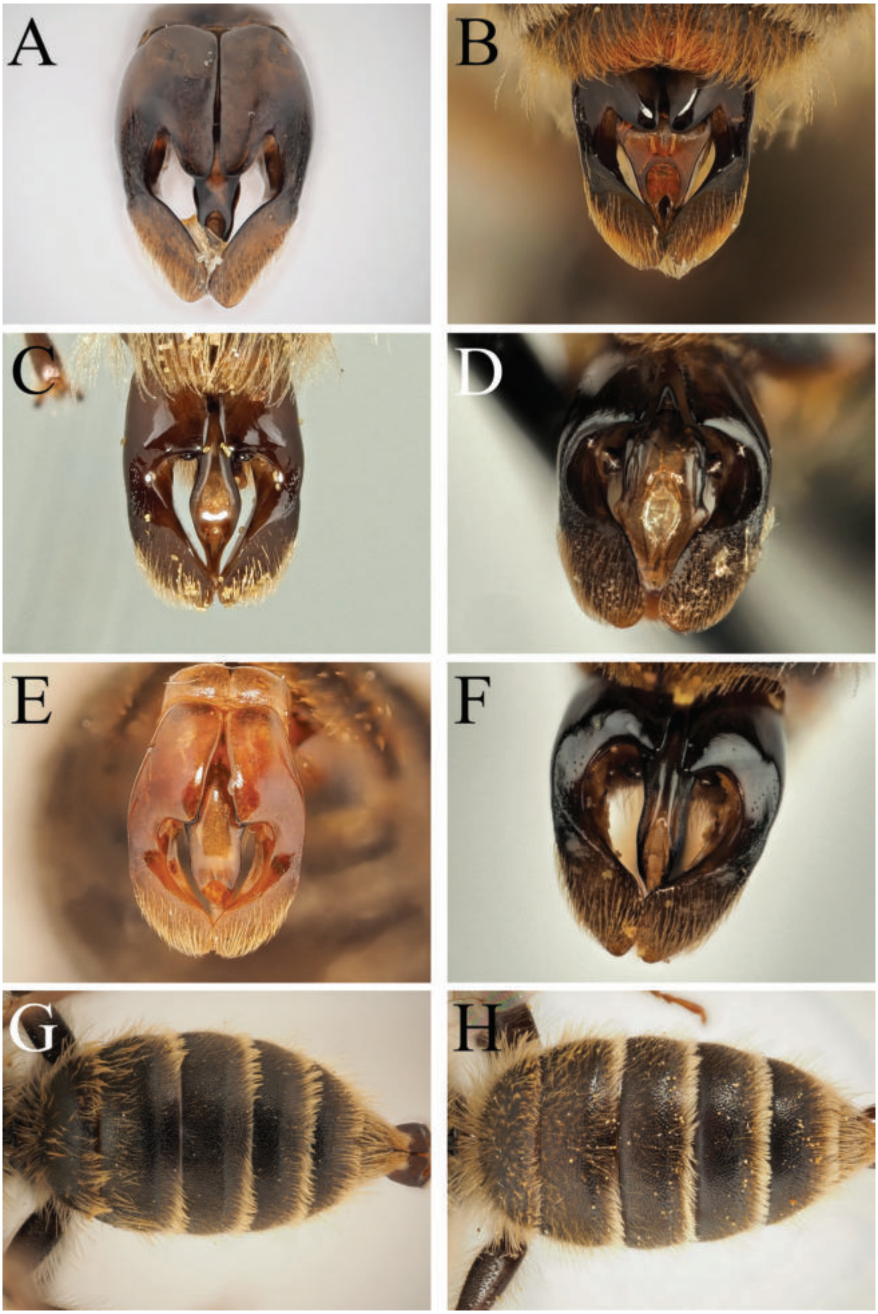

Figure 86. *Andrena* (*Taeniandrena*) *lusitania* Wood & Ortiz-Sánchez, 2022, male **A** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *lathyri* Alfken, 1900, male **B** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *gredana* Warncke, 1975, male **C** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *intermedia* Thomson, 1870 aggregate, male **D** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *levante* Wood & Praz, 2021, male **E** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *contracta* Wood, 2022, male **F** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *wilkella* (Kirby, 1802), male **G** terga, dorsal view; *Andrena* (*Taeniandrena*) *benoisti* Wood & Praz, 2021, male **H** terga, dorsal view.

129 Genital capsule with penis valves narrow basally, broad medially, and narrowing apically (Fig. 86C). Restricted to the Sistema Central and northern and western Iberia..***gredana* Warncke**

– Genital capsule different **130**

130 Penis valves broadened and gonocoxae with their inner margins diverging from their base, gonocoxae therefore forming a broad triangular opening basally (Fig. 86D, E)...**131**

– Penis valves not broadened or gonocoxae with their inner margins more or less parallel, sometimes slightly diverging apically **132**

131 Penis valves strongly broadened, occupying the majority of the space between the gonostyli (Fig. 86D). Gonostyli with strongly raised inner margin, this forming a distinct obtuse angle medially. Found across mountainous areas in eastern Spain.................................... ***intermedia* Thomson aggregate** (this likely represents a complex of an unknown number of species, potentially all of which are undescribed; the true *intermedia* may be absent from Spain)

– Penis valves not so strongly broadened, occupying ½ the space between the gonostyli (Fig. 86E). Gonostyli with weakly raised inner margin, not presenting a distinct angle. Restricted to southern and south-eastern Spain (Almería, Granada, Málaga, Murcia, Valencia). Univoltine (April–June)..***levante* Wood & Praz**

132 Genital capsule with weakly produced gonocoxal teeth (Fig. 86F). Penis valves very narrow, more or less parallel-sided. Restricted to the alpine zone of the Sierra Nevada (typically above 2000 m) .... ***contracta* Wood**

– Genital capsule different, species found elsewhere.................................**133**

133 A3 short relative to A4, approximately 0.6–0.7 times as long................**134**

– A3 long, more or less as long as A4, typically between 0.8–1.2 times as long...**136**

134 Clypeus densely covered with snow-white vestiture, in fresh specimens completely obscuring the underlying surface, particularly of the apical margin. Terga strongly shagreened, punctation obscure, T1 with declivity almost impunctate, any punctures sparse and obscure. Marginal areas of T2–4 almost impunctate. Currently known only from the steppe of central Spain (Guadalajara, Salamanca, Segovia). Univoltine (May–June) .... ***ovata* Schenck**

– Clypeus without such pubescence, the surface of the clypeus is usually clearly visible through the sparser pubescence. Terga with stronger more distinct punctation, including declivity of T1. Marginal areas of T2–4 distinctly punctate, at least basally...**135**

135 Terga with weak apical hair bands, widely interrupted on T2–3, complete on T4 (Fig. 86G). Smaller, 8–9 mm. Restricted to northern Portugal and Spain to the Pyrenees with isolated populations at elevation in the Sistema Central and Sistema Ibérico.. ***wilkella* (Kirby)**

– Terga with strong and thick apical hair bands, medially interrupted on T2, complete on T3–4 (Fig. 86H). Larger, 10–11 mm. Restricted to the Sistema Central to central and northern Portugal and north-western Spain

(Zamora). Not known from the Pyrenees or Cantabrian Mountains .... ***benoisti* Wood & Praz**

136 Hind tibiae and basitarsi lightened orange. Terga strongly shagreened, usually with punctures obscure and disappearing into underlying sculpture. A3 sometimes a little longer than A4. Larger, 10–12 mm. Univoltine (April–June) .....***russula* Lepeletier sensu lato** (including the distinct mitochondrial lineage from southern Portugal)

– Hind legs usually dark. Terga variable, often with abundant and distinct punctures. A3 variable. Smaller, 8–10 mm. Bivoltine (March-August) 137

137 A3 often shorter than A4 (Fig. 87E). Genital capsule with gonostyli produced into apical points (Fig. 87F). Currently only confirmed from the coast of southern Spain (Málaga). Bivoltine (probably February–April; May–June)[23] .... ***poupillieri* Dours**

– Genital capsule with gonostyli apically truncate, not produced into points. **138**

138 A4 usually equal or subequal to A3 in length (Fig. 87A). Terga less densely punctate, surface more finely shagreened, weakly shiny. Genital capsule comparatively less elongate, gonostyli broad with external margin usually straight (Fig. 87B). Internal margins of gonocoxae slightly divergent apically. Penis valve slightly broader basally. Throughout Iberia. Bivoltine (typically May–June; July–August) .... ***afzeliella* (Kirby)**

– A4 often slightly longer than A3 (Fig. 87C). Terga more densely punctate, shagreened and matt. Genital capsule comparatively more slender, gonostyli narrower, external margin weakly concave (Fig. 87D). Internal margins of gonocoxae usually parallel apically. Penis valve on average slightly narrower basally. Widespread throughout Iberia, most common in areas with an Atlantic climate and abundant Genisteae. Bivoltine (typically March–May; June–July) .... ***ovatula* (Kirby)**

139 (126) At least some tergal discs red-marked (Fig. 41G) **140**

– Tergal discs never red-marked, at most with tergal margins lightened **144**

140 A3 longer than A4 .... **141**

– A3 much shorter than A4, at most ¼ the length **143**

141 Head broad, inner margin of compound eyes diverging ventrally (Fig. 41F). Pronotum with strong humeral angle. Clypeus smooth and shiny with scattered punctures. Genital capsule unique, elongate, gonocoxae truncate with inner margin rounded, penis valves basally broad, strongly narrowing medially to become elongate and acutely pointed apically (Fig. 41H) .... ***florea* Fabricius**

– Without this combination of characters **142**

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[23] These three taxa are extremely challenging to separate in the male sex. Comparison to confidently determined or preferably barcoded specimens should be made, as well as association with females.

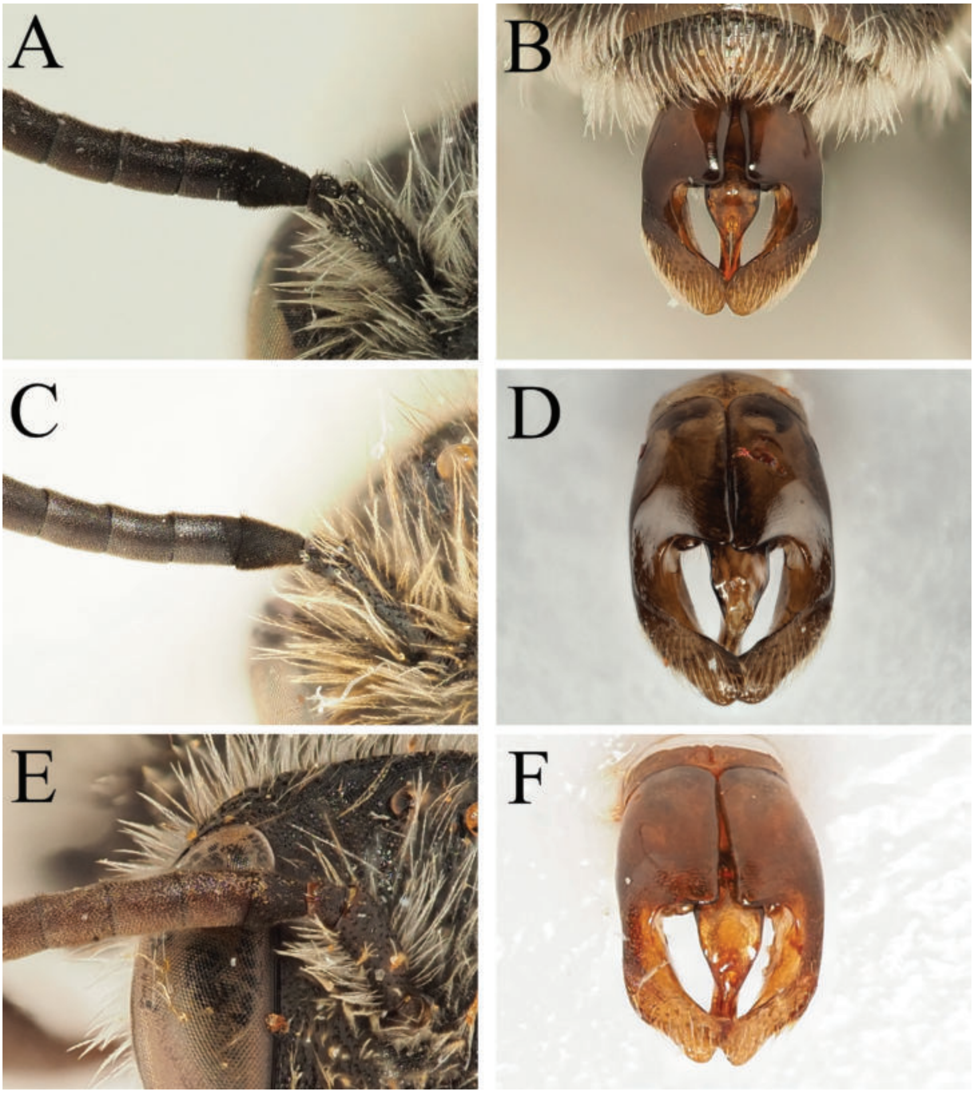

Figure 87. *Andrena* (*Taeniandrena*) *afzeliella* (Kirby, 1802), male **A** antennae, frontal view **B** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *ovatula* (Kirby, 1802), male **C** antennae, frontal view **D** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *poupillieri* Dours, 1872, male **E** antennae, frontal view **F** genital capsule, dorsal view.

142 Clypeus shagreened and matt. Mesonotum and disc of T1 strongly and densely punctate. Hind basitarsi lightened orange. Restricted to the Pyrenees, associated with *Campanula* (Campanulaceae) .... ***rufizona* Imhoff**

– Clypeus smooth and shiny. Mesonotum and disc of T1 weakly punctate with scattered punctures. Hind basitarsi dark. More widespread across Spain .... ***parviceps* Kriechbaumer** (*partim*, light form)

143 S8 apically truncate, lacking apical emargination. Mandibles always bidentate .... ***rosae*** **Panzer** (*partim*, light form)

– S8 with clear apical emargination. Mandibles unidentate (1st generation) or bidentate (2nd generation) .... ***trimmerana*** **(Kirby)** (*partim*, light form)

144 (139) Tergal discs with metallic blue reflections........ **145**

– Tergal discs dark, without metallic reflections, or at most with greasy greenish or bronzy reflections laterally (if greenish reflections present on clypeus, scutum, and scutellum, go to couplet 182), never with blue metallic reflections **147**

145 Tergal discs with abundant 'crater punctures' with raised rims. Pubescence of mesosoma and face light brown, never with abundant black and white hairs........ ***nigroolivacea*** **Dours**

– Tergal discs with simple punctures, without noticeably raised rims. Pubescence of mesosoma with abundant black and white hairs, on the mesosoma forming a striped pattern; white anteriorly and posteriorly, medially with a uniform black strip **146**

146 A3 0.6 times as long as A4. Facial hair shorter than the width of a compound eye. Antennal scape with intermixed black and white hairs. Bivoltine (April–May; July–August), restricted to mountains in northern Spain and the Pyrenees[24] .... ***barbareae*** **Panzer**

– A3 as long or almost as long as A4. Facial hair exceeding the width of a compound eye. Antennal scape with uniformly white hairs. Univoltine (April–May), more widespread across northern Portugal and Spain[24] ... ***cineraria*** **(Linnaeus)**

147 (144) Mandibles elongate, sickle-like, strongly crossing apically (Fig. 88A). Pronotum with strong humeral angle. Gena often expanded, broader than the width of a compound eye........ **148**

– Without this combination of characters; mandibles normal, not elongate and strongly crossing apically (Fig. 88B). Pronotum usually without a strong humeral angle. Gena usually normal, equalling or shorter than the width of a compound eye........ **167**

148 Genital capsule distinctive, gonostyli long and filiform, penis valves grossly expanded, occupying almost the entire space between the gonostyli (Fig. 88C). S8 elongate and strongly emarginate medially, forming a 'Y' shape. Rare, restricted to the Pyrenees........ ***bucephala*** **Stephens**

– Genital capsule and S8 otherwise........ **149**

149 A3 extremely short, at most ¼ the length of A4........ **150**

– A3 longer, never this short. If in doubt, then terga with well-defined and narrow light brown apical hair bands **153**

150 S8 apically truncate, lacking apical emargination. Mandibles always bidentate .... ***rosae*** **Panzer** (*partim*, dark form)

– S8 with clear apical emargination. Mandibles either unidentate or bidentate **151**

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[24] These two species are challenging to separate morphologically.

151 Mandible unidentate, lacking an inner subapical tooth. Gena usually with a long spine. Flying only in the spring (March-May, depending on elevation)................... ***trimmerana*** **(Kirby)** (*partim*, dark form, 1st generation)

– Mandible bidentate, with an inner subapical tooth. Gena usually without a spine, sometimes with a very short spine. Flying in the spring or the summer.. **152**

152 Flying in the spring (usually April to mid-June). Facial pubescence long. Rare, restricted to cooler parts of Iberia.............................. ***scotica*** **Perkins**

– Flying in the summer (usually mid-June to July). Facial pubescence short. Widespread throughout Iberia .... ***trimmerana*** **(Kirby)** (*partim*, dark form, 2nd generation)

153 Mandible unidentate, without inner subapical tooth. Sometimes there may be a hint of a weakly formed or ancient subapical tooth; this state should be treated as unidentate. Head often grossly enlarged **154**

– Mandible clearly bidentate, with a strong inner subapical tooth. Head not normally grossly enlarged.. **156**

154 A3 slightly shorter than A4. Clypeus in apical third bulging, surface smooth and shiny with scattered punctures, punctures separated by 1–4 puncture diameters. Hind tibiae and tarsi usually lightened orange. Northern and central Spain, in areas with deciduous forest. Associated with *Quercus* (Fagaceae) .... ***ferox*** **Smith**

– A3 clearly longer than A4. Clypeus even, without bulging apical part, underlying surface evenly shagreened and regularly punctate. Hind tibiae and tarsi dark.. **155**

155 Clypeus densely punctate, punctures separated by 0.5–1 puncture diameter. Clypeus apically occasionally with very small pale marking medially. Tergal discs with scattered punctures, punctures separated by 2–3 puncture diameters, underlying surface smooth and shiny. Bivoltine, flying April-May and again July-August[25] .... ***nuptialis*** **Pérez**

– Clypeus with sparser punctures, punctures separated by 1–2 puncture diameters. Tergal discs densely punctate, punctures separated by 1–2 puncture diameters, underlying surface shagreened, weakly shiny. Univoltine, typically flying March-June depending on altitude[25] .... ***vetula*** **Lepeletier**

156 A3 distinctly shorter than A4. Genital capsule with gonocoxal teeth pronounced but strongly truncate apically, quadrangular (Fig. 88D). Terga with well-defined and narrow apical light brown hair bands, these occupying only the apical part of the marginal areas (Fig. 88E) .... ***leptopyga*** **Pérez**

– A3 at least as long as A4, usually longer. Genital capsule either with less strongly pronounced gonocoxal teeth, or with gonocoxal teeth apically rounded. Terga with or without apical tergal hair bands........................ **157**

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[25] These two species are unrelated, but have converged on a quite similar morphology; more care is required than might be expected based on their divergent female morphology.

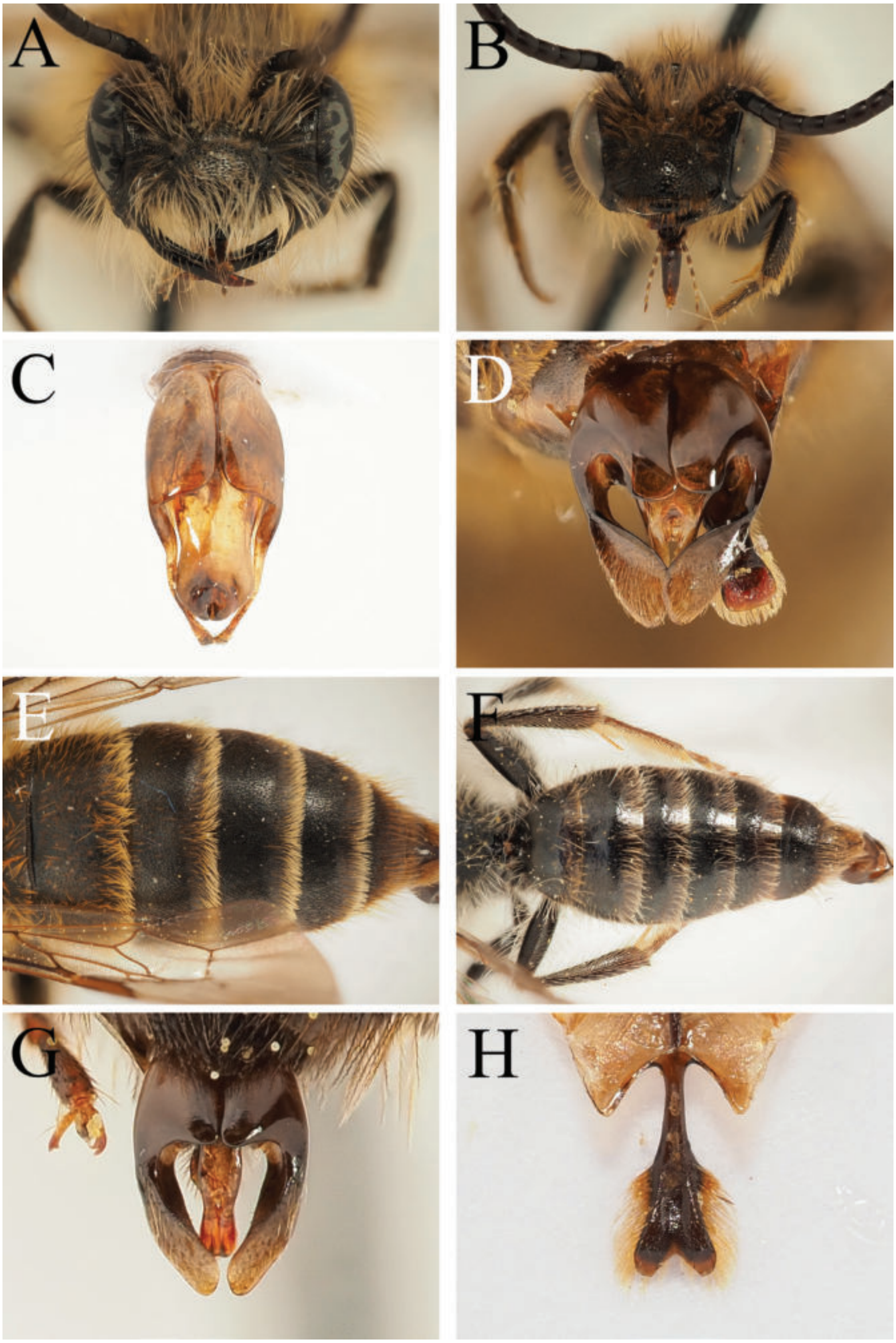

Figure 88. *Andrena* (*Andrena*) *helvola* (Linnaeus, 1758), male **A** head, frontal view; *Andrena* (*Chrysandrena*) *fulvago* (Christ, 1791), male **B** head, frontal view; *Andrena* (*Hoplandrena*) *bucephala* Stephens, 1846, male **C** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *leptopyga* Pérez, 1895, male **D** genital capsule, dorsal view **E** terga, dorsal view; *Andrena* (*Euandrena*) *angustior* (Kirby, 1802), male **F** tergal, dorsal view; *Andrena* (*Euandrena*) *lavandulae* Pérez, 1902, male **G** genital capsule, dorsal view; *Andrena* (*Lepidandrena*) *paucisquama* Noskiewicz, 1924, male **H** S8, dorsal view.

157 Marginal area of T2 broad, occupying ½ the length of the segment, strongly depressed, surface smooth and shiny (Fig. 88F). Found in areas with a temperate Atlantic climate across central, north-western, and northern Iberia..***angustior* (Kirby)**

– Marginal area of T2 never this broad; at most weakly depressed, surface structurally not clearly differentiated from the disc, never smooth and shiny...**158**

158 Genital capsule with gonocoxae apically rounded, gonocoxal teeth very slightly protruding at most (Fig. 88G). Facial pubescence intermixed light brown and black, brown medially, black apically and laterally. Usually smaller, 8–9 mm. Found in areas with a Mediterranean climate ....***lavandulae* Pérez**

– Genital capsule with more strongly projecting gonocoxal teeth, overall capsule more robustly built. Facial pubescence either black or pale, never mixed. Usually larger, 9–12 mm. Typically not found in areas with a Mediterranean climate, species of temperate deciduous forest (subgenus *Andrena* s. str.) **159**

159 Mandible at its base with a clearly pronounced tooth............................**160**

– Mandible at its base with either an angulation or straight **165**

160 A3 1.8 times longer than A4. Hind tarsi lightened orange. With a patchy distribution from northern Portugal and Spain to the Pyrenees, with an isolated population in the Sierra de Cazorla (Jáen)..............***fulva* (Müller)**

– A3 at most 1.3 times longer than A4, usually more or less equal in length. Hind tarsi dark to reddish..**161**

161 Propodeum with majority of hairs black, at most with scattered pale hairs.. ....**162**

– Propodeum with majority of hairs pale, at most with scattered dark hairs... ....**163**

162 S8 apically emarginate. Slightly smaller, 9–11 mm.........***praecox* (Scopoli)**

– S8 apically truncate. Slightly larger, 10–12 mm ....***apicata* Smith**

163 Basal mandibular tooth short. Apical margins of S2–4 with long loose hairs that do not form clear fringes, hairs longer than the length of the hind basitarsis. Restricted to northern Spain. Flying later in the year (June–August), associated with shrubs, particularly *Rubus* (Rosaceae).............***fucata* Smith**

– Basal mandibular tooth long. Apical margins of S2–4 with dense fringes composed of short hairs, these hairs not exceeding the length of the hind basitarsis. Flying earlier in the year (March-June).................................**164**

164 Hind tarsi reddish. Genital capsule more elongate, gonocoxal teeth comparatively weak. Restricted to areas around the Pyrenees and Cantabrian Mountains. Flying during March-May, associated with *Salix* (Salicaceae) ... .***mitis* Schmiedeknecht**

– Hind tarsi dark. Genital capsule more compact, gonocoxal teeth strongly produced. More widespread across northern Iberia into northern Portugal. Flying during May-June, associated with *Vaccinium* (Ericaceae)................. .... ***lapponica* Zetterstedt**

165 Mandible without any kind of angulation at its base. Mesosoma with bright reddish brown hairs, with some black hairs on the mesepisternum. Associated with *Salix* (Salicaceae) ....***clarkella* (Kirby)**

– Mandible at its base with an angulation. Mesosoma never with black hairs laterally. Associated with a wider range of flowering trees and shrubs........**166**

166 Mandible at its base with angulation forming a strong 90° angle. In fresh specimens, clypeus with golden hairs. Terga with marginal areas normal, marginal area of T3 occupying at most 30% of segment length. Restricted to the Pyrenees with an isolated population in the Sierra de Cazorla (Jáen) ....***helvola* (Linnaeus)**

– Mandible at its base with angulation rounded, forming an obtuse angle (c. 120°). In fresh specimens, clypeus with white hairs. Terga with marginal areas broad, marginal area of T3 occupying 60% of segment length. More widespread across central and northern Iberia into northern Portugal .... ***synadelpha* Perkins**

167 (147) Measured along ventral margin, A3 twice as long as A4............................**168**

– Measured along ventral margin, A3 longer or shorter than A4, but never twice as long..**193**

168 S8 unique, elongate on narrow step, apical portion medially constricted and apically strongly emarginate (Fig. 88H) ....***paucisquama* Noskiewicz**

– S8 different, not of this shape **169**

169 Fore margin of the clypeus upturned. Propodeal triangle broad and well-defined by raised lateral carinae, margins extending almost to the lateral edges of the metanotum, internal surface covered in raised irregular carinae of a similar width, thus appearing regular and consistent. Pronotum with weak or strong humeral angle. Genital capsule, see Fig. 45E, F (subgenus *Ovandrena*).....**170**

– Without this combination of characters...**171**

170 Larger, 9–10 mm. Tongue with outer surface of galea clearly punctate, punctures separated by 1–2 puncture diameters. Pronotum with humeral angle comparatively weak, and fore margin of the clypeus only weakly upturned. Sterna with weak and sparse fringes on apical margins. Tergal punctation comparatively larger and coarser. Genital capsule, see Fig. 45F ....***oviventris* Pérez**

– Smaller, 7–8 mm. Tongue with outer surface of galea more or less smooth and shiny, without obvious punctures. Pronotum with humeral angle comparatively strong, and fore margin of the clypeus more strongly upturned. Sterna with strong and dense fringes on apical margins. Tergal punctation comparatively fine. Genital capsule, see Fig. 45E ....***farinosa* Pérez**

171 Clypeus smooth and shiny over almost its entire surface, regularly punctate, punctures separated by 0.5–1 puncture diameters. Metasoma elongate, essentially parallel-sided, surface finely shagreened, more or less smooth and shiny, deeply punctate, punctures separated by 0.5–2 puncture diameters. Genital capsule with gonocoxal teeth apically diverging (Fig. 89A) ....***alluaudi* Benoist**

– Without this combination of characters...**172**

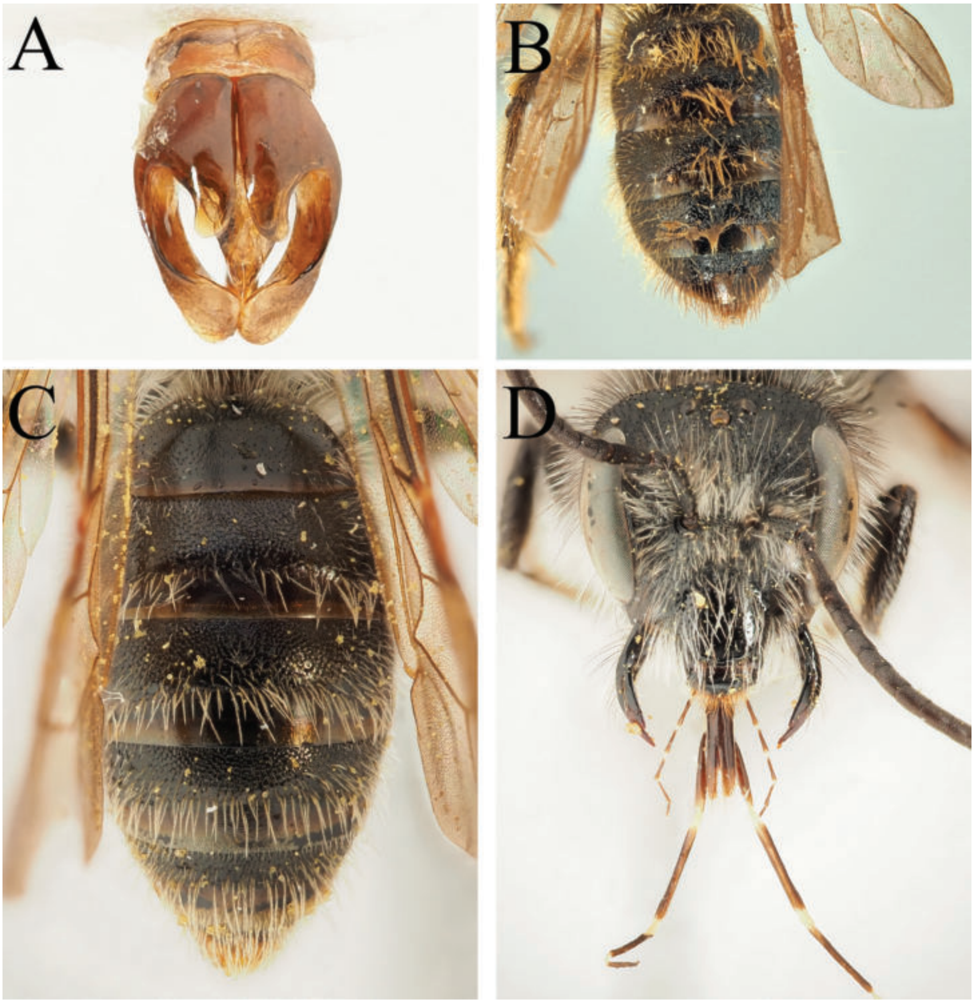

Figure 89. *Andrena* (incertae sedis) *alluaudi* Benoist, 1961, male **A** genital capsule, dorsal view; *Andrena* (*Euandrena*) *fortipunctata* Wood, 2021, male **B** terga, dorsal view; *Andrena* (*Aenandrena*) *hystrix* Schmiedeknecht, 1883, male **C** terga, dorsal view **D** *Andrena* (*Euandrena*) *solenopalpa* Benoist, 1945, male **D** face, frontal view.

172 Tergal margins distinctly depressed, medially occupying 40% of the visible segment (Fig. 89B, C). Tergal discs densely punctate, punctures separated by 0.5–1 puncture diameters; tergal margins impunctate, lightened hyaline brown, strongly contrasting tergal discs..**173**

– Tergal margins either not depressed, not impunctate, not lightened hyaline brown, or narrower...**174**

173 Tergal discs strongly humped, accentuating contrast with margins (Fig. 89B). Margins of T2–4 with irregular light brown hairs. Facial pubescence medially light brown, laterally black along the inner margins of the compound

eyes. Terga never lightened reddish laterally. Known only from mountainous areas in north-western, central, and south-eastern Spain (Léon, Ávila, Jáen) .... ***fortipunctata*** **Wood**

– Tergal discs not strongly humped (Fig. 89C). Margins of T2–4 basally with long whitish plumose hairs that arise from the junctions with the discs and overly the marginal areas without obscuring the underlying surface. Facial pubescence uniformly whitish. Terga often reddish laterally, view in profile. Widespread across Iberia .... ***hystrix*** **Schmiedeknecht** (*partim*)

174 Head elongate, mouthparts extremely long, twice the length of the head, labial palps alone equal the length of the head (Fig. 89D). Associated with *Lithodora* (Boraginaceae)... ***solenopalpa*** **Benoist**

– Head shorter, never with the labial palps equalling the length of the head... .... **175**

175 Gonostyli with outer margin concave, penis valves with weak lateral hyaline extensions (Fig. 90A). Terga strongly microreticulate, dull. Clypeus medially with unclear and slightly raised impunctate midline, otherwise densely punctate, underlying surface largely smooth and shiny. Restricted to areas close to the Pyrenees. Associated with *Symphytum* (Boraginaceae).............. .... ***symphyti*** **Schmiedeknecht**

– Without this combination of characters.. **176**

176 A4–13 ventrally covered with shiny scales, contrasting A3 which is ventrally dull (c.f. Fig. 88B). Tergal margins widely lightened yellow-orange hyaline. Scutellum with intermixed brown-orange and black hairs. Terga very finely shagreened, more or less smoothly shiny, regularly punctate, punctures separated by 1–2 puncture diameters.. ***fertoni*** **Pérez**

– Without this combination of characters... **177**

177 Face with pale hairs medially and black hairs along the inner margin of the compound eyes. Genital capsule with surface of the gonocoxae with distinctive latitudinal granular shagreen, this extending onto the basal parts of the gonostyli (Fig. 90B–D). Terga shagreened, with large scattered punctures on tergal discs, these almost becoming crater-like on T1, but without clearly raised rims. (former subgenus *Zonandrena*, *partim*).............................. **178**

– Without this combination of characters (for species with contrasting black hairs along the inner margin of the compound eyes, see the next couplet) **181**

178 Genital capsule with outer margins of gonostyli weakly emarginate (Fig. 90B, C) **179**

– Genital capsule with outer margins of gonostyli more or less straight, without emargination (Figs 15B–D, 90D)... **180**

179 Penis valves comparatively broad (Fig. 90B). Rare, restricted to the Pyrenees... ***gravida*** **Imhoff** (*partim*)

– Penis valves comparatively narrow (Fig. 90C). Restricted to steppic areas in central Spain... ***soror*** **Dours**

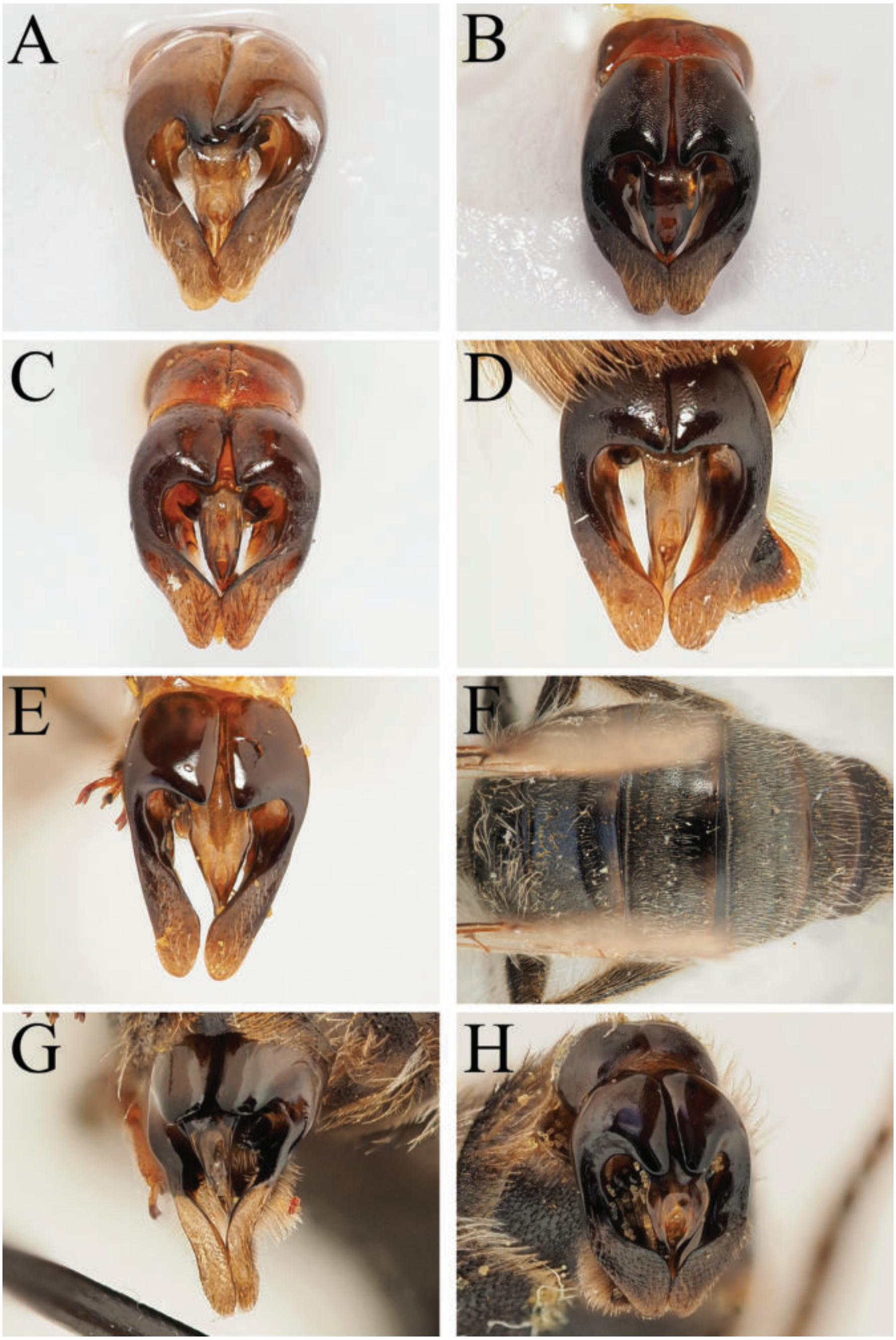

Figure 90. *Andrena* (*Euandrena*) *symphyti* Schmiedeknecht, 1883, male **A** genital capsule, dorsal view; *Andrena* (*Melandrena*) *gravida* Imhoff, 1832, male **B** genital capsule, dorsal view; *Andrena* (*Melandrena*) *soror* Dours, 1872, male **C** genital capsule, dorsal view; *Andrena* (*Melandrena*) *vulcana* Dours, 1873, male **D** genital capsule, dorsal view; *Andrena* (*Melandrena*) *bicolorata* (Rossi, 1790), male **E** genital capsule, dorsal view; **F** terga, dorsal view; *Andrena* (*Lepidandrena*) *baetica* Wood, 2020, male **G** genital capsule, dorsal view; *Andrena* (*Lepidandrena*) *pandellei* Pérez, 1895, male **H** genital capsule, dorsal view.

180 Genital capsule with penis valves comparatively narrow (Fig. 90D). Terga microreticulate, dull to weakly shiny. Punctures on disc of T2 less visible against background sculpture[26] .... ***vulcana*** **Dours**

– Genital capsule with penis valves comparatively broad (Fig. 15B–D). Terga shagreened, weakly shiny. Punctures on disc of T2 more clearly visible against weaker background sculpture[26] .... ***discors*** **Erichson**

181 Face predominantly white-haired, with black hairs along inner margin of compound eyes. Genital capsule elongate, relatively featureless (Fig. 90E). Tergal discs densely and finely punctate, punctures separated by 0.5 puncture diameters (Fig. 90F). Tergal margins slightly but distinctly depressed, with small, fine, and obscure punctures, the margins thus strongly contrasting the discs; underlying surface finely shagreened and weakly shiny **182**

– Without this combination of characters 183

182 Tergal discs with uniformly pale pubescence (Fig. 90F) .... ***bicolorata*** **(Rossi)**

– Tergal discs with intermixed black and white pubescence .... ***florentina*** **Magretti**

183 Terga densely and regularly punctate, punctures separated by up to 1 puncture diameter, underlying surface weakly shagreened to smooth and shiny. T2–4 with distinct white apical hair bands, often abraded and interrupted medially (remaining *Lepidandrena*) **184**

– Terga shagreened, with large ‘crater punctures’ with raised rims. Tergal margins without apical hair bands (remaining *Chlorandrena*) **186**

184 Genital capsule elongate, gonostyli extremely long, many times longer than wide (Fig. 90G). Hind basitarsi lightened orange .... ***baetica*** **Wood**

– Genital capsule with gonostyli compact, not extremely narrow and elongate (Fig. 90H). Hind basitarsi dark **185**

185 S8 with short hairs that do not noticeably project laterally. Tarsal segment 5 of the hind leg elongate and bent. Slightly larger, 10–11 mm .... ***curvungula*** **Thomson**

– S8 with long, laterally projecting hairs. Tarsal segment 5 of the hind leg not noticeably bent. Slightly smaller, 9–10 mm .... ***pandellei*** **Pérez**

186 Process of S8 large, with triangular-shaped lateral projections covered with projecting hair tufts (Fig. 91A; *taraxaci*-group) **187**

– Process of S8 large or small, but more or less parallel-sided, without triangular lateral projections or hair tufts (Fig. 91B–D) **189**

187 Ventral surface of S8 with long, ventrally projecting hairs, clearly visible in profile. Apex of S8 emarginate .... ***senecionis*** **Pérez**

– Ventral surface of S8 without ventrally projecting hairs. Apex of S8 rounded, never medially emarginate **188**

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[26] Separation of the these species is very challenging without access to confidently determined reference material.

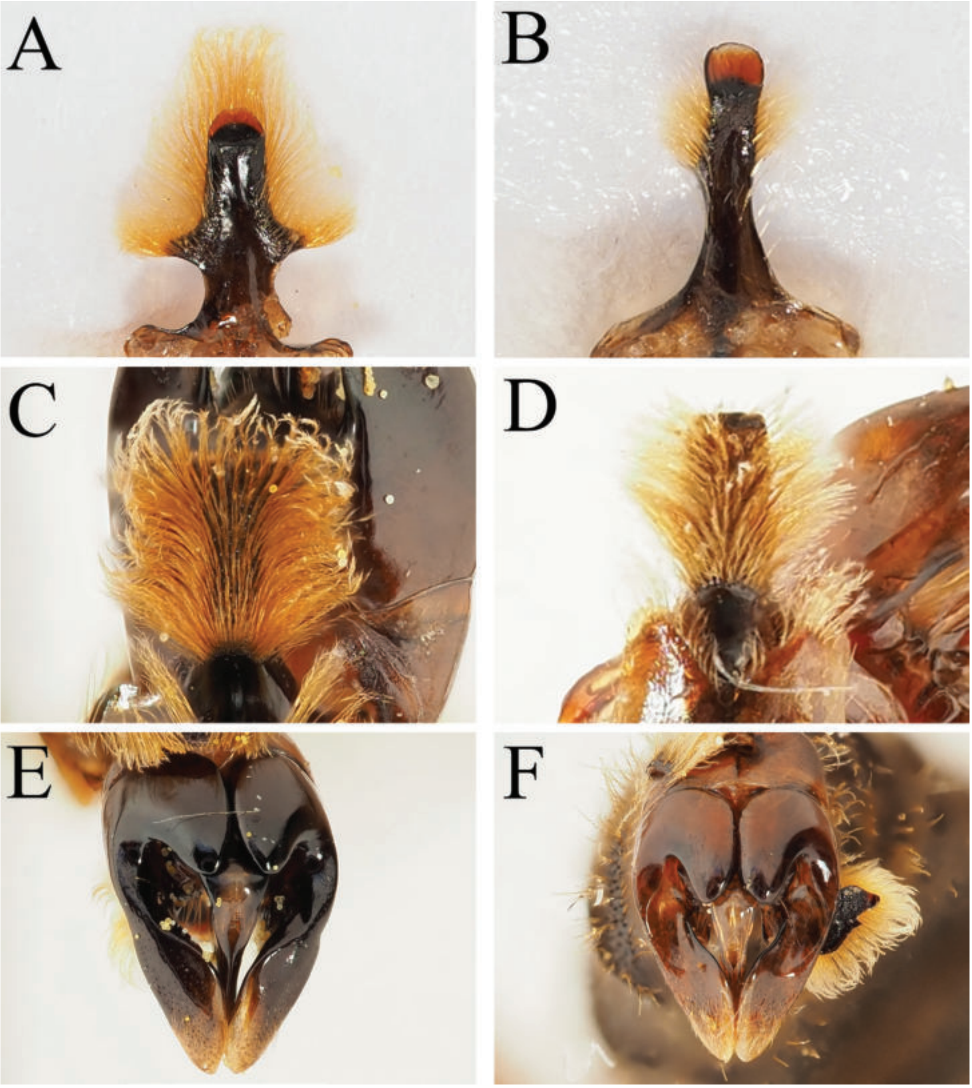

Figure 91. *Andrena* (*Chlorandrena*) *rhenana* Stöckhert, 1930, male **A** S8, dorsal view; *Andrena* (*Chlorandrena*) *cinerea* Brullé, 1832, male **B** S8, dorsal view; *Andrena* (*Chlorandrena*) *livens* Pérez, 1895, male **C** S8, ventral view **E** genital capsule, dorsal view; *Andrena* (*Chlorandrena*) *abrupta* Warncke, 1967, male **D** S8, ventral view; *Andrena* (*Chlorandrena*) *agnata* Warncke, 1967, male **F** genital capsule, dorsal view.

188 Apex of gonostyli with dense, deeply impressed punctuation, gonocoxal lobes strongly pronounced, apically pointed. Common throughout Iberia.. ....***rhenana* Stöckhert**

– Punctuation of gonostyli scattered, especially on the rim of the inner margin, gonocoxal lobes smaller, apexes broadly rounded. Rare, southern and south-eastern Spain only.. ***curtivalvis* Morice**

189 Process of S8 relatively short, ventral surface apically glabrous, viewed ventrally with hairs covering an area more or less as broad as long (Fig. 91B) .... ***cinerea* Brullé**

– Process of S8 relatively long, ventral surface entirely covered with hairs, viewed ventrally with hairs covering an area clearly longer than broad (Fig. 91C, D) **190**

190 Larger, 11–12 mm. S8 strongly broadened apically, here broader than the stem (Fig. 91C). Body dark, without metallic reflections **191**

– Smaller, 9–10 mm. S8 parallel-sided along its entire length, not apically broadened (Fig. 91D). Clypeus, scutum, scutellum, and tergal discs with obscure greasy green metallic reflections **192**

191 Gonostyli with inner margins more or less evenly rounded (Fig. 91E). Terga comparatively more strongly shagreened, weakly shiny. Distributed throughout Iberia .... ***livens* Pérez**

– Gonostyli with inner margins strongly flattened and produced into a raised ridge (Fig. 91F). Terga with shagreenation reduced, terga more strongly shiny in direct comparison. Rare, known only from as single specimen captured near to Madrid .... ***agnata* Warncke**

192 Clypeus strongly domed, underlying surface weakly shagreened laterally, smooth and shiny over the majority of its area; clypeus largely dark, with at most occasional hints of metallic green reflections. Terga with bases very weakly depressed. Found in dry to steppic areas in central Spain .... ***elata* Warncke**

– Clypeus weakly domed, underlying surface shagreened, weakly shiny; metallic green reflections present. Terga with bases strongly depressed. Found in areas close to or on the coast in southern Portugal and Spain .... ***abrupta* Warncke**

193 (167) Measured along ventral margin, A3 shorter than or as long as A4 .... **194**

– Measured along ventral margin, A3 slightly longer than A4 .... **215**

194 A3 extremely short relative to A4, at most $^{1}/_{5}$ the length (Fig. 81A). Terga dark. Genital capsule distinctive, with extremely narrow parallel-sided penis valves (Fig. 81B). Rare, known from eastern Spain (Jáen, Soria, Teruel) .... ***vaulogeri* Pérez** (*partim*, normal sized individuals)

– Without this combination of characters **195**

195 Fore margin of clypeus upturned. Gena slightly exceeding width of compound eye. T2–4 with dense white apical hair bands (Fig. 40G). Genital capsule compact, rounded, with gonocoxal teeth apically diverging, gonostyli apically broadened and flattened (Fig. 40H) .... ***blanda* Pérez**

– Without this combination of characters **196**

196 A4–13 ventrally covered with shiny scales, contrasting A3 which is ventrally dull (Fig. 88B) **197**

– A4–13 not noticeably different from A3, without shiny scales **200**

197 Smaller, 7–8 mm. Tergal discs finely shagreened, more or less smooth and shiny, with deep and distinct punctures, punctures on disc of T1 separated

by 1–2 puncture diameters, on discs of T2–4 separated by 0.5–1 puncture diameter. Tergal margins broadly lightened yellow-orange hyaline **198**

– Larger, 10–11 mm. Tergal discs shagreened to coarsely microreticulate, at most weakly shiny, with fine regular punctures or coarse 'crater punctures'. Tergal margins at most with their apical rims narrowly lightened hyaline brown **199**

198 Clypeus, scutum, and scutellum laterally shagreened, medially smooth and shiny (Fig. 88B). Restricted to temperate areas in northern Portugal and Spain ....***fulvago* (Christ)**

– Clypeus, scutum, and scutellum microreticulate and dull. Widespread across Iberia ....***hesperia* Smith**

199 Terga shagreened, weakly shiny, with fine and dense punctation. Tergal margins comparatively weakly depressed, with narrow tight apical white hair bands. Hind basitarsi dark. Throughout Iberia........ ....***hypopolia* Schmiedeknecht**

– Terga strongly microreticulate, with coarse 'crater punctures'. Tergal margins comparatively strongly depressed, with long loose white apical hair bands that exceed the length of the marginal areas. Hind basitarsi lightened orange. Restricted to high altitude sites (>1200 m) in the Pyrenees........ ....***ranunculorum* Morawitz**

200 Larger species, 12–14 mm, usually with abundant black, white, or brown pubescence, usually with entirely dark black facial hair. Ocelloccipital distance >2 times the diameter of a lateral ocellus. Terga always without apical hair bands, sometimes with lateral hair patches (*Melandrena* partim).... 201

– Smaller species, 9–10 mm, usually with subdued pubescence, facial hairs often pale, though dark in *A. lepida* and *A. propinqua*. Ocelloccipital distance often shorter, <2 times the diameter of a lateral ocellus. Terga with or without hair bands........**207**

201 Face and mesepisternum with long white pubescence, mesosoma dorsally with bright light brown pubescence. Univoltine, flying April-June. Restricted to temperate parts of northern Spain[27] ....***nitida* (Müller)**

– Without this pattern of pubescence; face either with extensive dark pubescence, or mesepisternum with dark pubescence, or mesosoma dorsally with dark pubescence........**202**

202 Body with only black and white pubescence **203**

– Body with at least some brown pubescence........**204**

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[27] Note, separation of *Melandrena* species in this group is usually made on the basis of colouration. However, these taxa are extremely variable, and certain characters that work in elsewhere in Europe do not work in Iberia. Caution should be taken; powerful genetic techniques are required to robustly delineate these species in an Iberian context.

203 Body typically more extensively dark haired, face and mesepisternum normally with entirely black hairs. T2–4 laterally with strongly contrasting dense patches of white pubescence[28] .... ***albopunctata* (Rossi)**

– Body often with extensive pale hairs, face sometimes white-haired with black hairs laterally, sometimes entirely black-haired. Terga often entirely black haired, laterally without dense patches of white pubescence. In pale forms, if T2–4 have loose white hair fringes laterally, then mesepisternum always white-haired[28] .... ***morio* Brullé**

204 Terga shagreened, obscurely punctate, with punctures disappearing into the underlying sculpture .... ***assimilis* Radoszkowski**

– Terga at most weakly shagreened, sometimes smooth and shiny, at least weakly shiny. Discs of T2–5 clearly and usually densely punctate, punctures typically separated by 1 puncture diameter **205**

205 Marginal areas of terga with narrow section of apical rim lightened hyaline-brown, tergal discs with weak bronzy reflections. Face with mixture of dark brown and black hairs .... ***nigroaenea* (Kirby)**

– Marginal areas of terga with apical rim dark, not lightened, tergal discs dark, without weak bronzy reflections. Face with uniformly black hairs **206**

206 Disc of T1 with dense punctures, punctures separated by up to 2 puncture diameters[29] .... ***limata* Smith**

– Disc of T1 with more scattered punctures, punctures usually separated by over 3 puncture diameters[29] .... ***thoracica* (Fabricius)**

207 A3 extremely short, at most 0.5 times the length of A4[30] **208**

– A3 longer, at least 0.8 times as long as A4, often as long as A4 .... **209**

208 Facial hair almost entirely black, with a few scattered light brown hairs around the antennal insertions. Clypeus densely punctate, punctures separated by 0.5 puncture diameters, underlying surface smooth and shiny. Widespread across Iberia .... ***lepida* Schenck**

– Facial hair intermixed light and dark. Clypeus more sparsely and irregularly punctate, punctures separated by 1–2 puncture diameters, underlying surface microreticulate and dull. Very rare, known only from one specimen from Cádiz .... ***rhypara* Pérez**

209 Genital capsule distinctive, elongate, basally narrowed (Fig. 92A). Tergal discs with punctation becoming sparser laterally, most clearly visible on T2 .... **210**

– Genital capsule otherwise. Tergal discs with uniform punctation **211**

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[28] These two species can be tricky to separate due to large colour variation within *A. morio* following the synonymy of the more extensively pale-haired *A. hispania*. Association with females should be made.

[29] These two species are very difficult to separate in the male sex, and positive determination is not possible in many cases.

[30] Note, male *Simandrena* are very difficult to identify; association should be made with females.

210 Face with predominantly dark hairs, with some light hairs intermixed around the antennal insertions. Scutum polished, shiny. Hind tarsi dark. Common throughout Iberia .... ***propinqua* Schenck**

– Face with entirely light hairs. Scutum shagreened and dull. Hind tarsi lightened orange. Restricted to temperate areas in northern Spain .... ***dorsata* (Kirby)**

211 Face with entirely bright pubescence, without any dark hairs laterally. Terga entirely smooth and shiny, without shagreenation .... ***combinata* (Christ)**

– Face with at least some dark hairs laterally. Terga often with shagreenation **212**

212 Terga entirely shagreened and dull to weakly shiny at most. Clypeus with fine granular shagreen, relatively shallowly punctate, medially with weak impunctate longitudinal midline. Discs of T2–4 densely punctate, punctures separated by 0.5 puncture diameters.......................... ***antigana* Pérez**

– Terga less strongly shagreened, weakly to strongly shiny. Structure of clypeus variable, from shagreened to smooth and shiny, more strongly and deeply punctate. Terga less densely punctate, punctures on discs of T2–4 separated by at least 1 puncture diameter **213**

213 Mesepisternum and propodeum with abundant black-brown hairs; remaining pubescence whitish. Scutum comparatively less strongly shagreened, weakly shiny. Restricted to areas close to the Pyrenees ....***thomsonii* Ducke**

– Mesepisternum, dorsum of mesosoma, and propodeum with bright yellowish pubescence, at most with occasional scattered black hairs. Scutum comparatively more strongly shagreened, dull.. **214**

214 Clypeus between the punctures smooth and shiny. Tergal discs without shagreen, smooth and shiny, clearly visible at the base of T2. More widespread across Iberia[31] .... ***congruens* Schmiedeknecht**

– Clypeus between the punctures shagreened, at most weakly shiny. Tergal discs shagreened, weakly shiny, most clearly visible on the base of T2. Restricted to the Pyrenees and Cantabrian Mountains[31]........................ ***confinis* Stöckhert**

215 (193) Genital capsule unique within the Iberian fauna (Fig. 92B). Restricted to the Pyrenees and Cantabrian Mountains ....***polita* Smith**

– Genital capsule otherwise **216**

216 Head elongate, only slightly wider than long. Clypeus shagreened and dull in its basal half, polished and shiny in its apical half (Fig. 54C). Mesepisternum laterally with long strongly plumose light brown hairs (Fig. 54A). Genital capsule simple, with penis valves progressively narrowing apically (Fig. 54F). Known only from south-western Spain (Cádiz, Sevilla), flying in the very early spring (January–March) .... ***ramosa* Wood**

– Combination of characters otherwise.. **217**

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[31] These two species are challenging to separate, and there may be taxonomic complexity in Iberia as well as across Europe. Further study is required.

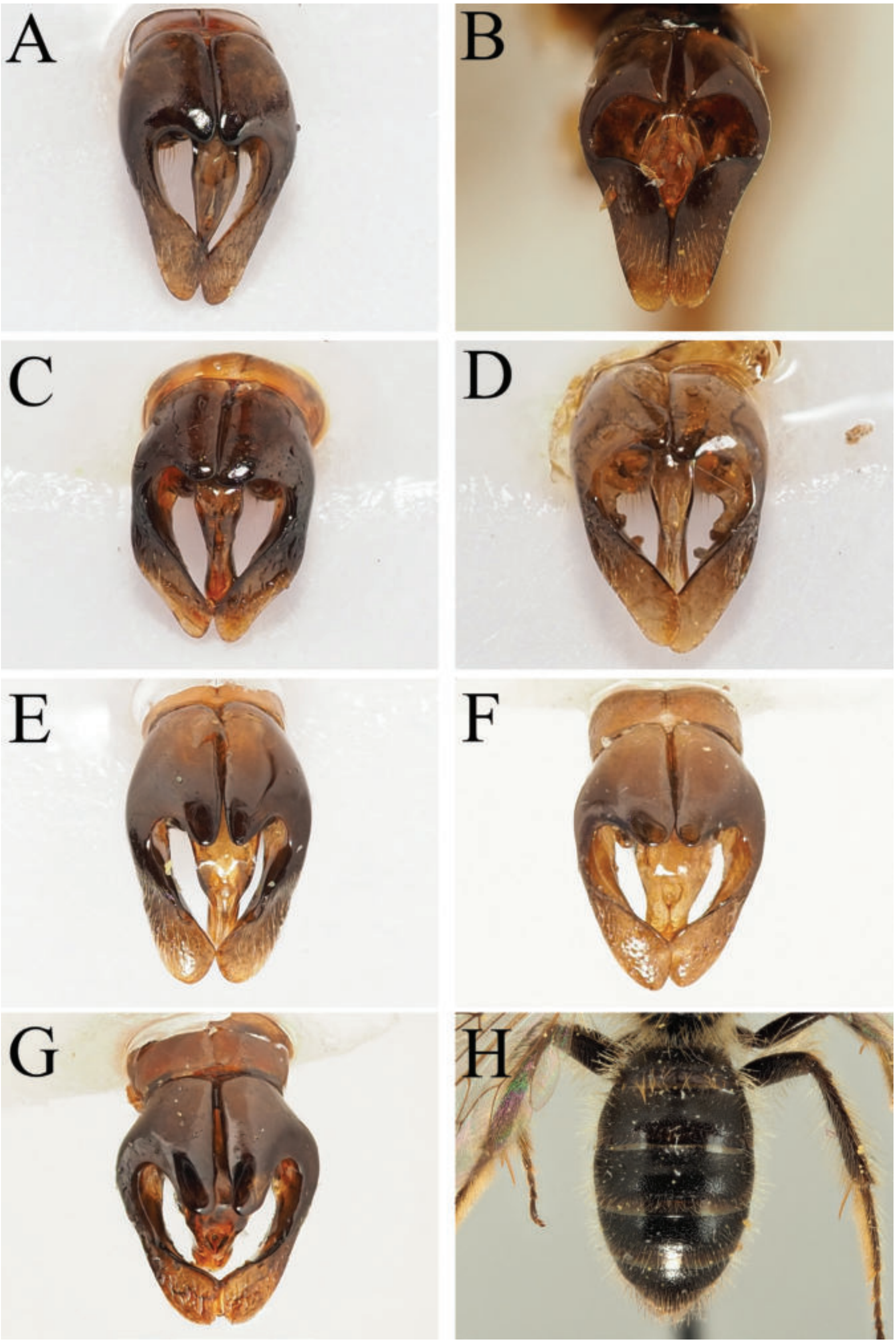

Figure 92. *Andrena* (*Simandrena*) *propinqua* Schenck, 1853, male **A** genital capsule, dorsal view; *Andrena* (*Ulandrena*) *polita* Smith, 1847, male **B** genital capsule, dorsal view; *Andrena* (*Euandrena*) *granulosa* Pérez, 1902, male **C** genital capsule, dorsal view **H** terga, dorsal view; *Andrena* (*Euandrena*) *bicolor* Fabricius, 1775, male **D** genital capsule, dorsal view; *Andrena* (incertae sedis) *corax* Warncke, 1975, male **E** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *parviceps* Kriechbaumer, 1873, male **F** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *argentata* Smith, 1844, male **G** genital capsule, dorsal view.

217 Clypeus domed, covered with dense network of coarse and strongly raised transverse wrinkles. Dorsolateral surface of propodeum with dense network of raised rugosity that is almost indistinguishable from the propodeal triangle, this network extending onto the lateral faces of the propodeum. Terga smooth and shiny with regular deep punctures, without a hint of shagreenation .... ***ampla* Warncke**

– Without this combination of characters **218**

218 Tergal margins distinctly depressed, depressions medially occupying 40% of the visible segment (Fig. 89C). Tergal discs densely punctate, punctures separated by 0.5–1 puncture diameters; tergal margins impunctate, lightened hyaline brown, strongly contrasting tergal discs. Margins of T2–4 basally with long whitish plumose hairs that arise from the junctions with the discs and overly the marginal areas without obscuring the underlying surface. Facial pubescence uniformly whitish. Terga often reddish laterally, view in profile .... ***hystrix* Schmiedeknecht** (*partim*)

– Without this combination of characters **219**

219 Penis valves narrow, more or less parallel-sided along their length (Fig. 92C, D; *Didonia* and remaining *Euandrena*) **220**

– Penis valves basally broadened, clearly wider basally than medially or apically (Fig. 92E–G) **225**

220 Head relatively elongate. Process of the labrum large, slightly wider than long. Clypeus domed, with large irregular punctures, punctures separated by 0.5–2 puncture diameters, with unclear impunctate longitudinal midline. In fresh specimens, terga with clear unbroken apical hair fringes. Bivoltine, March-April and again in June-July .... ***mucida* Kriechbaumer**

– Head less elongate. Process of the labrum smaller, more clearly wider than long. Clypeus more weakly domed, shiny to shagreened. Terga without apical hair fringes **221**

221 Apical margins of T1–5 widely lightened hyaline-yellow (Fig. 92H). Terga impressed basally and apically, thus tergal discs appear humped. Species associated with Cistaceae **222**

– Tergal margins at most with apical margins narrowly lightened yellowish. Tergal discs comparatively flat. Species not strongly associated with Cistaceae **223**

222 Base of terga and tergal margins comparatively strongly impressed, margins clearly separated from disc by a visible 'step' (Fig. 92H). Tergal discs coarsely and densely punctate, punctures separated by 2 puncture diameters[32] .... ***granulosa* Pérez**

– Base of terga and tergal margins comparatively weakly impressed, margins not clearly separated from discs by a visible 'step', almost level with discs medially. Tergal discs less densely punctate, punctures separated by 3–4 puncture diameters[32] .... ***vulpecula* Kriechbaumer**

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[32] These two species are difficult to separate morphologically. Comparison with confidently determined reference material should be made.

223 Gonostyli apically truncate, outer margin forming an acute point. A3 only slightly longer than A4. Pubescence entirely light brown with exception of occasional dark hairs laterally on the face. Restricted to temperate areas close to the Pyrenees..***rufula* Schmiedeknecht**

– Gonostyli with outer margin rounded, never forming an acute point. A3 visibly longer than A4..**224**

224 Light hairs on dorsal parts of mesosoma, terga and sterna yellowish white in fresh specimens. Erect hairs on disc of T4 usually predominantly dark. Facial pubescence often entirely dark. Bivoltine, can be recorded between March and August. Widespread across Iberia[33] ...... ***bicolor* Fabricius sensu lato** (two mitochondrial lineages are present in *A. bicolor*; to date, only the southern lineage has been found in Iberia)

– Light hairs on dorsal parts of mesosoma, terga and sterna snow white, without yellowish hue even in very fresh specimens. Disc of T4 at most with a few isolated, erect dark hairs. Face always with some grey-white hairs medially, at least between and around antennal sockets. Univoltine, April-June. Restricted to mountainous areas in northern and north-western Spain[33]...***allosa* Warncke** (note, the Spanish taxon may be distinct from populations in Central Europe)

225 Face medially with white hairs, laterally with clear line of black hairs along the inner margin of the clypeus. Genital capsule with outer margins of gonostyli weakly emarginate. Rare, restricted to the Pyrenees ....***gravida* Imhoff** (*partim*)

– Face entirely pale-haired, at most with scattered black hairs laterally. Genital capsule with outer margins of gonostyli straight, without emargination **226**

226 Terga very weakly shagreened, more or less smooth and shiny. Tergal discs with extremely scattered punctures, punctures separated by 3–4 puncture diameters or more. Genital capsule, see Fig. 92F...***parviceps* Kriechbaumer** (*partim*, dark form)

– Terga either more strongly microreticulate (at least on discs of T2–3) or clearly and densely punctate, punctures separated by 1–2 puncture diameters...**227**

227 Tergal discs finely microreticulate, with obscure and scattered punctures, punctures separated by 2–4 puncture diameters. Tergal margins with narrow broadly interrupted hair fringes apically.......................***barbilabris* (Kirby)**

– Tergal discs at most finely shagreened, more or less smooth and shiny, clearly and regularly punctate, punctures separated by 1–2 puncture diameters. Tergal margins with narrow interrupted or broad uninterrupted hair bands apically **228**

228 Tergal discs with punctures slightly sparser, separated by 2 puncture diameters. T2–4 apically with broad uninterrupted apical white hair bands, these

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[33] Note, the Spanish male of *A. allosa* is unknown, therefore this couplet is based on the key of Praz et al. (2019) for the Alps.

exceeding the length of the tergal margins and obscuring the underlying surface. Ocelloccipital distance equals the diameter of a lateral ocellus. Genital capsule, see Fig. 92G. Restricted to mountainous areas of central and northern Spain................................***argentata* Smith** (*partim*, large individuals)

– Tergal discs with punctures slightly denser, separated by 1 puncture diameter. T2–4 apically with widely interrupted narrow lateral hair fringes. Ocelloccipital distance equals 2 times the diameter of a lateral ocellus. Genital capsule, see Fig. 92E. More widespread in central and southern Iberia........ ....***corax* Warncke**

Discussion

At 228 species, the Iberian fauna is slightly larger than those of Greece (c. 220) and Israel (c. 220), though the fauna of Israel is likely to eventually be larger than that of Iberia following ongoing revisions (Pisanty et al. 2022a). Within the Old World fauna, it is much smaller than that of Turkey which has an estimated 376 species (Wood 2023b), but this is less surprising as Turkey is larger (783,000 km^2 versus 583,000 km^2), sits at the interface of Europe and Asia, hosts an even greater diversity of habitats, and is likely at the centre of diversity for this genus (Pisanty et al. 2022b). Iberia nevertheless hosts one of the top five largest *Andrena* faunas globally.

There are a number of outstanding problems that remain to be resolved, in addition to those highlighted above. Members of the subgenus *Avandrena* Warncke remain difficult to interpret due to their morphological variation and rarity in collections. *Andrena* (*Avandrena*) *avara* Warncke, 1967 sensu stricto was described from Morocco and also occurs in southern Iberia. Two additional subspecies were described from Spain, *A. avara gavia* Warncke, 1974 (*locus typicus* Madrid in central Spain) and *A. avara liturata* Warncke, 1974 (*locus typicus* Sierra de Guadarrama in central Spain), as well as two additional subspecies from North Africa. These may all represent valid species; molecular revision of this subgenus across the West Palaearctic is necessary to define species boundaries, and also to establish whether members of the *Avandrena* that lack spines on the posterior face of the hind femur truly belong here (Pisanty et al. 2022b). Many other groups have subspecies which Warncke described from Iberia, most pertinently *A.* (*Micrandrena*) *pandosa trigona* Warncke, 1975, *A.* (*Notandrena*) *langadensis albipila* Warncke, 1967, and *A.* (*Truncandrena*) *medeninensis donata* Warncke, 1967. These may also represent valid species, but without genetic data it is unwise to raise them to species status, as the results presented here illustrate that the relationships between Iberia, North Africa, and the rest of continental Europe are not always straightforward.

A total of 33 of the 228 *Andrena* species recorded here are endemic to the peninsula (14.5%). Twenty-two of the species are true Spanish endemics (9.6% endemic), whereas no species are endemic to Portugal. Of these 33 species, 31 of them were described after 1967 in just a handful of publications by a very limited number of authors (Warncke 1967, 1975a; Wood et al. 2020a, 2021, 2022a; Wood and Ortiz-Sánchez 2022; Wood 2022; the current work). Only the endemic *A. pruinosa* and *A. cyanomicans* (see Kratochwil 2021) were described earlier (Erichson 1835; Pérez 1895). The fact that so many of Iberia's endemic species have only been described recently makes it difficult to conclude on a likely final pattern of richness. As our ability to distinguish between cryptic taxa has increased, so has our ability to quickly travel to areas with unusual climates, botanical communities, or biogeographical histories. A defining characteristic of bees of the genus *Andrena* is their ability to very rapidly adapt their behaviours to local conditions over evolutionary time, be that in the use of a novel or locally abundant host plant, changing their emergence date or voltinism, or surviving in drier, wetter, hotter, or colder environments. This ability likely underpins their extremely high speciation rate (Bossert et al. 2022; McLaughlin et al. 2022). For example, species described from Iberia in just the last few years include those restricted to saline soils (*Andrena juliana*), a species which uses generic Brassicaceae species but which flies at the unusual time of December (*Andrena gades*), an early emerging taxon restricted to south-western Spain which has avoided capture until very recently due to its flight period of January–March (*Andrena ramosa*), a specialist of late-flowering Apiaceae which flies during September–October (*Andrena foeniculae*), and specialists of little-used botanical families such as Crassulaceae and Geraniaceae (*Andrena omnilaevis* and *Andrena erodiorum*). Altogether, this means that until all unusual habitats and mountainous areas have been thoroughly searched across the entirety of the bee season, new species are almost guaranteed to continue to be found.

It is possible however to comment more broadly on the biogeography of Iberian bees and notable distributional patterns. Warncke (1975a) identified four major biogeographic zones on the peninsula (excluding the Balearic Islands); a) north-western and northern Iberia from Coimbra to the Pyrenees, this area hosting Central European species, b) the northern *meseta* (*Meseta Norte*), or "Old Castille" (formerly known as Castilla la Vieja), the area of elevated open habitats north of the Sistema Central to the Cantabrian range, c) the southern *meseta* (*Meseta Sur*), or "New Castille" (formerly known as Castilla la Nueva) to the Ebro Valley, the lower area of open habitats south-east of the Sistema Central to the Ebro Valley, separated by the Sistema Ibérico, and d) the coastal zone from Coimbra in the west to Cádiz in the south up to Barcelona in the north-east, this area possessing a subtropical climate with hot summers and hosting Mediterranean taxa. These categorisations are broadly correct but do not fully capture the diversity of Iberian habitats and some of the patterns of endemism and micro-endemism. As a corollary, Warncke (1975a) writes that in the driest and warmest parts of Iberia some species have evolved into their own subspecies. It is worthwhile to highlight these areas in light of taxonomic developments in the intervening years.

The most substantial change since Warncke's (1975a, 1976) Iberian revision is the study of mountain refugia and their associated fauna. The Serranía de Ronda/Sierra de las Nieves and Sierra Nevada all host endemic *Andrena* species that have diverged from Iberian or from European/North African species (*A. contracta*, *A. ghisbaini*, *A. isolata*, and *A. ortizi*). The Sistema Central to the mountains in north-western Iberia (Serra do

Gerês, Cantabrian Mountains, etc) host endemic species that prefer cooler temperatures and are associated with herbaceous plants on acidic soil (*A. benoisti*, *A. gredana*, *A. omnilaevis*). In eastern Spain, the mountain ranges of the Sistema Ibérico, Sierra de Cazorla, and smaller ranges are understudied and support distinct species (*A. levante*) and subspecies whose status should be further investigated (*A. hattorfiana nigricauda* Wood, 2021). Because the eastern mountain ranges of Spain are somewhat isolated latitudinally, with intervening low elevation areas, it is likely that many of the species present here at elevation have experienced interrupted gene flow in their recent evolutionary history (e.g. subgenus *Taeniandrena*, Wood et al. 2021; Praz et al. 2022). The links between these montane populations should be investigated to establish their status. Members of the *A. intermedia* Thomson, 1870 aggregate may well be distinct, and populations present on the Sierra Nevada -> Sierra de Cazorla -> Sistema Ibérico -> Pyrenees may each represent a different species. Whether this pattern hold true for other groups requires further study.

The elevated plateau of central Spain clearly hosts relictual *Andrena* faunal elements. This is most clearly seen for two subgenera, *Nobandrena* Warncke, 1968 and *Parandrenella* Popov, 1958. *Nobandrena* consists of 10 species from Central Europe to Central Asia (western limit Switzerland), with one species endemic to central Spain (*A. funerea* Warncke, 1975), predominantly in the provinces of Ávila, Madrid, Salamanca, and Segovia. Likewise, *Parandrenella* consists of nine species from eastern Central Europe to Central Asia and Pakistan (European western limit is Slovenia, with an additional species in north-western Africa from Morocco to Tunisia; see Scheuchl et al. 2011, also Wood et al. 2020b), with one species endemic to central Spain (*A. taxana* Warncke, 1975), known only from the provinces of Cuenca, Madrid, and Soria. *Andrena funerea* and *A. taxana* therefore represent what must have been a broader distribution for these subgenera prior to the Quaternary period, both subgenera having estimated crown ages of around 10 million years (Pisanty et al. 2022b).

More broadly, Iberia hosts several predominantly eastern species in steppic or dry areas, such as *A. lateralis* (Spain and Portugal, southern Balkans to the Central Asia), *A.* (*Melandrena*) *soror* Dours, 1872 (Spain, Morocco, Turkey), and *A. urdula* (Spain, Morocco, and Greece). Iberia has strong faunal links to Morocco, and particularly the Middle Atlas. Due to the nature of European mountain chains, outside of Iberia, raised steppic areas are rare or cover only very small areas. In Central Spain, Morocco, and Turkey, extensive raised areas (the *mesetas* of Old and New Castille) of steppic habitat can be found. This elevated steppe differs from the Great Eurasian Steppe that runs from the Pannonian basin (predominantly eastern Austria, Hungary, southern Slovakia, western Romania, northern Serbia) to Mongolia and northern China, and hosts a fauna that supports the same evolutionary lineages (e.g. *Nobandrena* and *Parandrenella*), but often contains different species, many of which are endemic. This link between Iberia and Morocco can be seen particularly strongly in the Middle Atlas. In addition to the finding of *A. relata* in the Middle Atlas (Wood et al. 2020b), another species previously considered to be endemic to Spain, *A. nebularia*, can be found on the high steppe in the eastern Middle Atlas. This link to the Middle Atlas can also be seen on the Sierra Nevada for *A. isolata* and *A. ortizi* which are genetically most closely related to what are undescribed species in the Middle Atlas. Additional genetic work and further surveys in the Middle Atlas are likely to strengthen these links further, as well as further surveys on the Sierra Nevada and the mountains of southern Spain.

The extraordinary nature of central Spain and its rich *Andrena* fauna is well-illustrated by both historical (particularly those of Dusmet that were revised by Warncke 1975a, 1976) and recent collections. During a single eight-day period from the 13th to 19th of May 2021 in the provinces of Ávila, Guadalajara, Madrid, Segovia, and Toledo I collected a total of 70 *Andrena* species, including the Iberian endemic *A. baetica*, *A. benoisti*, *A. corax*, *A. elata*, *A. funerea*, *A. lecana*, *A. murana*, *A. parata*, *A. pruinosa*, and *A. varuga* and also the restricted *A. lateralis*, *A. monilia*, *A. nebularia*, *A. soror*, *A. relata*, and *A. urdula*. Whilst large parts of the Sistema Central mountain range are protected as nature reserves or regional parks, the same is not true for the steppe habitats at lower altitudes, both north and south of this mountain range. Most collecting sites were habitat fragments sandwiched between urban development or intensive agriculture, though some formed a mosaic with land under a lower-intensity management regime. The areas south of Madrid that were so extensively collected by Dusmet and which represent the *loci typici* for many of the species described by Warncke have either been lost to urban development or are threatened by its encroachment (e.g. *Andrena montarca* was described from Montarco which is now a suburban park). Given the endemic nature of this fauna, these areas are deserving of a greater level of protection than they currently receive.

Away from central Spain, there are more obvious links between southern Spain and the North African *Andrena* fauna. Warncke (1976) recorded three predominantly North African taxa in the extreme south of Spain, specifically *A.* (*Notandrena*) *microthorax* Pérez, 1895 (Cádiz), *A.* (*Truncandrena*) *minapalumboi* Gribodo, 1894 (Cádiz, Alicante), and *A. rhypara* (Cádiz). I have seen no other material of these species, and their current status in Spain is unclear; they may be locally extinct. In contrast, recent workers have discovered three North African species in southern Spain, namely *A.* (*Truncandrena*) *varia* Pérez, 1895 (Córdoba; Ortiz-Sánchez 2020), *A. laurivora* (Huelva and Sevilla; Wood et al. 2021), and *A. melacana* (Albacete, Cádiz, Granada, Málaga; Wood and Ortiz-Sánchez 2022). Given the lack of historical and contemporary collecting in southern Spain, it is very difficult to answer whether or not these species were always present, whether the newly detected species are recent arrivals, or whether there is a constant turnover of North African species in southern Spain that regularly colonise and then become locally extinct. Increased recording of *Andrena* specifically and Iberian bee species more broadly is required in order to better understand faunal interchanges across the Strait of Gibraltar.

Finally, the difference between the size of the Portuguese (128) and Spanish (228) *Andrena* faunas is large and notable. Though Portugal has a higher density of *Andrena* species due to its much smaller size, it hosts no endemic *Andrena* species compared to the 22 species endemic to mainland Spain. As highlighted above, the Portuguese

Andrena fauna is so much smaller due to the almost complete absence of high northern mountains and their associated Euro-Siberian fauna (the Serra da Estrella reaches to 1,993 m but is isolated from the high Cantabrian Mountains of northern Spain), the lack of elevated steppe (limited to north-eastern Portugal around Almeida or the Douro valley), the lack of high mountains in the south (the Sierra de las Nieves reaches 1,919 m and the Sierra Nevada 3,479 m), and finally the absence of the very hot and dry Mediterranean habitat from Cádiz to Alicante and Valencia that hosts both North African species as well as restricted endemic species. When taken collectively, it is this enormous variety of habitats, isolated mountains, and Atlantic and Mediterranean influences that has shaped and generated the rich Iberian *Andrena* fauna, and continues to provide taxonomic surprises and ecological delights.

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Supplementary material 1

Iberian *Andrena* species checklist

Authors: Thomas J. Wood

Data type: National checklist

Explanation note: Iberian *Andrena* species checklist, with national totals for Portugal and Spain, details on *loci typici* for species described from Iberia, and dietary niche classifications.

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SHORT COMMUNICATION

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Resident parasitoids associated with Drosophilidae in Michigan tart cherry orchards and woodland edges

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Abstract

Knowledge of the distribution and abundance of resident parasitoid species of *Drosophila* flies constitutes an important base for developing and implementing a biological control program for *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), an invasive pest that attacks ripening thin-skinned wild and cultivated berries and stone fruits. For this purpose, a field survey was conducted to identify the parasitoid community associated with *D. suzukii* infested sites in tart cherry orchards and woodlots in west, northwest, and central Michigan. Sentinel traps baited with *D. suzukii* larvae and pupae in banana slices were deployed in the center of tart cherry orchards, in woodlots adjacent to tart cherry orchards, and in woodlots isolated from any known commercial host of *D. suzukii*. Traps were placed from the beginning of July to the end of October 2021. Three parasitoid species that are known to use drosophilids as hosts were recovered from these traps. *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae) and *Leptopilina boulardi* Barbotin, Carton & Keiner-Pillault (Hymenoptera: Figitidae) emerged from the infested bananas. *Leptopilina heterotoma* (Thomson) was collected as an adult in a sentinel trap. Among these wasps, only *P. vindemiae* successfully parasitized *D. suzukii* pupae in the laboratory. This pupal parasitoid was abundant and widely distributed in both cherry orchards and woodlots. The highest number of *P. vindemiae* was collected from orchards, followed by woodlots adjacent to orchards, with woodlots without nearby cultivated fruit having the lowest detections. These findings suggest that future release of augmentative or classical biological control agents for *D. suzukii* could be successful in orchards postharvest to control late-season populations of this pest.

Keywords
biological control, sentinel trap, spotted wing drosophila, wasp

Introduction

Since its first detection in Michigan in 2010, spotted-wing *Drosophila*, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), has rapidly become the number one pest of small fruits and cherries in Michigan. Due to a zero tolerance for detectable larvae in these fruits, growers have relied almost entirely on calendar-based spray programs to protect their valuable crops from *D. suzukii* damage prior to harvest (Van Timmeren and Issacs 2013). These intensive spray programs target the adult flies but have also disrupted existing IPM programs developed for other insect pests, with potential cascading effects on the environment, especially non-target organisms (Tait et al. 2021). Moreover, these high-input control strategies are costly for growers, particularly those that are growing processing fruits with a lower profit margin such as tart cherry. All these factors have motivated researchers to search for effective and environmentally sustainable long-term solutions to prevent crop damage by *D. suzukii*.

Biological control is a vital component of an IPM strategy of invasive insect pests (Lee et al. 2019) and remained unutilized in the framework of *D. suzukii* management until recently (Gabarra et al. 2015; Woltz et al. 2015). Explorations for potential classical biological control agents in Japan, South Korea, and China, where *D. suzukii* is native or endemic, found three dominant larval parasitoids that predominately attack *D. suzukii*: *Asobara japonica* Belokobylskij (Hymenoptera: Braconidae), *Ganaspis brasiliensis* (Ihering) and *Leptopilina japonica* Novkovic & Kimura (Hymenoptera: Figitidae) (Wang et al. 2020a). In addition, over 50 frugivorous drosophila parasitoids have been reported worldwide, and several common larval drosophila parasitoids in the Americas and Europe have been evaluated against *D. suzukii* with most of them failing to develop from this host due to its strong host immune defense (Wang et al. 2020b). In the meantime, both *G. brasiliensis* and *L. japonica* have been unexpectedly detected in British Columbia, Canada and the state of Washington outside their presumed native range of Asia (Abram et al. 2020).

Of the known pupal parasitoids of drosophilids, two have been found to attack and develop successfully from *D. suzukii*: *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae) and *Trichopria drosophilae* Perkins (Hymenoptera: Diapriidae) in Spain (Gabarra et al. 2015), Italy (Miller et al. 2015), Mexico (Garcia-Cancino et al. 2020), California (Wang et al. 2016), and Oregon (Miller et al. 2015). Both species are cosmopolitan and readily parasitize *D. suzukii* pupae inside fruit as well as in soil (Wang et al. 2016).

In comparison, information is currently lacking regarding the composition and distribution of resident parasitoid species of Drosophilidae in Michigan. This knowledge is important for the implementation of biological control against *D. suzukii*, especially prior to classical biological control agent releases. Moreover, this information will also aid in determining any possible non-target effects of parasitoids new to this region, with potential spillover effects to other Drosophilidae as well as potential interactions among resident and future introduced parasitoids (Hougardy et al. 2020). Thus, the objective of our survey was to determine the presence and biological control status of resident parasitoid populations in Michigan cherry orchards and natural habitats using sentinel banana traps infested with larvae or pupae of *D. suzukii* as hosts, in support of the development of biological control programs that may include future augmentative releases of parasitoids to suppress populations of *D. suzukii*.

Material and methods

Insect colony

A *D. suzukii* colony was established, originating from adult flies collected from infested cherry fruit from a commercial orchard near South Haven, Michigan during the summer of 2020. The colony was maintained on a standard solid cornmeal diet (Dalton et al. 2011) in 50 ml polystyrene vials (Genesee Scientific, CA) in a growth chamber set to 22 °C, 45% relative humidity (RH), and a 16:8 (L:D) photoperiod.

Preparation of sentinel traps

Larval and pupal parasitoids of *D. suzukii* were sampled using sentinel traps described by Miller et al. 2015 with some modifications. About 20–24 fresh banana slices (2–3 cm thick, 20–25 g total) were exposed to 300 to 400 adult *D. suzukii* in a white mesh cage (34 × 34 × 61 cm with a vinyl window, BioQuip Products, Compton, CA) in a rearing room kept at 22 °C and 55% RH, with a 16:8 (L:D) photoperiod. These flies were allowed to oviposit directly onto the banana slices for 2–3 days. Afterwards, each infested banana slice was transferred into a plastic cup (118 ml) with a small piece of sponge (2 × 4 × 5 cm) at the bottom to absorb excess liquid and a piece of paper towel lining the sides of the cup to provide pupation sites. Each cup was then covered by a lid with a hole (2.5 cm diam.) in the center plugged with a foam plug (Genesee Scientific, San Diego, CA) for air exchange. Half of the cups were kept in the rearing room for 4–5 days, allowing larvae to develop into the pupal stage; the other half were held in a growth chamber at 13 °C and 55% RH, with a 16:8 (L:D) photoperiod to slow larval development and ensure there would be first or second instar stages present when deployed in the field. Prior to field deployment, lids with plugs were replaced with lids modified with a 4 cm diameter opening covered with a piece of nylon mesh (mesh opening: 830 micron, 55% open area; Component Supply, Sparta, TN) through which parasitoids could pass while adult *D. suzukii* were kept inside based on the laboratory observation. All sentinel traps consisted of a pair of these sentinel trap cups, each with a banana slice infested with *D. suzukii* larvae or pupae, placed in an orange delta trap (Great Lakes IPM, Vestaburg, MI) which served as a shelter in the field.

Sampling locations and duration

The survey was carried out at 3 sites in west Michigan, 7 sites in central Michigan, and 6 sites in northwest Michigan, with a total of 26 sentinel traps deployed (see Suppl. material 1). Nine traps were deployed at the edge of woodlots, not adjacent to any tart cherry orchards, instead surrounded by corn and/or soybean fields. The remaining traps were deployed either all within or adjacent to tart cherry orchards. Each site was at least 280 m apart from any other site being monitored in this study. At 3 cherry orchards in west Michigan, however, two traps were placed in or adjacent to cherry orchards to compare wasp capture in these habitats. Here, one trap was placed in the center of the orchard, and the other was placed at the edge of an adjacent woodlot at least 60 m apart. Traps in central and west Michigan were deployed on 9 July and taken down on 15 October 2021. In northwest Michigan, nine sentinel traps were deployed in 9 different natural habitats containing wild mulberry, raspberry, blackberry, pin cherry, and/or honeysuckle, all directly adjacent to tart cherry orchards, from 22 July to 15 September 2021. All sentinel cups in each trap were collected and replaced weekly.

Rearing and identifying parasitoids

After one week in the field, sentinel cups from west and central Michigan were transported back to the rearing room at Michigan State University campus and carefully examined for possible trapped adult parasitoids before their lids were switched to those with foam plugs described as above to prevent exit or entry of any insects. Four weeks later, cups were examined every couple days, for up to 2 weeks, and all parasitoids emerged were collected and counted. Representative morphospecies of emerging parasitoids were collected using an aspirator and identified to their family or genus level, then presented with numerous 1–2 instar larvae or at least 20 pupae of *D. suzukii* reared in a diet for oviposition for 4 days to test their ability in parasitizing these *D. suzukii* life stages. In the meantime, voucher specimens emerged from sentinel cups were placed in 70% ethanol before being sent to Dr. Matthew Buffington (USDA-ARS, Beltsville, MD) for species identification.

Sentinel cups collected from northwest Michigan were transported to a laboratory at the Northwest Michigan Horticulture Research Center in Traverse City and assembled in the same way described as above. Once wasps started to emerge, these cups were delivered to campus of Michigan State University for identification and ovipositional tests, however the number of emerging wasps over time was not counted; only the presence or absence of wasp species was recorded.

Statistical analysis

Wasp emergence over a 14-week sampling period from sentinel traps in Michigan was combined and square root transformed to meet assumptions of normality and homoscedasticity (SAS Institute 2021). An ANOVA compared the numbers of *P. vindemiae* emerged: 1) between 5 traps in orchards vs. 12 traps at the edge of woodlots, and 2) between 3 traps in woodlots adjacent to orchards vs. 9 traps from woodlots without adjacent orchards (SAS Institute 2021). Analysis was not possible on any other species captured due to insufficient sample size.

Results

In total, 1 adult parasitoid was captured, at least 1876 parasitoids were reared out from the sentinel cups. Three species of parasitoids were either found in traps or emerged from cups baited with sliced banana infested with drosophila larvae or pupae: *Pachycrepoideus vindemiae* Rondani (Hymenoptera: Pteromalidae), *Leptopilina boulardi* Barbotin, Carton & Keiner-Pillault, and *Leptopilina heterotoma* (Thomoson) (Hymenoptera: Figitidae). Large numbers of *P. vindemiae* and *L. boulardi* emerged from sentinel cups within 3–4 weeks after initial field collection. *Pachycrepoideus vindemiae* was present in all trapping sites, but *L. boulardi* was only found in northwest Michigan. A single specimen of *L. heterotoma* was found in a sentinel cup immediately following field collection in a commercial cherry orchard in west Michigan.

The first emergence of *P. vindemiae* was from sentinel traps deployed at central Michigan sites during the week of 23 July. This species was abundant both in west and central Michigan throughout the sampling period (Fig. 1) and present in all 26 sentinel traps including those deployed in the northwest region at least once during the survey period. In total, 1319 *P. vindemiae* emerged from sentinel traps at sites in west Michigan compared to 557 *P. vindemiae* in central Michigan. Sentinel traps placed in orchards had significantly higher *P. vindemiae* emergence than those in the woodlots ($F_{1,15} = 5.14$, $P = 0.04$) (Fig. 2A). Woodlots adjacent to orchards had significantly more *P. vindemiae* emerged than woodlots without cherry orchards nearby ($F_{1,10} = 7.83$, $P = 0.02$) (Fig. 2B).

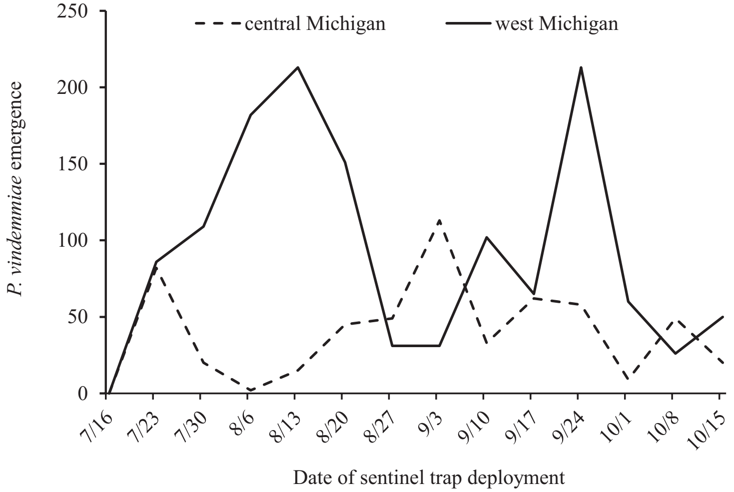

Figure 1. Total *P. vindemiae* emergence from weekly *D. suzukii* pupal sentinel traps in west Michigan (n = 6) and central Michigan (n = 11).

Pachycrepoideus vindemiae successfully reproduced using *D. suzukii* pupae as its host under laboratory conditions. Hundreds of *L. boulardi* emerged from sentinel cups deployed in the northwest region, but none of them were able to reproduce on *D. suzukii* larvae.

Discussion

This survey presents the first baseline data on the current field presence and seasonal occurrence of resident parasitoids of Drosophilid flies in Michigan. As expected, *P. vindemiae* was abundant and prevalent in Michigan since it attacks other pupae of many Dipteran fly families including Drosophilidae (Wang et al. 2004; Rossi Stacconi et al. 2013; Miller 2015). Under controlled and optimal laboratory conditions, females of this species are capable of parasitizing nearly 600 *D. suzukii* pupae during their lifetime (Bezerra Da Silva et al. 2019). However, a field survey revealed low levels of

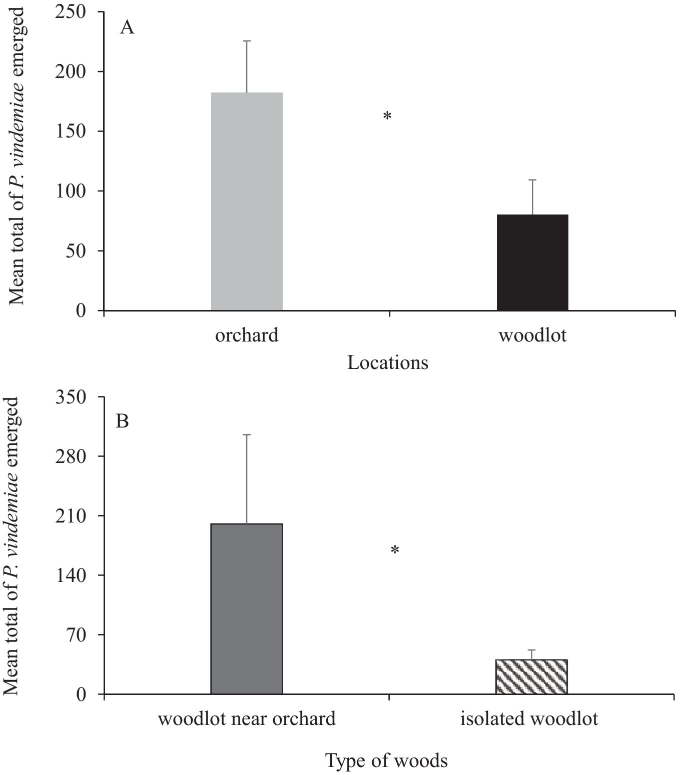

Figure 2. Mean total numbers of *P. vindemiae* (+SEM) emerged during a 14-week sampling period between sentinel traps placed in orchards vs. in woodlots regardless of orchards nearby (**A**), and between sentinel traps placed in woodlots adjacent to orchards and in those without orchards nearby (**B**). Asterisk indicates a significant difference between trap locations (P < 0.05).

parasitism of *D. suzukii* pupae in both North America and Europe (Lee et al. 2019; Wang et al. 2021), likely due in part to its relatively wide host range (Wang et al. 2021).

Larval parasitoids such as *L. boulardi*, *L. heterotoma*, and *Asobara tabida* (Nees) are important natural enemies of many endemic Drosophilidae species, but rarely successfully parasitize *D. suzukii* larvae (Girod et al. 2018). Although, hundreds of *L. boulardi* emerged from sentinel traps originally baited with *D. suzukii* larvae in northwest Michigan, none of them successfully reproduced on *D. suzukii* in the laboratory due to a strong immune response by the host. This indicates that other drosophilid species re-colonized *D. suzukii* infested banana slices, attracting larval parasitoids such as *L. boulardi* and *L. heterotoma* for oviposition. Indeed, other Drosophilidae including *D. melanogaster* were observed emerging from some of the sentinel traps after being incubated in the laboratory.

One potential reason why *D. suzukii* is so destructive to cultivated fruit crops is the absence of a significant natural enemy in invaded regions. Recently, *G. brasiliensis*, a species-specific larval parasitoid imported from Asia (Daane et al. 2016; Giorgini et al. 2019) that attacks early instar *D. suzukii* larvae (Wang et al. 2018), has been approved for release in Michigan as a classical biological control agent. While it is expected to take time for new natural enemies such as *G. brasiliensis* to suppress *D. suzukii* populations, resident pupal parasitoids such as *P. vindemiae* and *T. drosophilae* could play an important role through augmentative releases in combination with releases of new natural enemies. Interestingly, *P. vindemiae* has recently been found to parasitize and successfully develop on all preimaginal stages of *G. brasiliensis* (Hougardy et al. 2022), which could also potentially affect the establishment and success of *G. brasiliensis*.

Importantly, *P. vindemiae* was found most abundantly within cherry orchards after harvest, suggesting that they can navigate this agroecosystem despite presumable remnants of chemical applications commonly present in these systems. However, this may also imply that they are present during the growing season when regular insecticide applications are applied, suggesting possible disruption of this biological control from chemical exposure. More information is needed to elucidate the effects of pesticide, both in-season and post-harvest, on the success of current and future biological controls for *D. suzukii*. Additionally, *P. vindemiae* was more commonly associated with woodlots adjacent to cultivated cherry, likely because *D. suzukii* and other *Drosophila* populations are higher in areas with greater access to host fruit. This study serves as baseline information for the resident parasitoid community of Drosophilidae in the tart cherry agroecosystem and provides guidance on landscape factors that influence establishment of future augmentative and classical biological control releases.

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Supplementary material 1

Endemic parasitoids associated with Drosophilidae in Michigan tart cherry orchards and woodland edges

Authors: Juan Huang, Heather Leach, Matthew Buffington, Nikki Rothwell, Julianna K. Wilson

Data type: table (docx. file)

Explanation note: The location and description of each sentinel trap.

Link: https://doi.org/10.3897/jhr.96.103160.suppl1

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RESEARCH ARTICLE

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Genetic variation and phylogenetic relationships of commercial populations of *Bombus ignitus* (Hymenoptera, Apidae) with wild populations in Eastern Asia

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Abstract

The bumblebee, *Bombus ignitus* (Hymenoptera, Apidae), plays a vital role in pollination in Northeast Asia, including Korea, China, Japan, and Far East Russia. Understanding the genetic makeup of the population can aid in its conservation. This study explores the DNA barcode region of cytochrome C oxidase subunit I (COI) of *B. ignitus* in commercial populations from Korea and Japan. The results reveal low intraspecific genetic diversity among commercially reared populations, with a maximum sequence divergence of 0.3%. Analysis of a 458-bp region of the COI gene, including 384 previously reported sequences, identified 20 haplotypes with the highest sequence divergence of 2.01% in East Asia. Commercial populations show a genetic similarity primarily with the Japanese population. Cross-mating with native populations could result in competition and genetic contamination, leading to reduced fitness and sensitivity to future environmental conditions. Morphological similarities make monitoring of such effects challenging. This study provides a basis for further research on population studies, conservation, and commercialization of local populations of *B. ignitus* for better pollination services while minimizing risks of reducing genetic diversity and increasing competition between native and introduced populations.

Keywords

Bombus ignitus, Bumblebee, COI, wild populations, commercial population

Introduction

Bumblebees, play a critical role in pollinating many agricultural crops (Grixti et al. 2009; Hou et al. 2009). *Bombus ignitus* is an important pollinator species throughout its distributional range, including Korea (Yoon et al. 1999), China (An et al. 2010; Zhang et al. 2018) and Japan (Asada and Ono 2000) where it is used commercially in pollination of greenhouse plants (Cooley and Vallejo-Marin 2021). It plays a significant role in the pollination of various crops such as tomatoes, strawberries, and blueberries (Toni et al. 2020). The decline of *B. ignitus* populations could have adverse effects on agricultural production and ecosystem health in Korea, highlighting the need for conservation measures. However, *B. ignitus* populations in Korea are threatened by various factors, including habitat loss, fragmentation, and pesticide exposure (Carvell et al. 2006; Wu et al., 2010). Furthermore, the introduction of non-native bumblebees such as *B. terrestris* for pollination purposes has further exacerbated the decline of the species through competition for food, spread of diseases, and hybridization with native populations (Dimou et al. 2008; Whittington et al. 2004; Ings et al. 2005; Kanbe et al. 2008; Tsuchida et al. 2019; Keum et al. 2020). These negative impacts have led some countries to ban the introduction of foreign bumblebee species and promote the use of local pollinators instead (Velthuis and Doorn 2006).

Maintaining genetic diversity in local populations is essential for survival and fitness in different environmental conditions, such as climate changes and food availability (Kawecki and Ebert 2004). Inbreeding can occur in populations with lower genetic diversity, leading to inbreeding depression and reduced fitness, including lower reproductive rates, slower growth rates, and less flexibility in adapting to different environmental conditions (Zayed and Packer 2005). Failure to adapt could ultimately lead to extinction. Therefore, knowledge of genetic diversity and geographic relationships of *B. ignitus* is crucial for long-term conservation, artificial selection, and the development of effective conservation strategies (Lee et al. 2006; Goulson et al. 2008; Zayed 2009; Whitehorn et al. 2009; Goka 2010; Habel et al. 2014).

Mitochondrial DNA is inherited maternally and characterized by a relatively fast mutation rate. It exhibits high genetic variation between related species and low intraspecific variation (Moritz et al. 1987). Among mitochondrial genes, Cytochrome oxidase subunit I (COI) has emerged as the most interesting and widely used gene due to its lower mutation rates and high incidence of nucleotide substitution at the third codon position compared to other protein-coding genes (Yi et al. 2002; McClellan 2000). Prior studies have demonstrated that Japanese populations of *B. ignitus* form a distinct clade that is genetically divergent from Korean and Chinese populations, using COI and microsatellites (Shao et al. 2004; Tokoro et al. 2010; Oh et al. 2013). Additionally, Han et al. (2018) used DNA barcoding part of COI to determine that the original stocks of commercially bred *B. ignitus* in Belgium were from Japan. This study aims to assess the genetic diversity of commercial populations of *B. ignitus* in Korea and Japan and explore the phylogenetic relationships between these populations and wild East Asian populations of *B. ignitus* using both newly collected samples and previously deposited sequences in GenBank. Understanding the genetic diversity and relationships between populations, is helpful to develop strategies for conservation, artificial selection and improving the fitness of *B. ignitus* populations in the face of environmental changes.

Materials and methods

Sample collection

In this study 35 worker bees (one individual from each colony) were collected from three different commercial populations of *B. ignitus* in South Korea and Japan. All populations were acquired from Biobest (Belgium) between 2017 and 2018, as presented in Table 1. Voucher specimens were stored at -20 °C in 100% ethanol until DNA extraction. All analyzed samples are stored in ethanol and deposited in the insect collection of Andong National University, South Korea.

DNA extraction, primer, PCR, and sequencing

Total DNA was extracted from the hind leg of each of the 35 samples using the DNeasy Blood and Tissue kit (Qiagen, Germany). We used Polymerase Chain Reaction (PCR) to amplify a 658-bp region of the COI gene that corresponds to the "DNA Barcode" region (Herbert et al. 2003). The universal primer set LCO-1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO-2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Flomer et al. 1994) was used in the PCR reaction, and AccuPower PCR PreMix (Bioneer, Daejeon, Korea) was used as the PCR master mix.

Thermocycler conditions consisted of initial denaturation step for 5 minutes at 95 °C, followed by 35 cycles of denaturation at 95 °C for 30 seconds, annealing at 52 °C for 30 seconds, and extension at 72 °C for 30 seconds, and a final extension step for 5 minutes at 72 °C. Sequencing was performed commercially by BIONICS (Seoul, South Korea). All sequences were generated in both directions by Sanger sequencing.

Sequence analysis and genetic diversity estimates

The consensus sequence was assembled from forward and reverse sequences using BIOEDIT v7.0.5.2 (Hall 1999) and all sequences were aligned in MEGA7 (Kumar et al. 2016) using ClustalW. COI sequences of this study have been archived on the GenBank under accession numbers MN022949–MN022985 and MN423343–MN423360 (Table 1, Suppl. material 1: appendix S1).

The within-locality diversity estimates in terms of haplotype diversity (H), mean number of pairwise differences (MPD), and nucleotide diversity (π) which reflect genetic diversity within each locality were analyzed for commercially reared populations of *B. ignitus* based on 658 bp of COI sequences using DNAsp v5 (Librado and Rozas 2009). Because commercial populations are isolated from each other and even from wild populations, we did not calculate the pairwise fixation indices and migration rates.

Table 1. Sampling information of the *B. ignitus* and GenBank accession numbers.

Locality	No. of samples	Accession No.
Commercial – Korea A* (BIKOA1–BIKOA15)	15	MN022949-58, MN022981-85
Commercial – Korea B* (BIKOB1–BIKOB10)	10	MN022959-68
Commercial – Japan** (BIJA01–BIJA10)	10	MN022969-76, MW080642-3

* Commercial stocks imported from a Belgian company and kept in Korea. ** Commercial stocks imported from a Belgian company and kept in Japan.

Network construction

In order to evaluate the phylogenetic relationship between commercial and wild populations of *B. ignitus*, all previously reported *B. ignitus* COI sequences in the nucleotide database of the National Centre for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov) were also included in our analysis. Only sequences that overlapped part of the gene by 458 bp were selected for analysis. To construct the most reliable haplotype network, all frequencies of the sequences in Tokoro et al. (2010) were included (Suppl. material 1: appendix S2). The final dataset included 419 sequences, consisting of 35 from the present study and 384 from GenBank (Suppl. material 1: appendix S1).

Since *B. terrestris* is closely related to *B. ignitus* (Cameron et al., 2007), this species was used as an outgroup to root the tree. The evolutionary distances between haplotypes were calculated using Kimura's 2-parameter model (Kimura 1980) implemented in MEGA7 (Kumar et al. 2016). Bayesian analyses were conducted in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2011), using the HKY+G mutation model which were selected by jModeltest 2.1.10 (Darriba et al. 2012). The analyses were performed for 5×10^6 generations, with four chains each. Trees were sampled every 500 generations with 25% burn-in. A haplotype network was constructed using median-joining method (Bandelt et al. 1999) in Network software version 5.0.0.1 to infer the relationships among haplotypes and their geographical distribution.

Results

Sequence analysis and genetic diversity estimates

The Commercial-Japan population was found to have no genetic diversity, as all ten individuals possessed the same haplotype (H9). Although most individuals of Commercial-Korea A and Commercial-Korea B possessed H9 haplotype, two more haplotypes occurred. In terms of π and HD, all three localities displayed low estimates and the highest nucleotide diversity (π = 0.00058) and haplotype diversity (HD = 0.362) were found in Commercial-Korea A population and the estimates of Commercial-Korea B (π = 0.00031) was as low as nearly half of that obtained from Commercial-Korea A (Table 2).

Table 2. Within locality diversity estimates in commercially reared populations of *B. ignitus* based on 658-bp partial COI gene.

Locality	N	NH	HF	HD	NP	MPD	π
Japan	10	1	H9, 1.0	–	–	–	–
Korea A	15	3	H5, 0.067; H9, 0.8; H11, 0.13	0.362	2	0.3809	0.00058
Korea B	10	2	H9, 0.9; H5, 0.1	0.2	1	0.2	0.00031

– Zero estimates were obtained either by one haplotype or by in individual from corresponding locality; N: number of sampled individuals; NH: Number of haplotypes; HF: Haplotype frequency; HD: Haplotype diversity; NP: Number of polymorphic sites; MPD: Mean number of pairwise differences; π: Nucleotide diversity

Genetic variation based on 458-bp of COI gene

A total of 20 haplotypes was obtained from 419 studied sequences (Suppl. material 1: appendix S3). The most divergent haplotypes (H18 versus H2) differed by 9 substitutions (2.01%) across the 458-bp sequence region (Suppl. material 1: appendix S3). The highest within country genetic distances were found in China (8 substitutions) followed by 4 substitutions in Korean and Japanese and 2 within Belgian commercial haplotypes. Sequence alignments revealed 17 variable sites; of these, 13 substitutions (76.5%) were transitions (A↔G, C↔T), whereas four (23.5%) were transversions (three T↔A switch and one G↔C switch) (Suppl. material 1: appendix S2, S3).

Phylogenetic and Haplotype analysis

Upon analyzing a 458 bp segment of the COI gene, eight haplotypes from South Korea were identified. Five haplotypes were exclusive to Korean populations, while six were exclusive to Japanese populations. Haplotypes 1 and 4 were shared between Korean and Chinese wild populations, and haplotype 5 was shared between Korean populations and two Belgian commercially reared populations (Table 2, Suppl. material 1: appendix S2). Additionally, four haplotypes were exclusive to Chinese populations, and one haplotype was shared between Japanese and Belgian populations (Fig. 1).

The phylogenetic tree demonstrated that all *B. ignitus* sequences obtained from Korea are grouped together with haplotype 5 from Belgium (commercial) and four Chinese haplotypes forming a separate clade (posterior probability = 50). The other two Chinese haplotypes (H2 and H3) are clustered with haplotype 8 from Japan (posterior probability = 72). Haplotypes from China belong to two different clades. Only a few sub-clusters are well supported and the phylogenetic relationships of the rest of haplotypes remained unresolved (Fig. 2).

Discussion

The results of the study indicate that the Belgian commercial population of *B. ignitus* has low genetic diversity, which is likely the result of repeated inbreeding for

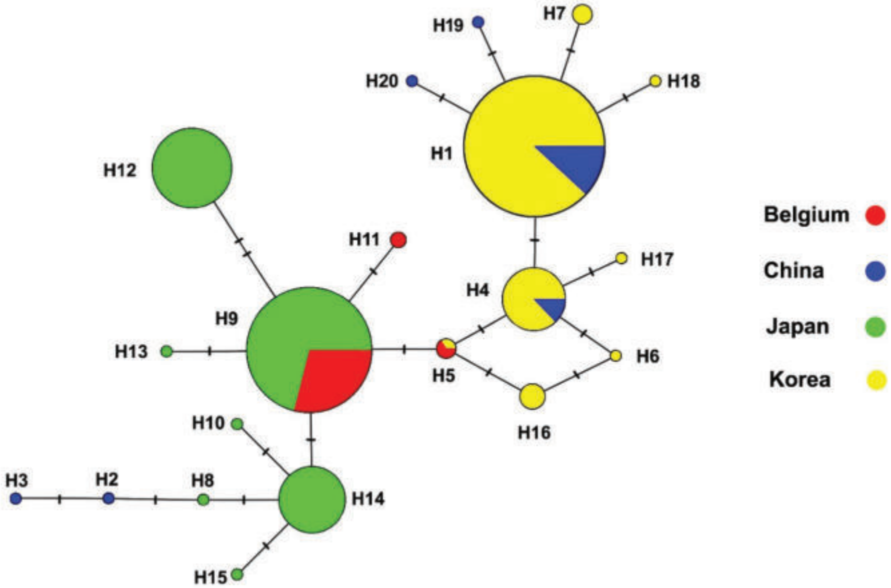

Figure 1. Median joining haplotype network of *B. ignitus* based on 458-bp partial COI gene. Each circle represents one haplotype and the size is proportional to its frequency among the studied sequences. Small black dashes represent mutational steps (Belgium = commercial population).

commercial purposes. (Hedrick and Kalinowski 2000; Cole 2003). The dominant haplotypes in Korea and China are H1 and H4, which differ in one nucleotide substitution, and other Korean haplotypes are derived from these two haplotypes (Fig. 1). These two haplotypes are also the most frequent haplotypes in China. The most widespread haplotypes with highest frequency are likely the oldest ones and appear in the center of haplotype network while recently derived haplotypes distributed in the restricted localities forming a star-shape phylogeny (Watterson and Guess 1977). Thus Haplotype 1 is the most widespread haplotype in Korea and China and Haplotype 9 is the oldest and most widespread haplotype in Japan and Belgium commercially reared populations (Fig. 1) which suggests that the commercial populations have close relatedness to Japanese wild populations. Han et al. (2018) also revealed that the Japanese sequence from Honshu made one cluster with Belgian sequences.

We found that haplotype 5 is shared between Belgian (commercial) and Korean populations and it is phylogenetically closely related to Korean haplotypes. Among the three commercial populations studied here, the Commercial-Korea A population showed the highest haplotype and nucleotide diversity (Table 2). Since high genetic diversity is known to play a crucial role in enabling populations to adapt to new environmental conditions (Suaraz and Tsutsui 2008; Handley et al. 2011), this population appears to be particularly well-suited for utilization in variable environments for the purpose of pollinating agricultural products. However, it is important to consider the potential risks associated with widespread introduction of alien populations of *Bombus ignitus*

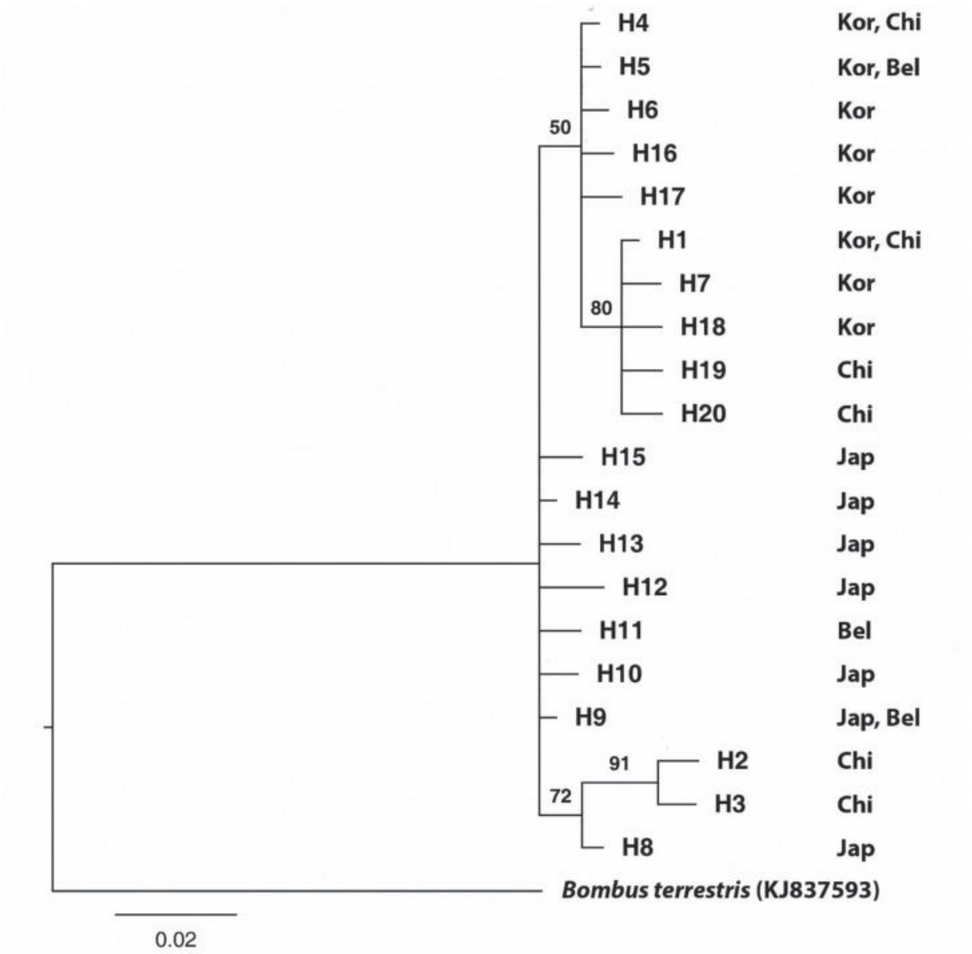

Figure 2. Bayesian inference of 458-bp partial COI gene of the haplotypes of *B. ignitus*. Numbers represent posterior probability. Bel: Belgium (commercial), Chi: China, Jap: Japan, Kor: Korea.

originated from Japan, due to the potential risk of their escape from greenhouses. These include the loss of genetic variation within native populations, decrease in adaptation rate, and disruption of population structure of local populations. Additionally, releasing alien populations can result in competition for food and the spread of diseases and parasites, which may reduce the size of local populations (Dimou et al. 2008). Hybridization between alien and native populations is also a major concern, as it can alter genetic diversity, viability, and productivity of the populations. Furthermore, this phenomenon can reduce individual fitness, negatively impacting the ability of populations to adapt to future environmental changes (Rhymer and Simberloff 1996; Laikre et al. 2010).

The importation of the European bumblebee, *B. terrestris*, to Japan as a pollinator for tomato production has resulted in negative impacts on native bumblebee populations. The species is currently widespread in Hokkaido and has interfered reproductively with native bumblebees, leading to declines in populations of *B. hypocrita* (Inoue et al. 2008; Kondo et al. 2009). As a result of these risks, Williams et al. (2012) proposed preventing the movement of *B. patagiatus* from China into Japan and *B. hypocrita* from Japan into China for pollination services. At the population level, the ongoing release of introduced bees could increase the dominance of the alien population in relation to local bumblebee communities. Additionally, due to the morphological similarities of the female castes of *B. ignitus* and *B. ardens* (Mohamadzade Namin et al., 2021) and similarities of alien populations of *B. ignitus* with native ones, monitoring the adverse effects of the introduction on local populations can be challenging. Therefore, it is essential to carefully weigh the potential risks and benefits of introducing alien bumblebees for pollination services, and to implement measures to minimize negative impacts on native bumblebee populations. While steps are taken to minimize the impact of insecticide spraying on bumblebees, releasing alien populations can have significant negative ecological and genetic consequences. Thus, it is important to thoroughly evaluate the potential risks and benefits before introducing alien populations and to take measures to minimize negative impacts on native populations. This can include monitoring of the introduced populations and implementing strategies to prevent hybridization with native populations, as well as developing alternative solutions for pollination services that do not rely on the introduction of alien species.

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Supplementary material 1

Information for COI sequences of *Bombus ignitus* from this study and NCBI-Genbank database

Authors: Saeed Mohamadzade Namin, Jiaxing Huang, Jiandong An, Chuleui Jung

Data type: phylogenetic (.docx file)

Link: https://doi.org/10.3897/jhr.96.102569.suppl1

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RESEARCH ARTICLE

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A taxonomic re-assessment of the widespread oriental bumblebee *Bombus flavescens* (Hymenoptera, Apidae)

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Abstract

Bombus flavescens Smith is one of the most widespread bumblebee species in the Oriental region. Due to colour polymorphisms, this species or species-complex has been a challenge for taxonomy. This study aims to assess the taxonomic status of the *flavescens*-complex using evidence from COI barcodes and morphology. We then reconstruct its biogeographic history from a phylogenetic analysis of populations across the current range, combining COI with 16S and nuclear PEPCK data. Despite a large range of polymorphisms across its distribution, the results show that *B. flavescens* is a single species based on algorithmic species delimitation methods, and it is clearly separated from its sister species, *B. rotundiceps* Friese. We suggest that *B. flavescens* diverged from its sister lineage in the Himalaya and dispersed into Southeast Asia in the Pleistocene. Conservation of the widespread *B. flavescens* will need to consider its several unique island populations.

Keywords

COI, Museum specimens, Polymorphism, *Pyrobombus*

Introduction

Bumblebees (genus *Bombus* Latreille) are well-studied pollinators, especially in temperate regions (Williams et al. 2014; Rasmont et al. 2021). They can also be found in both subtropical and tropical areas in Central and South America, and Asia (Williams 1998), although taxonomic knowledge gaps and the relative rarity of bumblebees in these areas still constrain our understanding of their biogeography and ecology.

The taxonomic studies of bumblebees in Asia, based on morphological evidence only, have been considered highly problematic, due to colour pattern polymorphism within the same species (Huang et al. 2015b; Ding et al. 2019) and cryptic species (Williams et al. 2020, 2022a). Moreover, the same colour pattern is also observed from different species which are co-existed in same locality (Hines and Williams 2012). Therefore, these confusions of taxonomic delimitation of Asian bumblebees require molecular evidence (Williams et al. 2012). Taxonomic status of bumblebees has been revised and various new species have been recently described in Asia, based both morphology and molecular evidence (Williams et al. 2020, 2022a, c; Williams 2022).

Bombus flavescens Smith is a Southern Asian species of the subgenus *Pyrobombus* Dalla Torre (Williams 1998). While the type locality of *B. flavescens* is Zhoushan, China (Smith 1852), this taxon is found in many other countries in the Himalaya and Southeast Asia with tropical low montane habitats, including Nepal, India, Bhutan, Myanmar, Thailand, Laos, Vietnam, Malaysia, and the Philippines (Starr 1992; Williams 1998, 2022; Williams et al. 2009; Koch and General 2019).

Most frequently, *B. flavescens* is a predominantly black pubescence (or hair) bumblebee with an orange tail (the area of hairs covering posterior part of metasoma) and legs in workers and queens. Males often (e.g., in parts of China and in the Himalaya) show a predominantly pale yellow (flavescent) hair pattern with orange legs (Fig. 1), although they sometimes exhibit the widespread dark pattern of the females. However, the colour pattern of hair varies across its wide area of distribution (Fig. 2), which has caused taxonomic problems for more than a century and led to the formal description of local variants (Frison 1934). For example, the name *B. alienus* Smith in China (Fig. 2E; morphologically synonymised by Williams (2022)) was applied to a specimen with an anterior yellow band on its metasoma (terga 1–2 or T1–2) whereas specimens of from the Philippines (Fig. 2G), with yellow hair covering the side of the mesosoma and metasoma (T1–2) but without the orange tail, have been described as *B. baguionensis* Cockerell (morphologically synonymised by Williams (1998)). In addition, a form with an entirely body, covered with uniformly orange hairs, has been described as *B. rufoflavus* Pendlebury (Fig. 2J; provisionally synonymised by Williams (1998), based on morphology). Further names were published for colour patterns resembling the typical *B. flavescens*: *B. mearnsi* Ashmead from Mindanao in the Philippines (morphologically synonymised by Pittioni (1949)); *B. bakeri* Cockerell from Negros (Fig. 2H; morphologically synonymised by Frison (1925)); and *B. tahanensis* Pendlebury from the Tahan mountains of Malaysia (Fig. 2I; morphologically synonymised by Frison (1934)). Apart from this high level of colour variation, other morphological characters, including shape of labrum, punctures on clypeus, and male genitalia, are relatively similar

Figure 1. Holotype male of *B. flavescens*, deposited in the entomological type collection at the Natural History Museum, London (NHMUK 014025381). Scale bar: 5 mm.

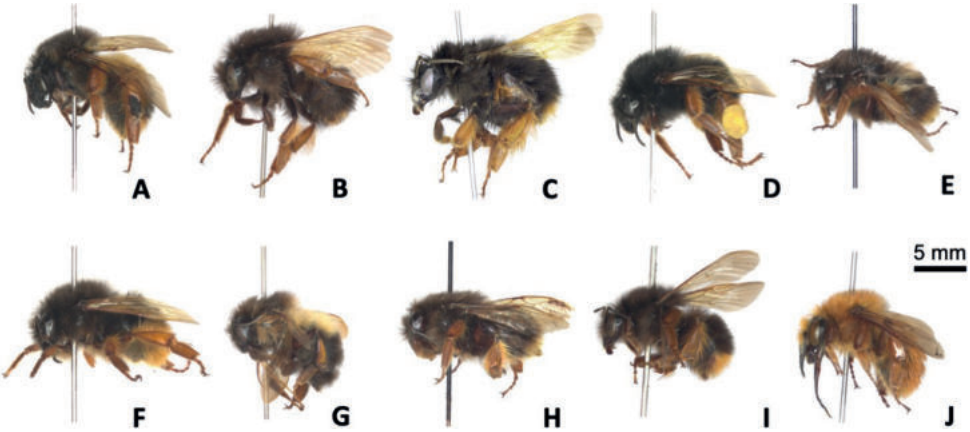

Figure 2. Colour variation of *B. flavescens* workers with their unique specimen identifiers **A** India (FLA#5) **B** Nepal (NHMUK 010814958) **C** Thailand (CT#1024) **D** Kunming, China (FLA#6) **E** *alienus*; Fujian, China (NHMUK 010815023) **F** Taiwan (FLA#4) **G** *baguionensis*; Luzon, the Philippines (CT#932) **H** *bakeri*; Negros, the Philippines (ZMA.INS.758600) **I** *tahanensis*; Gunung Tahan, Malaysia (NHMUK 010820651) **J** *rufoflavus*; Cameron highlands, Malaysia (NHMUK 010814574). Some images are reversed. Scale bar: 5 mm.

(Williams 1998; Thanoosing 2022). Yet, at various times through the 20th century different intraspecific names have been applied to describe minor *B. flavescens* variants (Frison 1925, 1928, 1934; Bischoff 1936; Chiu 1948; Pittioni 1949; Table 1) although they are clearly grouped together because of their morphological similarity (Williams 1998).

Table 1. List of *Bombus flavescens* names.

Author	Name
Smith (1852)	*Bombus flavescens*
Smith (1854)	*Bombus alienus*
Ashmead (1905)	*Bombus mearnsi*
Friese (1905)	*Bombus rufocaudatus*
Cockerell (1917)	*Bombus geei*
Cockerell (1920)	*Bombus irisanensis* var. *baguionensis*, *Bombus bakeri*
Pendlebury (1923)	*Bombus tahanensis*, *Bombus rufoflavus*
Frison (1925)	*Bremus mearnsi*, *Bremus mearnsi* var. *bakeri*, *Bremus irisanensis* var. *baguionensis*
Hedicke (1926)	*Bombus imuganensis*
Frison (1928)	*Bremus* (*Pratobombus*) *baguionensis*, *Bremus* (*Pratobombus*) *baguionensis* var. *imuganensis*
Dover (1929)	*Bremus rufoflavus*
Skorikov (1933)	*Pratobombus flavescens*
Frison (1934)	*Bremus mearnsi* var. *deflectus*, *Bremus mearnsi* var. *ditutus*, *Bremus mearnsi* var. *bakeri*, *Bremus mearnsi* var. *geei*
Bischoff (1936)	*Bombus* (*Pratobombus*) *mearnsi* ssp. *chekiangensis*
Chiu (1948)	*Bombus mearnsi* var. *deflectus*, *Bombus mearnsi* var. *ditutus*, *Bombus mearnsi* var. *bakeri*, *Bombus mearnsi* var. *geei*, *Bombus mearnsi* var. *subrufus*, *Bombus mearnsi* var. *luteus*
Pittioni (1949)	*Bombus flavescens* f. *dilutior*

Colour-pattern variation of bumblebees can be controlled by differential gene expression of, e.g., the *Abd-B* and *nubbin* genes affecting pigment generation during pupal development (Rahman et al. 2021). However, the evolutionary forces determining variation in colour pattern among *B. flavescens* populations remain unclear. Selection for mimicry might take a major role in driving evolutionary differences because the colour pattern of *B. flavescens* locally matches other bumblebee species in the same areas (Williams 2007). For example, on Luzon lsland, *baguionensis* shows a similar pattern to *B.* (*Megabombus*) *irisanensis* Cockerell, and in the Malay Peninsula, *rufoflavus* resembles *B.* (*Megabombus*) *montivagus* Smith with a similar predominantly orange pattern of both pubescence and underlying sclerites, which had been named *B. maxwelli* Pendlebury (Hines and Williams 2012).

Orange body colour (pubescence and sclerites) and enlarged ocelli in Hymenoptera are often associated with a nocturnal or crepuscular lifestyle, for example, *Megalopta* bees and *Apoica* wasps in Central and South America (Roubik 1989; Williams 2007; Warrant 2008). Interestingly, male and female nocturnal carpenter bees, *Xylocopa* (*Nyctomelitta*) *myops* Ritsema, show a pattern closely similar to the orange pattern bumblebees. This carpenter bee is found in Malaysia, Singapore, and Borneo, based on specimens in the Natural History Museum, London (NHMUK) collection and records by Ascher et al. (2022). Similarly, the two orange pattern bumblebees in Malaysia, *rufoflavus* (*B. flavescens*) and *maxwelli* (*B. montivagus*), might be active nocturnally also, at least in part (Williams 2007). Species of the subgenus *Nyctomelitta* Cockerell display relatively large ocelli compared to day-flying carpenter bees (Cockerell 1929; Michener 2007). However, the ocelli of the orange pattern bumblebees remain to be assessed in this regard. Observation of a night-flying bumblebee had been claimed in Myanmar (Doria 1886), but this record is a misidentification of the carpenter bee, *X.* (*Nyctomelitta*) *tranquebarica* (Fabricius) (Cameron 1910). Therefore, genuine evidence of nocturnal bumblebees has yet to be recorded in Southeast Asia.

The colour-pattern diversity of *B. flavescens* must be seen in light of the complex biogeography of its distribution range across the Southeast Asian mainland and the Philippines. The most recent common ancestor (MRCA) of the *flavescens* species complex has been placed into the Miocene epoch around eight million years ago (Ma), presumably on the mainland (Hines 2008) with two possible dispersal routes to the Philippines (Starr 1989): 1) through the Sundaland route, via Borneo–Sulawesi from the South; or 2) across the Luzon strait via Taiwan from the North. When global temperatures increased after the last glacial maximum (LGM), bumblebees likely became restricted to highlands (e.g., the Cameron Highlands, Malaysia) and diverged in allopatry. At the same time, as the sea level rose and submerged land bridges across Sundaland (Voris 2000; Sathiamurthy and Voris 2006; Woodruff 2010), populations of bumblebees on the Philippines were even further isolated.

This study seeks to clarify genetic patterns within the *flavescens*-complex, to establish the species status of geographically separated lineages and to infer biogeographic scenarios for bumblebees in Southeast Asia more generally. Species-level entities in bumblebees have been delimited by morphological, molecular (e.g., Williams et al. (2019, 2020)), and chemical approaches, the latter using Cephalic Labial Gland Secretions or CLGS (e.g., Brasero et al. (2021), Ghisbain et al. (2021)). Given the challenges of morphology for taxonomic assessment of the *flavescens*-complex, molecular data are required to resolve the species status of sub-lineages and their relationships. In addition, this study aims to clarify the question about the nocturnal lifestyle in *B. flavescens*, using morphological examination of their ocelli.

Methods

Sampling

Museum and institutional specimens of the *flavescens*-complex (Table 1) were examined for morphological analysis. Collecting information was recorded and made available at the NHMUK Data Portal (https://doi.org/10.5519/qd7f4uuw and https://doi.org/10.5519/isxh6saw). Additional records were obtained from reliable sources, including: 1) published literature (Williams et al. 2009, 2010); 2) major natural history collections, including the Naturalis Biodiversity Center (NMNL; Bakker F, Creuwels J), the Smithsonian Institution (USNM; Orrell T, Informatics Office), the University of Illinois at Urbana-Champaign (INHS; McElrath T), and the Taiwan Forestry Research Institute (TFRI; Lu S), available on the Global Biodiversity Information Facility (GBIF) (GBIF.org 2021). Records with unclear locality information and clear geographic outliers were ignored. For example, there is a record of *B. flavescens* from Japan (e.g., GBIF occurrence 3801818589; McElrath 2022), far outside the established range of *B. flavescens*, based on the specimen records by Williams (1998, 2022).

COI barcode data of *B. flavescens* and relatives were obtained from public databases (Suppl. material 1) and newly sequenced from pinned or fresh specimens (Table 2).

Table 2. List of specimens included, species name, ID, deposit place (KKIC = Kasetsart Kamphaeng Sean Insect Collection, PHW = Paul H. Williams Research Collection, CUNHM = Chulalongkorn University Natural History Museum Collection, NMNL = Naturalis Biodiversity Center Collection), sex/caste (w = worker, m = male), locality, collecting date, and COI GenBank accession number.

Species	Project ID	Collection (specimen ID)	Sex/caste	Locality	Collecting date	GenBank accession
B. flavescens	CT#662	KKIC	w	Thailand, Nakorn Pathom?	7/5/2017	OP355718
	CT#669	KKIC	m	Thailand, Loei	13/4/2016	OP355719
	CT#926	PHW	w	Malaysia, Gunung Tahan	NA	OP355720
	CT#1018	NMNL (ZMA.INS.758598)	w	Philippines, Negros	4/5/1953	OP355722
	CT#1023	CUNHM (BSRU-AB-9609)	w	Thailand, Chiang Mai	15/2/2021	OP355723
	CT#1024	CUNHM (BSRU-AB-9610)	w	Thailand, Chiang Mai	15/2/2021	OP355724
	FLA#2	PHW	w	Philippines, Luzon	27/4/1986	OP355725
	FLA#3	PHW	w	Taiwan, Tai Chung	5/5/1980	OP355726
	FLA#4	PHW	w	Taiwan, Nantou	24/6/1989	OP355727
	FLA#5	PHW	w	India, Uttar Pradesh	6/5/1990	OP355728
	FLA#6	PHW	w	China, Kunming	8/4/2018	OP355729
	FLA#7	NMNL (ZMA.INS.773029)	w	Bhutan, Lungtenphu	10/6/1996	OP355730
	FLA#10	PHW	w	Philippines, Luzon	27/4/1986	OP355731
B. rotundiceps	CT#960	CUNHM (BSRU-AB-1268)	m	Thailand, Chiang Mai	17/6/2019	OP355721
	ROT#1	PHW	w	India, Uttar Pradash	6/5/1990	OP355732
	ROT#2	PHW	w	India, Uttar Pradash	6/5/1990	OP355733
	ROT#3	PHW	w	China, Guangxi	3/6/2016	OP355734
	ROT#4	PHW	w	China, Guangxi	5/6/2016	OP355735

The samples were selected to represent the geographical distribution and all major colour pattern variants of *B. flavescens* (Fig. 3). *Bombus flavescens* belongs to the *pratorum*-group (Williams 1998). Thus, closely related species in the *pratorum*-group (Cameron et al. 2007; Williams et al. 2009, 2010), were included in the dataset: *B. ardens* Smith, *B. pratorum* (Linnaeus), *B. pyrenaeus* Pérez, *B. modestus* Eversmann, *B. nursei* Friese, *B. biroi* Vogt, *B. wangae* Williams et al., and *B. rotundiceps* Friese. The status of *B. nursei* as a distinct species was suggested in Williams (2022). Thirty COI sequences (> 600 bp) of *B. flavescens* and the relatives were downloaded from the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007) and the National Center for Biotechnology Information (NCBI) database (GenBank; Sayers et al. 2022) (Suppl. material 1). Nine *B. flavescens* sequences from China were provided by co-author MO, sequenced from freshly collected specimens. Thirteen further *B. flavescens* and five *B. rotundiceps* specimens from museum and institution collections were selected for sequencing (Table 2). The identifier numbers were applied to the studied specimens: 1) "CT#*n*" for Southeast Asian bumblebee specimens 2) "FLA#*n*" and "ROT#*n*" refer to *B. flavescens* and *B. rotundiceps* specimens from outside Southeast Asia, respectively.

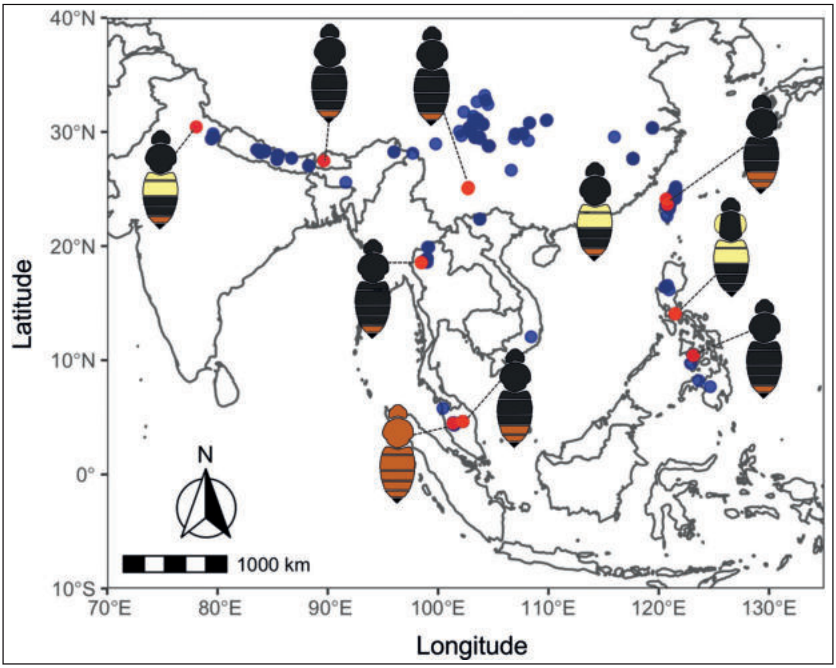

Figure 3. Map showing the distribution of *B. flavescens* with the pattern of hair colour in the dorsal view. The blue dots represent the records from museum collections, literature, and GBIF database (n = 702). The red dots represent the localities of barcoded specimens.

DNA extraction

Pinned and fresh specimens of *B. flavescens* and *B. rotundiceps* were selected for DNA extraction. For the recent specimens (< 20 years old), the tissue sources were a right front leg or a whole body for high DNA concentration yield. Each leg sample was ground using a small pestle in a microcentrifuge tube, whereas the whole-body sample was directly put in a microcentrifuge tube without specimen damages. The tissue samples were incubated at 56 °C for 24 hours in the ATL buffer with Proteinase K enzyme. Genomic DNA was extracted using the Qiagen DNeasy Blood and Tissue Kit, following the kit protocol. DNA quality and quantity were assessed using the Nanodrop spectrophotometer (Thermo Scientific ND8000) and the Agilent 2200 TapeStation system (Agilent Technologies, Inc.).

For older specimens (> = 20 years old), genomic DNA was likely to be degraded and all DNA extraction steps were performed inside a laminar flow chamber using dedicated UV sterilised equipment and consumables different from those used with modern bumblebee DNA. The DNA extraction method followed Sproul and Maddison (2017) using the Qiagen QIAamp Micro Kit, but without the use of carrier RNA. For each specimen, the right front leg was cleaned with sterile water, frozen with liquid nitrogen, and then ground with a small pestle. The samples were incubated in ATL buffer with Proteinase K at 55 °C for 24 hours. A blank sample (only the ATL buffer with the enzyme) was included for each extraction batch as a contamination control. Samples were eluted from the column twice with 15 µl AE buffer and incubated at room temperature for 10 minutes. The DNA concentration was measured using the Qubit fluorometer high sensitivity (Invitrogen) and samples were stored at -20 °C.

Primer design, amplification, and sequencing

For the recent specimens, PCR was performed to amplify the full length of COI amplicons (658 bp) using primers LepF1 and LepR1 (Hebert et al. 2004) and an annealing temperature at 50 °C. For older specimens, due to the DNA degradation, three pairs of primers were newly designed for amplifying partial COI contigs (150–300 bp), using Primer3 software (Untergasser et al. 2012). The COI sequence of *B. flavescens* (GenBank accession number: GU085209) was used as a reference sequence for the first two pairs of primers. The third pair was designed based on the partial mitogenome of *B. pratorum* (GenBank accession number: KT164684). There are three pairs of new primers for partial COI amplification (contig) in this study (Table 3): 1) FLA1: ParCOI_246_FLA_F1 (Tm° = 66.2 °C) and ParCOI_416_FLA_R1 (Tm° = 63.7 °C), 2) FLA2: ParCOI_349_FLA_F2 (Tm° = 64.2 °C) and ParCOI_662_FLA_R2 (Tm° = 66.6 °C), and 3) PRA1: ParCOI_1816_PRA_F1 (Tm° = 61.7 °C) and ParCOI_1994_PRA_R1 (Tm° = 65.5 °C). These primers were tested for amplification efficiency (Suppl. materials 2–4). The annealing temperature for the pair FLA1 and FLA2 was set at 65 °C and PRA1 was set at 63 °C.

The PCR products were sequenced in both forward and reverse directions using ABI technology at the NHMUK's sequencing facility. The sequences were edited using MEGA version 7.0.26 (Kumar et al. 2016: https://www.megasoftware.net/), to trim low-quality bases near the ends of the traces. The COI barcodes have been deposited in GenBank (Table 2).

Phylogenetic analysis and species delimitation

The aligned dataset was analysed to determine the best-fitting nucleotide substitution model using jModelTest software version 2.1.6 (Darriba et al. 2012). Phylogenetic trees were constructed using Bayesian Inference (BI) with MrBayes version 3.2.2 (Ron-

Table 3. Newly designed primers were used in this study, including gene, primer name, strand (F = forward, R = reverse) and primer sequence.

Gene	Primer name	Strand	Primer sequence
Partial COI	ParCOI_246_FLA_F1	F	5'– CCTGACATAGCTTTCCCACGA –3'
	ParCOI_416_FLA_R1	R	5'– TGCAATATCAACTGAAGGTGATG –3'
	ParCOI_349_FLA_F2	F	5'– CAGGATGAACTGTTTACCCTCCT –3'
	ParCOI_662_FLA_R2	R	5'– TGGATCACCTCCTCCTATTGGA –3'
	ParCOI_1816_PRA_F1	F	5'– TTCGTATAGAATTAAGTCATCCTGGT –3'
	ParCOI_1994_PRA_R1	R	5'– TCGTGGAAAAGCTATATCAGGTGAT –3'

quist and Huelsenback 2003). Markov Chain Monte Carlo (MCMC) chains were run for 10 million generations and sampled every 1000th generation. The first 10% was discarded as burn-in. The phylogenetic trees were visualised using FigTree version 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). Bumblebee species from closely related subgenera (Cameron et al. 2007) were used as outgroups, including *B.* (*Bombus*) *terrestris* (Linnaeus) and *B.* (*Alpinobombus*) *polaris* Curtis. The outgroup sequences were generated by Thanoosing (2017).

Poisson Tree Process (PTP) analysis is used to identify likely species coalescents. The test establishes the transition from long branches defining between-species diversification to short branches within species (estimated from the number of substitutions on branches) (Zhang et al. 2013; Kapli et al. 2017). The proportion of between- and within-species sampling was in a range where the PTP analysis performs well (Luo et al. 2018). The PTP analysis was run on the bPTP server (https://species.h-its.org; accessed 2021) under default parameters. The analysis was restricted to unique haplotype sequences in order to avoid introducing misleading 'zero-length' branches. The input phylogenetic tree was estimated using MrBayes rooted with *Bombus terrestris*. Results from the PTP analysis were compared to the Generalised Mixed Yule Coalescent (GMYC), which uses the branching rate rather than the number of nucleotide changes to establish the species-to-population transition (Pons et al. 2006). The required ultrametric tree was obtained with BEAST (Bouckaert et al. 2019) using the same dataset as for the PTP analysis. The clock rate was set at 0.0177 using the divergence rate from tenebrionid beetle COI (Papadopoulou et al. 2010). The GMYC analysis was run in the splits package of R (Ezard et al. 2009; https://r-forge.r-project.org/projects/splits/).

Biogeographic analysis

To reconstruct phylogenetic trees for biogeographic scenarios of *B. flavescens*, more genetic markers were added to the dataset, including mitochondrial 16S rDNA (16S) and nuclear phosphoenolpyruvate carboxykinase (PEPCK). Due to a lack of fresh specimens, most of 16S and PEPCK sequences for relatives of *B. flavescens* were retrieved from GenBank, especially from the dataset compiled by Cameron et al. (2007) (Suppl. material 5). 16S and PEPCK were not available from existing sources for three species; *B. rotundiceps*, *B. wangae*, and *B. nursei*. *Bombus nursei* is rare in inaccessible areas of the western Himalaya (Williams, 1991, 2022), and *B. wangae* also is a rare bumblebee from Sichuan (Williams et al. 2009). For *B. rotundiceps* and additional *B. flavescens*), the 16S and PEPCK were amplified using primers 16SWb (Dowton and Austin 1994) /874–16SIR (Cameron et al. 1992), and FHv4/RHv4 (Cameron et al. 2007) and sequenced in both directions (Table 4).

An ultrametric tree was constructed based on the combined dataset of COI (unique haplotypes), 16S and PEPCK (Suppl. material 6), using *BEAST (Ogilvie et al. 2017). If not available from the same individual, sequences in these three datasets were concatenated for different representative from the same area of distribution. For PEPCK, the sequence was partitioned for introns and exons. The closely related

Table 4. List of 16S and PEPCK sequences, included species, ID, and the 16S and PEPCK GenBank accession numbers, generated in this study.

Taxa	Project ID	16S	PEPCK
B. flavescens	CT#926	OP354521	-
	CT#1023	OP354523	OP382631
	FLA#6	OP354524	OP382632
B. rotundiceps	CT#960	OP354522	OP382630

B. (*Pyrobombus*) *lepidus* Skorikov, based on Cameron et al.'s (2007) tree, was used as an outgroup. The nucleotide substitution model for each fragment was selected according to the BIC criterion. The BEAUti software (Bouckaert et al. 2019) was used to generate an input file for BEAST. Trees were estimated under a strict clock and a Calibrated Yule Model as a species tree prior with the birth rate prior drawn from a Gamma distribution. Due to a lack of fossil evidence for the subgenus *Pyrobombus*, the clock was calibrated from molecular rate estimates based on five genes by Hines (2008), placing the origin to approximately 8.5 +/- 1 Ma. Accordingly, the prior distribution was 10.1–6.86 Ma (5% tails). The MCMC algorithm was run for 500 million generations and sampled every 5000th generation. The trace file was visualilsed using Tracer (Rambaut et al. 2018). A 20% burn-in was discarded using TreeAnnotator (Bouckaert et al. 2019) to construct the maximum clade credibility tree.

S-DIVA analysis (Yu et al. 2010) and BioGEOBEARS with DIVALIKE+J model (Matzke 2013a, 2013b, 2014) in the RASP package (Yu et al. 2020) were used to estimate biogeographic scenarios for the *flavescens*-complex and their relatives. The biogeographical distributions were divided into 11 principal areas, based on bumblebee global biogeography (Williams 1996), areas of endemism in Southeast Asia and the distributions of *flavescens*-complex and their relatives (Table 5): 1) Europe (A), 2) Central Asia (B), 3) North and Central China and North Asia (C), 4) Korean peninsula and Japan (D), 5) South China (E), 6) Himalaya (F), 7) Thailand (G), 8) Peninsular Malaysia (H), 9) Taiwan (I), 10) Luzon (J), and 11) Negros (K). These areas were chosen so that the maximum range size for any species was limited to three of these areas, due to acknowledged problems with the methods in inheriting broader distributions (Lamm and Redelings 2009). Then, the dispersal-corridor model was created with possible bumblebee permitted dispersal routes (Fig. 4). According to this model, the possible dispersal areas in this study are AB, ABC, ABF, AC, ACD, ACE, BEF, BF, BFG, CD, CDE, CE, CEF, CEG, CEI, EF, EFG, EFI, EG, EGH, EGI, EI, EIJ, FG, FGH, GH, GHK, HJK, HK, IJ, IJK, and JK. The burnin was set at 20%. Then, the *BEAST trees were used as the input trees.

Morphological study of ocelli in the *flavescens*-complex

The idea of the nocturnal lifestyle in the orange pattern bumblebees, *rufoflavus* (*B. flavescens*) and *maxwelli* (*B. montivagus*) from Peninsular Malaysia, has been introduced by

Table 5. Principal areas of endemic distribution of the *flavescens*-complex and their relatives in this study.

Area	Principal ranges included	Species recorded
A	Europe	*B. pratorum*, *B. pyrenaeus*
B	Central Asia	*B. biroi*
C	North China, and North Asia	*B. modestus*
D	Korea peninsula and Japan	*B. ardens*, *B. modestus*
E	South China	*B. flavescens*, *B. lepidus*, *B. rotundiceps*, *B. wangae*
F	Himalaya	*B. flavescens*, *B. lepidus*, *B. nursei*, *B. rotundiceps*
G	Thailand	*B. flavescens*, *B. rotundiceps*
H	Peninsular Malaysia	*rufoflavus* (*B. flavescens*), *tahanensis* (*B. flavescens*)
I	Taiwan	*B. flavescens*
J	Luzon	*baguionensis* (*B. flavescens*)
K	Negros	*bakeri* (*B. flavescens*)

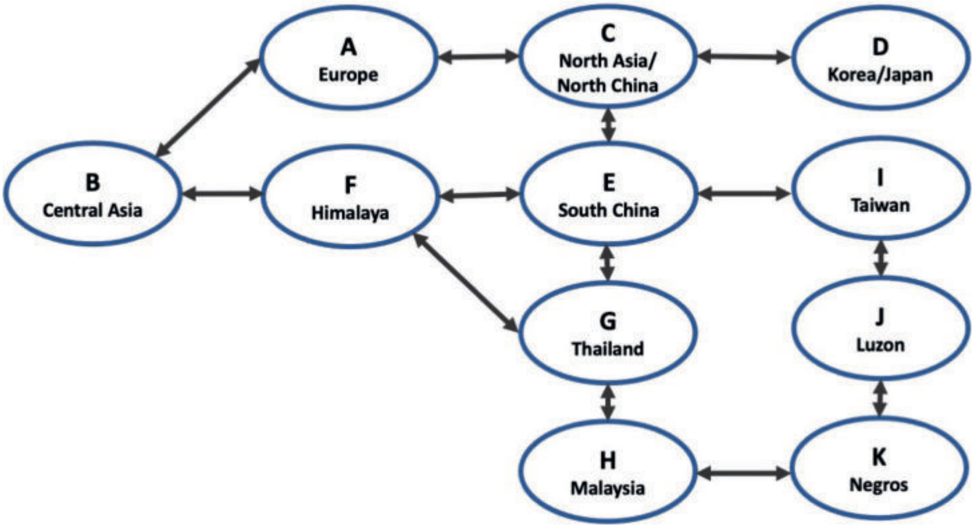

Figure 4. A corridor-dispersal model diagram of the *flavescens*-complex and their relatives in this study.

Williams (2007). Although orange hair pattern can be recognised in diurnal bumblebees (e.g., *B. humillis* Illiger, *B. pascuorum* (Scopoli), and *B. muscorum* (Linnaeus)), *rufoflavus* and *maxwelli* show the uniformly orange pattern both of pubescence and sclerites uniquely. This orange pattern can be recognised in the female specimens of nocturnal carpenter bees, *X. myops*, mentioned in Williams (2007), which can be also found in Peninsular Malaysia. For this reason, we selected the female specimens of *X. myops* and their related species, *X. tranquebarica* from the NHMUK collection, included in this study to test the idea.

Due to the sexual dimorphism bias and the availability of male specimens, only female or worker specimens were chosen in this study. Female *flavescens*-complex specimens (n = 107) together with its relative, *B. rotundiceps* (n = 12), outgroups including the diurnal *B. irisanensis* (n = 4), the orange pattern *B. montivagus* (taxon *maxwelli*) (n = 3), and the nocturnal carpenter bees, *X. myops* (n = 20) and *X. tranquebarica* (n = 12), were selected for

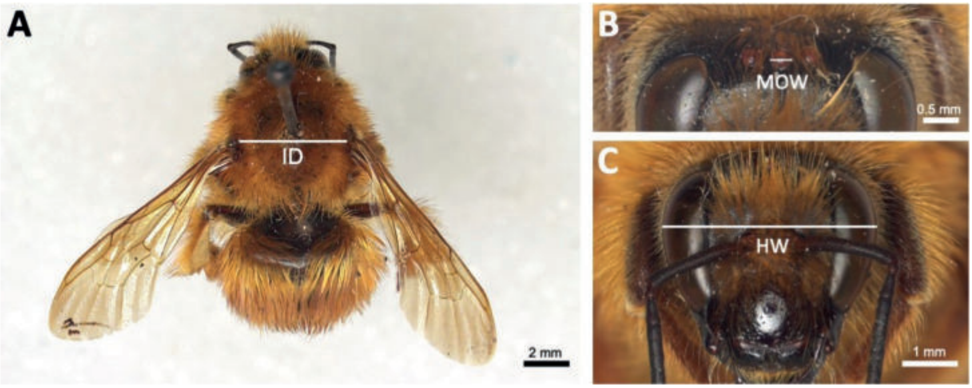

Figure 5. The measurement of morphological characters **A** dorsal aspect: intertegular distance (ID) **B** frontal aspect: median ocellus width (MOW) **C** frontal aspect: head width (HW). The specimen shown is *B. flavescens*, NHMUK 010814574, from the Cameron Highlands, Malaysia.

morphological character measurement, including median ocellus width (MOW), intertegular distance (ID), and head width (HW) (Fig. 5), under a Wild Heerbrugg M4A stereomicroscope, calibrated with ocular and stage micrometres. The specimens of the *flavescens*-complex were divided into eight groups: 1) Thailand (n = 4), 2) *baguionensis* (n = 15), 3) Himalaya (n = 16), 4) China (n = 20), 5) Taiwan (n = 6), 6) *bakeri* (n = 6), 7) *rufoflavus* (n = 20), and 8) *tahanensis* (n = 20). The data are available in the Suppl. material 8.

The morphological values, including MOW, the ratio between MOW and ID (MOW:ID), and the ratio between MOW and HW (MOW:HW), were visualized in box plots using R package ggplot2 (Wichham 2016). To test for differences between species, and within the *flavescens*-complex, statistical tests were performed in R (R core team 2021). First, a Shapiro-Wilk normality test was used to examine the distribution of data of each of the *flavescens*-complex taxa and each bee species. Where the data showed a normal distribution, an ANOVA test and Tukey test were then performed. A Kruskal-Wallis test and Dunn's test were used instead if the data were not normally distributed. The Dunn's test was conducted using the R package *FSA* (Ogle et al. 2022).

Results

DNA extraction, amplification, and sequencing

Genomic DNA was extracted successfully for most specimens of the *flavescens*-complex and *B. rotundiceps*. Most of the old samples were degraded and had relatively low DNA concentrations (< 10 ng/µl). The three amplicons obtained with new primer pairs PRA1, FLA1, and FLA2 were assembled into a single contig. However, there was a 25-base pairs gap between the first (PRA1) and second (FLA1) fragments, and the 5' part of the COI barcode region (88 base pairs) was not amplified at all. COI sequences were generated for 18 collected specimens with top BLAST hits to the subgenus *Pyrobombus*.

Phylogenetic analysis and species delimitation

The final dataset of the *flavescens*-complex and relatives comprised 57 COI sequences, including 25 unique haplotypes. The resulting 575 bp alignment was used to construct the BI phylogenic tree under the GTR+Γ model selected by jModelTest (BIC = 4596) (Fig. 6). *Bombus rotundiceps*, sampled from China, Nepal, India, and Thailand, was the reciprocally monophyletic sister group of the *flavescens*-complex. The latter included four regional clades: 1) Thailand and Himalaya, 2) China, 3) Malaysia, and 4) the Philippines and Taiwan.

The unique haplotype COI dataset was used to estimate the input tree for the species-delimitation analysis. The nucleotide substitution model of this dataset was GTR+Γ (BIC = 3877). Species delimitation using PTP returned each of the nine species as a separate entity, with Bayesian support values between 0.14–1.00 (Fig. 6). In contrast, the GMYC lumped the *flavescens*-complex and *B. rotundiceps*, as well as the *B. modestus* and *B. wangae* species pair (Fig. 6). All analyses recovered the *flavescens*-group, including *B. flavescens s. str.*, *B. baguionensis*, *B. bakeri*, *B. rufoflavus*, and *B. tahanensis*, as a single species.

Biogeographic analysis

The phylogenetic analysis was based on three loci (see supplement for missing data in 16S and PEPCK; Suppl. material 6) and 26 terminals, including the outgroup. Tree searches were conducted under partitioning and separate model choice for COI (575 bp), 16S (551 bp), PEPCK introns (483 bp), and PEPCK exons (369 bp). The resulting maximum clade credibility tree showed a deep separation of the *B. flavescens*/*B. rotundiceps* clade from their closest relatives, *B. pratorum* and *B. ardens*, estimated at 6 +/- 2 Ma (Fig. 7). Within the *flavescens*-complex the early split in was occupied by the Malaysian group. The extant members of the *flavescens*-complex diversified during a time interval approximately 1–2 Ma. However, there is some uncertainty about relationships among the four regional groups, as in the COI tree the Thai and Himalayan groups were sister to the China, Malaysia, the Philippines and Taiwan groups.

Although DEC model was the best fit model for the BioGEOBEARS analysis in this study (the highest AICc wt; Suppl. material 7), we selected DIVALIKE+J model instead (the second high AICc wt; Suppl. material 7). The DIVALIKE+J model supports widespread founder-event speciation at nodes (Yu et al. 2020) which fits the distribution changes of bumblebees (Williams et al. 2020, 2022b).

Results from S-DIVA and DIVALIKE+J showed that there was uncertainty in ancestral areas of *B. flavescens* and relatives, with more than one possible ancestral area suggested in both scenarios (Figs 8, 9). There were only four nodes (III, XI, XIV, and XVI; Fig. 8) for which we identified a single ancestral area in S-DIVA, whereas the DIVALIKE+J result (Fig. 9), only node XI showed a single ancestral area. The results suggested that the ancestral area for the MRCA of the *pratorum*-group was likely to be in area covered by Europe, Central Asia, and the Himalaya (ABF) in S-DIVA, and Central Asia (B) in DIVALIKE+J with low probability. This group diversified in the late Miocene.

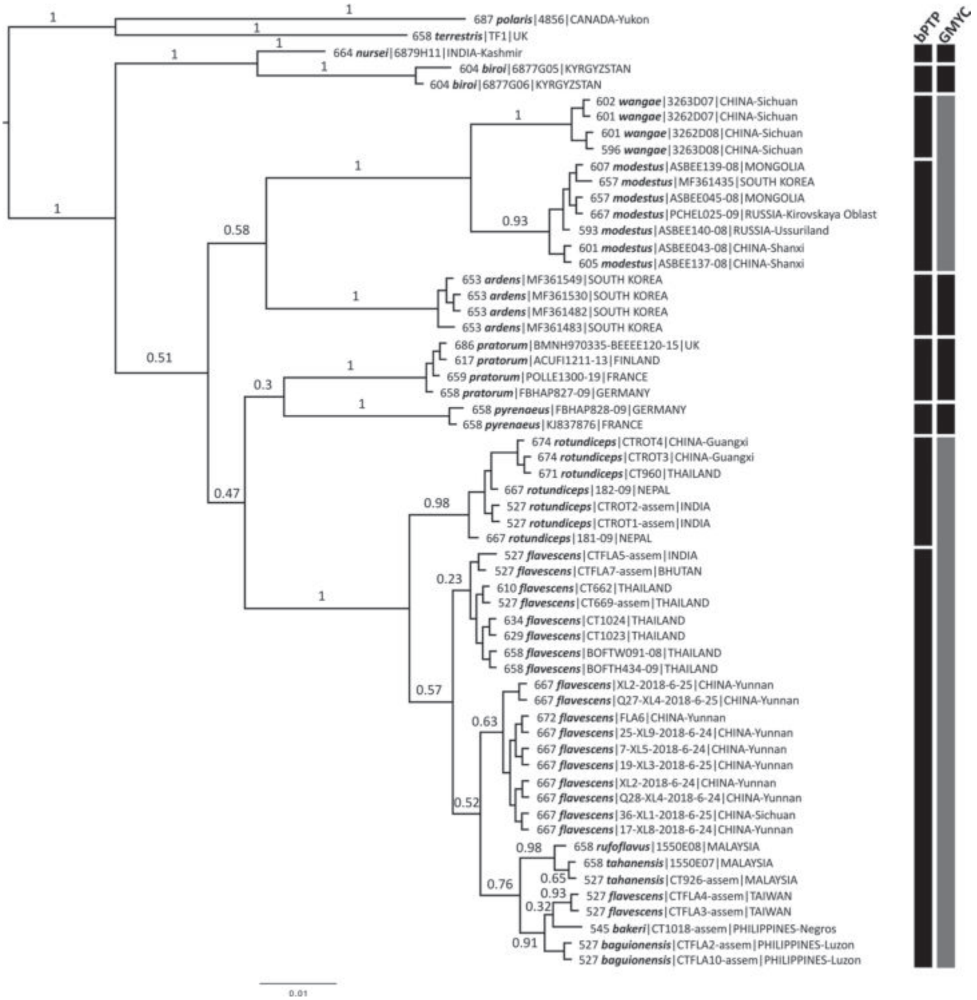

Figure 6. Bayesian inference (BI) phylogenetic tree based on a 575 bp fragment of COI in MrBayes. MCMC chains were run for 10 million generations, sampled every 1000th generation. Burn-in fraction is 10%. The posterior probabilities are shown above the branches. The tip of the tree shows the sample label including the sequence length, a taxon name, an identifier code from the database, and its geographic origin. The results of species delimitation methods are shown in the right-hand side columns. The black and grey bars within the same columns indicate the same species.

For the *flavescens*-complex, the S-DIVA biogeographic scenario illustrated that the MRCA of *B. rotundiceps* and *B. flavescens* (Node IX; Fig. 8) might have occurred in the Himalaya (F) around 1.5 Ma during the Pleistocene epoch. Next, the MRCA of *B. flavescens* in the S-DIVA analysis was inferred to be in the FGH areas, including Himalaya, Thailand, and Peninsular Malaysia (Node X; Fig. 8) at around 1 Ma. However, the DIVALIKE+J biogeographic scenario suggested that the group might

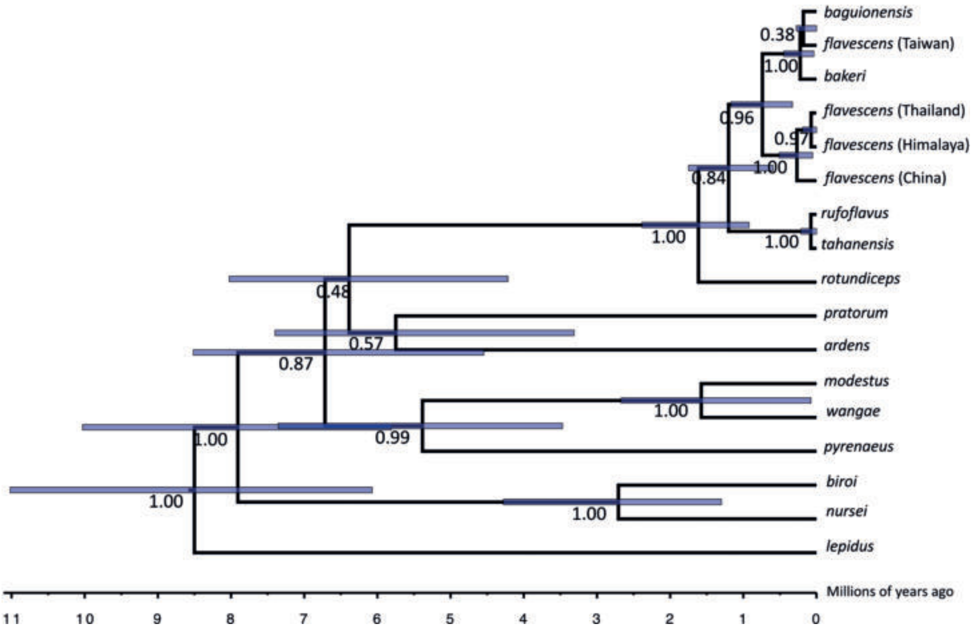

Figure 7. The maximum clade credibility tree of *B. flavescens* and their closely related species, reconstructed with *BEAST from gene trees for the COI, 16S, and PEPCK genes and calibrated using estimate time from Hines (2008). The MCMC chains were run for 500 million generations, sampled every 5000th generation. Burn-in fraction is 20%. The posterior probabilities are shown under the nodes. Blue bars represent the 95% confidence limits on the estimate dates of divergence. *Bombus lepidus* is the outgroup.

have originated in Malaysia (H), but with low probability. The DIVALIKE+J showed higher support for a Peninsular Malaysian origin (Node X; Fig. 9).

The diversification of the *B. flavescens* populations began after 1 Ma, resulting in three distinct clades: 1) *rufoflavus+tahanensis* from Malaysia (Node XI, Figs 8, 9); 2) *flavescens s. str.* from Thailand, Himalaya and China (Node XIII, Figs 8, 9); 3) *baguionensis+bakeri+flavescens s. str.* from Taiwan (Node XV, Figs 8, 9). According to our corridor-dispersal model diagram (Fig. 4), the S-DIVA showed that the *B. flavescens* used all possible corridors between E–K, except the corridor H–K, the Sundaland route, whereas the DIVALIKE+J included the corridor H–K as a permitted route.

Morphological study of *Bombus flavescens* ocelli

The carpenter bees, *Xylocopa tranquebarica* and *X. myops*, had a significantly larger median ocellus than the bumblebees (Fig. 10). *Bombus irisanensis* clearly showed the smallest median ocellus and *B. flavescens*, *B. rotundiceps*, and *B. montivagus* exhibited similar median ocellus sizes (Fig. 10).

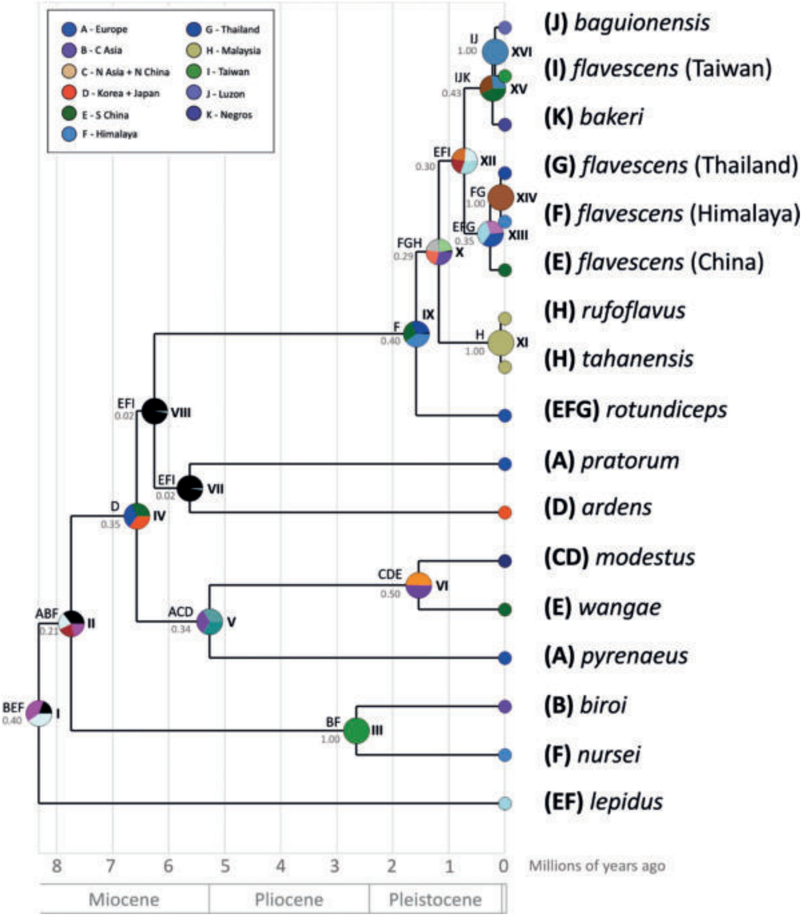

Figure 8. Biogeographic scenarios for the *flavescens*-complex and its close relatives by S-DIVA analysis. The input tree is reconstructed with *BEAST from gene trees for the COI, 16S, and PEPCK genes and calibrated using estimate time from Hines (2008). The internal nodes are represented in Roman numerals. The colours of the nodes represent the possible ancestral areas. The area codes used are given in Table 5. The most likely ancestral areas are represented above the nodes with the probabilities below.

For the *flavescens*-complex (Fig. 11), the Shapiro-Wilk normality test suggested that the MOW was not normally distributed ($W = 0.93$, $p\text{-value} < 0.05$), whereas the MOW: ID and MOW: HW did not differ significantly from a normal distribution ($W = 0.99$, $p\text{-value} = 0.28$ and $W = 0.99$, $p\text{-value} = 0.45$ respectively). There was a significant difference within the MOW of the *flavescens*-complex (Kruskal-Wallis test, chi-squared = 36.217, $p\text{-value} < 0.05$; Dunn's test, $p\text{-value} < 0.05$), including the taxa *baguionensis-rufoflavus*, *baguionensis-tahanensis*, Himalaya-*rufoflavus*, and Himalaya-*tahanensis*. For the MOW: ID, nine pairs were significantly different (ANOVA, F-value = 6.781, $p\text{-value} < 0.05$; Tukey test, $p\text{-value} < 0.05$): *bakeri*-China, *rufoflavus*-China, *tahanensis*-China, *bakeri*-Himalaya , *rufoflavus*-Himalaya, *tahanensis*-Himalaya, Taiwan-*bakeri*, Taiwan-*rufoflavus*, and Taiwan-*tahanensis*. In addition, only two pairs

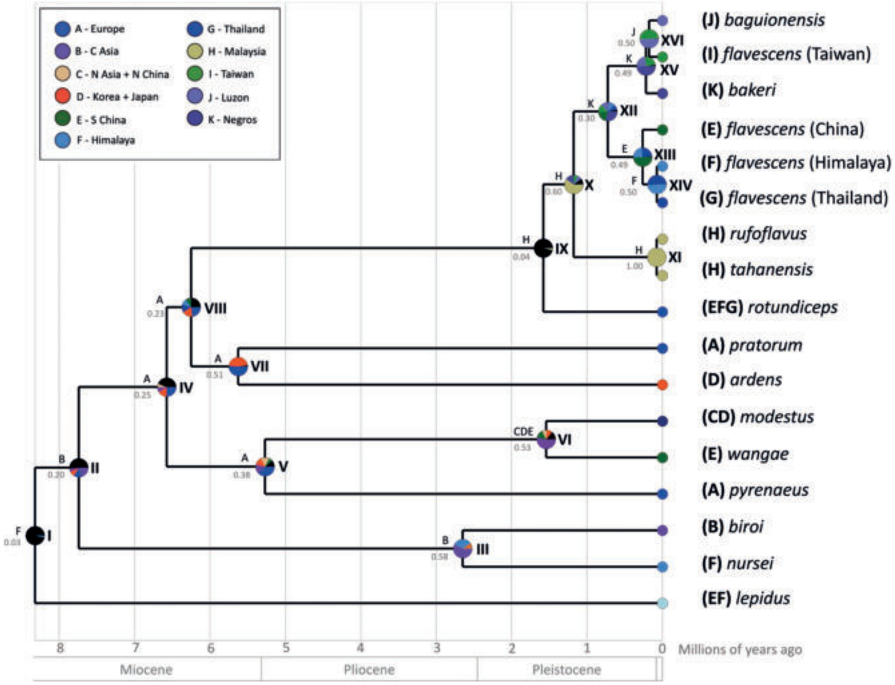

Figure 9. Biogeographic scenarios for the *flavescens*-complex and its close relatives by BioGeoBEARS with DIVALIKE+J analysis. The input tree is reconstructed with *BEAST from gene trees for the COI, 16S, and PEPCK genes and calibrated using estimate time from Hines (2008). The internal nodes are represented in Roman numerals. The colours of the nodes represent the possible ancestral areas. The area codes used are given in Table 5. The most likely ancestral areas are represented above the nodes with the probabilities below.

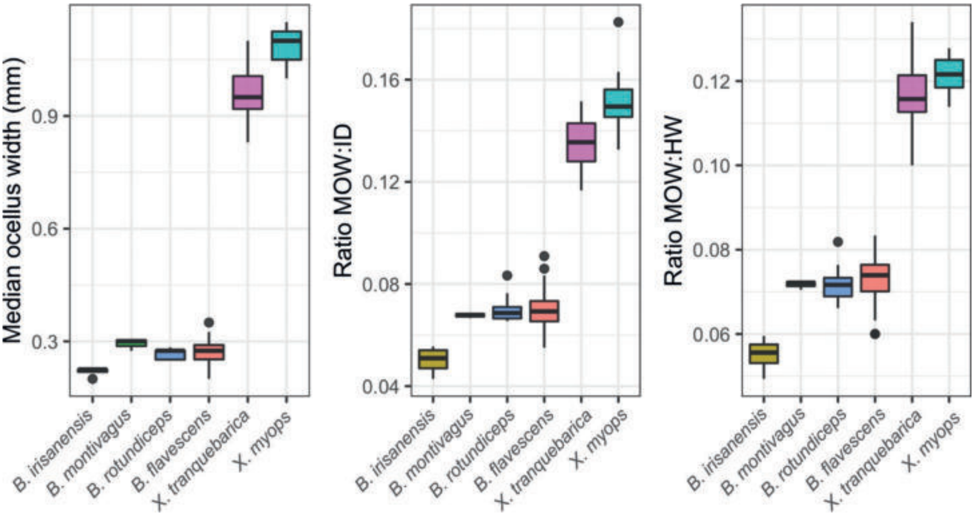

Figure 10. Box plots showing the median ocellus width (MOW), the ratio between MOW and intertegular distance (MOW:ID), the ratio between MOW and the head width (MOW:HW) of *B. irisanensis*, *B. rotundiceps*, *B. flavescens*, *B. montivagus* taxon *maxwelli*, *Xylocopa tranquebarica*, and *X. myops*.

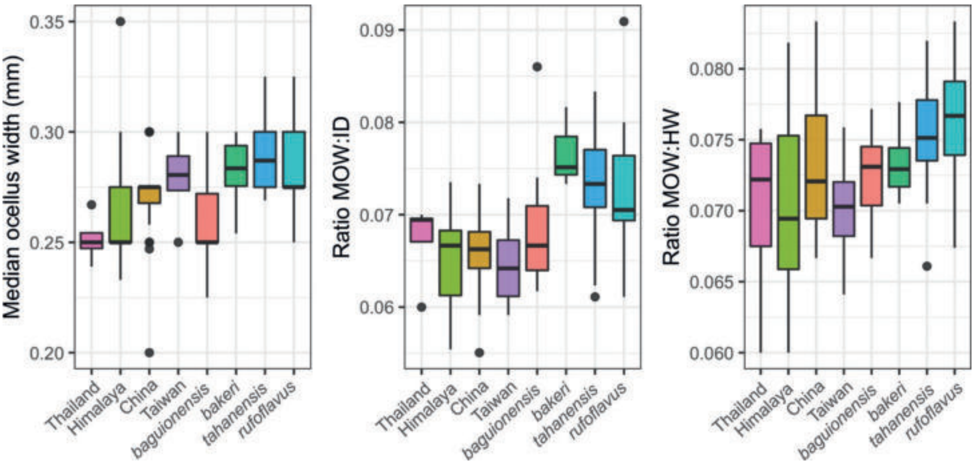

Figure 11. The box plots of the median ocellus width (MOW), the ratio between MOW and intertegular distance (MOW:ID) and the ratio between MOW and head width (MOW:HW) among *Bombus flavescens* population: Thailand, China, Himalaya, Taiwan, *baguionensis*, *bakeri*, *rufoflavus*, *tahanensis*.

of taxa were significantly different in MOW:HW (ANOVA, F-value = 3.701, p-value < 0.05; Tukey test, p-value < 0.05), *rufoflavus*-Himalaya, and *tahanensis*-Himalaya.

Discussion

Species status of the *flavescens*-complex

The status of species within the *flavescens*-complex taxa has been debated for nearly a century. Theodore Frison (1895–1945), an American entomologist wrote in his work in 1934, "*This species of bumblebee* [*B. flavescens*] *has been a problem to most persons who have attempted to determine…*" (Frison 1934). Our results for the COI-barcode tree (Fig. 6) support that the *flavescens*-complex is a monophyletic group, including the populations in China, the Himalaya, and Southeast Asia. The PTP and GMYC results group the *flavescens*-complex together as one species. This demonstrates that *B. flavescens s. l.* includes high intraspecific variation in colour pattern across its distributional range. The species-delimitation analyses confirm the conspecific status of the various geographical and morphological variants named as *B. baguionensis*, *B. bakeri*, *B. tahanensis* and *B. rufoflavus* by previous authors. Although this study did not include the taxon *mearnsi* from Mindanao, the taxon *mearnsi* also is expected to be a synonym of *B. flavescens* as morphologically suggested by Pittioni (1949), similar to the taxon *bakeri* from Negros, another population from the southern Philippines islands.

There is a discrepancy between the number of species recognised by PTP and GMYC. The GMYC analysis lumped 1) *B. flavescens* and *B. rotundiceps* 2) *B. modestus* and *B. wangae*, as single species, whereas PTP split them into four species. GMYC requires an ultrametric tree, which distorts the tree and branch lengths (Fujisawa and Barraclough 2013). For this, the closely related sister taxa which establish their own short clade might be identified as the same species. In contrast, the PTP keeps the original tree shape, and should be considered more reliable between the two approaches (Williams 2021), in this instance.

Nevertheless, when we investigate the morphological evidence of these four taxa, their morphological characters are unique (Williams 1998; Williams et al. 2009, 2010). The males of *B. wangae* and *B. modestus* are distinct, especially in their genitalia, which the gonostylus of *B. modestus* is broader than *B. wangae*. For the *B. flavescens* and *B. rotundiceps*, their male genitalia are also different: the gonostylus of *B. flavescens* is broad with round inner margin, whereas the gonostylus of *B. rotundiceps* is narrower with straight inner margin. In this case, the PTP results show congruence with the morphological characters whereas GMYC does not. Then, we suggest that the PTP analysis corroborates more consistently morphologically recognisable species for these bumblebees. For further study, if fresh male specimens of *B. flavescens* are available, chemical evidence, including, CLGS, is recommended as an alternative approach for defining the species recognition, whether it shows agreement with the molecular delimitation in this study.

Fresh specimens of *B. flavescens* and their relatives are not available from enough samples because of the rarity of these bees. Bumblebees in subgenus *Pyrobombus* are active particularly early in the year (Williams et al. 2014), so subgenus *Pyrobombus* sampling can only be conducted in a relatively short period. The accessibility of their habitats in Southeast Asia is also relatively limited and no records have been reported during recent decades, especially for *B. flavescens* from Gunung Tahan, Malaysia, and from Negros and Mindanao in the Philippines. Moreover, although the *flavescens*-complex is widely distributed, recorded in at least eleven countries, it is difficult to obtain specimens from some countries, because of limits imposed by local or international regulations. Therefore, old museum specimens are the best available option for clarifying genetic relationships within this group. However, these specimens were collected between 1980 and late 1990. The DNA of those specimens has become degraded through time (Pääbo 1989). It is difficult to extract the DNA from old specimens with standard protocols. However, numerous DNA extraction techniques for old insect specimens have been developed (Gilbert et al. 2007; Thomsen et al. 2009; Ballare et al. 2019). Next generation sequencing would help to obtain DNA sequences from historical specimens (Nazari et al. 2016; Prosser et al. 2016; Sproul and Maddison 2017; Call et al. 2021), but a high DNA quantity is required (Goodwin et al. 2016). According to our results, the DNA concentration of the samples in this study was not high enough for the sequencing requirement. The newly designed primers in this study were successful for the *flavescens*-complex and *B. rotundiceps*. The primers can amplify the DNA from specimens up to 70 years old. From our results, fresh specimens or pinned specimens less than 20 years old are recommended for use as DNA sources as the first option. Museum specimens are an alternative way if fresh specimens are not available. However, using museum specimens requires additional molecular processes, for example, extra-sterilisation of equipment and laboratory space, and conducting negative extraction and PCR controls. This is the first time that at least the partial COI barcodes of the *flavescens*-complex populations from the Philippines from both North and South islands have been retrieved. This information is invaluable because this is the key to resolving cryptic status among this group, but it also provides a workflow for approaching other difficult bee groups for which only old specimens are available.

Orange pattern bumblebees in Peninsular Malaysia

In the Cameron Highlands, Malaysia, several orange pattern bumblebees have been recorded, including the *rufoflavus* form of *B. flavescens* (Fig. 2J) and the *maxwelli* form of *B. montivagus*. Their fulvous hair and sclerite colour might relate to the nocturnal lifestyle of hymenopterans, similar to the nocturnal carpenter bees in subgenus *Nyctomelitta* (Williams 2007). In this study, the ocelli of *B. flavescens* populations were similar in size (Fig. 11) which did not match the hypothesis of enlarged ocelli, whereas the nocturnal carpenter bees have much more distinctively enlarged ocelli (Fig. 10). However, in the context of the variation among *B. flavescens* populations, the median ocellus of both Malaysian populations, *B. flavescens* taxon *rufoflavus* and taxon *tahanensis*, were significantly larger than the populations at higher latitudes, including from Himalaya and Luzon Island (Fig. 11). The results showed a gradient of ocellar size within the *B. flavescens* populations from high latitude (smaller ocellus) to low latitude (larger ocellus): MOW, MOWID, and MOWHW differed significantly between low latitude (0°–20°N) and high latitude (>20°N) group (MOW: Mann-Whitney U test, $p\text{-value} = 0.037$; MOWID: ANOVA, $F\text{-value} = 30.49$, $p\text{-value} < 0.05$; MOWHW: ANOVA, $F\text{-value} = 8.573$, $p\text{-value} < 0.05$).

Although there is a significant difference between low-latitude and high-latitude populations of *B. flavescens*, intraspecific variation of ocellar size in bumblebee populations has been reported before for *B. terrestris* (Kapustjanskij et al. 2007), without any evidence for nocturnal behavior in this well-known species. This also suggests that ocellar size might not be a good diagnostic character to distinguish species in bumblebees; it may be that it is relatively plastic to local selection regimes. The ocelli are visual organs that detect polarized light in low-light conditions (Wellington 1974; Roubik 1989). Ocellar size shows a negative correlation with light intensity (Kerfoot 1967; Warrant et al. 2006; Kapustjanskij et al. 2007), and there are a high number of nocturnal and crepuscular bees in tropical or low latitude areas (Dorey et al. 2020). The trend seen here towards larger ocellar size in the tropics might be evidence that bumblebees are more active in low-light conditions, for example, in the early morning or late afternoon, to avoid heat stress, as is suggested for *B. breviceps* Smith and *B. haemorrhoidalis* Smith (Williams 1991; Thanoosing 2022). Larger ocelli can also be observed in other tropical forest bees, for example, stingless bees, because sunlight is filtered by the tree canopy, thereby reduced in the understory (Streinzer et al. 2016).

Numerous light traps were run at night on the Cameron Highlands recently by researchers (Musthafa et al. 2021) and by tourist services (e.g., Cameron Service: https://cameronservice.blogspot.com/), but no bumblebees have been observed at traps. Consequently, a nocturnal or crepuscular lifestyle of the orange pattern bumblebees in the Cameron Highlands remains unsupported.

Apart from orange *B. flavescens*, another bumblebee, *B. montivagus* taxon *maxwelli*, and a variation of the diurnal hornet *Vespa velutina* Lepeletier taxon *divergens*, in the same locality, are also orange in colour (Hines et al. 2012; Perrard et al. 2014). In addition, not only the orange pattern but also the black hair with a red tail pattern of *B. flavescens* in South China (Fig. 2D) is recognised in the colour variation of *V. velutina* taxon *nigrithorax* (Perrard et al. 2014). For this reason, the colour patterns of *B. flavescens* might potentially be a result of Müllerian mimicry.

Biogeography of *Bombus flavescens*

Pyrobombus is a bumblebee subgenus in which five species groups are found in the Old and New World (Williams 1998). *Bombus flavescens* and its relatives are in the '*pratorum*-group'. This group is the sister group to the '*lepidus*-group' (Cameron et al. 2007). The groups originated in the Palearctic and Oriental regions, in the late Miocene (~11 Ma), and the *lepidus*-group is entirely restricted to the Oriental region (Williams 1998). In this study, biogeographic analyses show that the origin of the *pratorum*-group is likely to be in the Oriental region, specifically around the Qinghai-Tibetan Plateau (QTP) or Himalaya. Then, during the late Miocene and early Pliocene, the diversification of this group occurred. This is coincident with the period when the monsoon climate in this area intensified (Zhou et al. 2018), which also accelerated the diversification of bumblebee food plants in the Oriental region (Yu et al. 2015; Ma et al. 2016; Matuszak et al. 2016). Our results show that there were dispersal events between the Oriental (E, F, G, H, I, J, and K; Fig. 8) and the Palearctic region (A, B, C, and D; Fig. 8), for example, the clade of *biroi*+*nursei*, *pyrenaeus*+*modestus*+*wangae*, and *pratorum*+*ardens*. In addition, there are the lineages of *B. nursei* and *B. wangae* that reinvaded the Oriental Region: *B. nursei* from the west and *B. wangae* from the east. *Bombus nursei* prefers subalpine meadow habitats similar to *B. biroi* (Williams 1991; Williams 2022). This dispersal pattern between the Oriental and Palearctic regions during the Miocene-Pliocene can be observed in other bumblebee subgenera, for example, in subgenera *Mendacibombus* (Williams et al. 2018) and *Melanobombus* (Williams et al. 2020).

Only the group *rotundiceps*+*flavescens* has been restricted to the Oriental until now. The divergence between *B. rotundiceps* and *B. flavescens* was in the Pleistocene (ca 1.5 Ma). The climate in Southeast Asia during the late Pliocene and Pleistocene was cooler than the present day (Morley 2012). This might have given the opportunity for temperate and montane flora to colonise these areas. At the same time, the MRCA of *B. flavescens* dispersed southward into Southeast Asia or Sundaland, following suitable habitat (A; Fig. 12). *Bombus flavescens* is likely to have dispersed to and colonised the Philippines islands when the islands or the Pleistocene Aggregate Island Complex (PAIC), including Luzon, Negros-Panay or Visayan, and Mindanao, were connected in the LGM (Brown et al. 2013). This study supports that *B. flavescens* dispersed to the Philippines by the

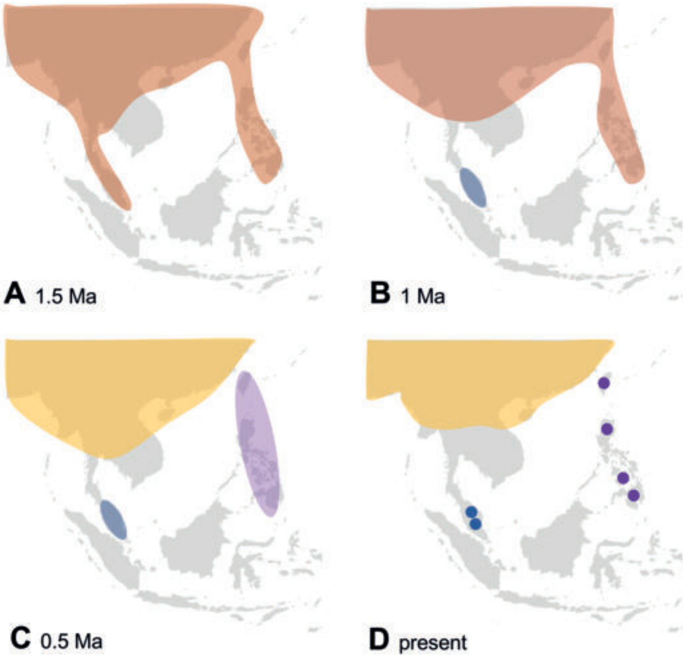

Figure 12. Biogeographic scenarios of *Bombus flavescens* through time **A** the most recent ancestor of *B. flavescens* dispersed through Southeast Asia or Sundaland around 1 Ma (orange) **B** the Malaysian population was isolated on the highland of the peninsula due to the temperature rising around 1 Ma (blue), at that time, the populations in Taiwan and Philippines were connected to the mainland populations (orange) **C** the bridge between the mainland and Taiwan was submerged, the Taiwan-Philippines populations were isolated around 0.5 Ma (purple) **D** at present day, *B. flavescens* populations distribute in the subtropical of Southeast Asia, China and Himalaya (yellow), on the Highlands of Malay peninsula (blue), and the islands of Taiwan and the Philippines (purple).

Taiwan-Luzon route in the same way as *B. irisanensis*, the other species in the Philippines. The oscillation of sea level and raising of global temperature in the late Pleistocene facilitated the population isolation and higher latitude immigration of *B. flavescens* (B, C; Fig. 12). First, the populations from the North (Luzon) and the South (Negros and Mindanao) were separated, because the South population (taxon *bakeri*) is the sister of the North population (taxon *baguionensis*) and the Taiwan group (Fig. 7). Then, the populations on the North of Philippines and Taiwan were isolated when the sea submerged the bridges, so that the populations in Southeast Asia were captured in montane refuges as biological islands until the present, similar to the populations on the Cameron Highlands and Gunung Tahan mountain in Malaysia (D; Fig. 12).

Biogeography of bumblebees in Southeast Asia

Many lineages of bumblebees in Southeast Asia might are hypothesised to have originated around the QTP, then dispersing into the region via the Himalaya–Hengduan corridor (Williams 1985; Hines 2008; Williams et al. 2022). The bumblebee fauna at the Northern border and highlands of the Southeast Asian region is similar to the fauna of the Himalaya and Southern China, adjacent neighbours both spatially and genetically (Williams et al. 2009; Williams et al. 2010; Hines and Williams 2012; Streinzer et al. 2019; Williams 2022). The subgenera *Orientalibombus* Richards and *Alpigenobombus* Skorikov are mainly restricted to the North of the Southeast Asian region, whereas the subgenera *Megabombus* Dalla Torre, *Melanobombus* Dalla Torre, and *Pyrobombus* are more widely distributed throughout the region (Williams 1998).

The long-faced subgenus *Megabombus* crown group might have originated around 13 Ma (Hines 2008). Then, two independent lineages of subgenus *Megabombus* diverged in Southeast Asia approximately between 4.25–1.5 Ma, based on molecular dating (Huang et al. 2015a). The lineages are 1) a *trifasciatus*-group: *B. montivagus*, *B. albopleuralis* Friese, *B. burmensis* (Skorikov) in the North of Southeast Asia and the Malay Peninsula, and 2) a *senex*-group: *B. irisanensis* on Luzon Island, in the Philippines. However, due to a lack of genetic information on *B. senex* Vollenhoven and *B. melanopoda* Cockerell, the phylogenetic relationship between mainland and Sumatran subgenus *Megabombus* remains relatively unresolved (Huang et al. 2015a). Consequently, the biogeography of Sumatran subgenus *Megabombus* bumblebees remains unclear.

Nonetheless, the link between the Southeast Asian mainland and the Indonesian islands can be explained by the phylogenetic relationship of two subgenus *Melanobombus* sister species, *B. eximius* Smith and *B. rufipes* Lepeletier of the *rufipes*-group. The MRCA of the *rufipes*-group lineage diverged from the other subgenus *Melanobombus* lineages around 16 Ma and was distributed in the Himalaya and QTP (Williams et al. 2020). Speciation within the *rufipes*-group is likely to have occurred around 1 Ma in the Pleistocene epoch, after the Sundaland land bridge was submerged, isolating part of the *rufipes*-group on Sumatra and Java (Williams et al. 2020).

Southeast Asian bumblebees in the subgenus *Pyrobombus* are also distributed both on the mainland and on the islands of the Philippines, for example, *B. flavescens*. There is no record of subgenus *Pyrobombus* on the islands of Indonesia and adjacent areas. A member of subgenus *Pyrobombus* had been recorded on the Andaman Islands, named *B. andamanus* Gribodo (Gribodo 1882). However, this is a mislabeled specimen of a Nearctic bumblebee, *B. bifarius* Cresson (Williams 1998).

Conclusion

Genetic information proved crucial for the study of bumblebees in Southeast Asia. This is the first gene-based study to address the taxonomic status of *B. flavescens*, which is highly variable in hair colour. This study confirms that the populations of *B. flavescens* on the Asian mainland and on the islands are parts of the same species. Despite this, a trend among *B. flavescens* populations can be observed towards larger ocelli at lower latitudes. This might only reflect local selection based on foraging in the low-light conditions within dense forest, or in more early morning or twilight activity in warmer environments. *Bombus flavescens* originated in the Himalaya and dispersed to Southeast Asia during the Pleistocene. Its constituents, various regional colour forms, diversified through an allopatric divergence process. *Bombus flavescens* is a useful model for studying the biogeography of bumblebees in Southeast Asia, many of which are less known. Nevertheless, more genetic information is required to investigate the conservation of endemic populations of *B. flavescens*.

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Supplementary material 1

List of COI sequences from databases, research and collaboration, including the accession number or ID, the original sequence length and country

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Sequence ID (word document)

Link: https://doi.org/10.3897/jhr.96.104715.suppl1

Supplementary material 2

Primer testing

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Text (word document)

Explanation note: Testing newly designed primers in this study.

Link: https://doi.org/10.3897/jhr.96.104715.suppl2

Supplementary material 3

Primer testing with gradient annealing temperatures

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Experimental (word document)

Explanation note: The samples were *B. breviceps* (CT#552) and *B. flavescens* (CT#662). The brightness of gel electrophoresis is presented in symbols: *** = strong, ** = medium, * = weak, NS = unsuccessful.

Link: https://doi.org/10.3897/jhr.96.104715.suppl3

Supplementary material 4

Polymerase chain reaction temperature profile of different pairs of primers in this study

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Experimental (word document)

Link: https://doi.org/10.3897/jhr.96.104715.suppl4

Supplementary material 5

List of 16S and PEPCK sequences from GenBank with the accession number, the original sequence length, and country

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Sequence ID (word document)

Link: https://doi.org/10.3897/jhr.96.104715.suppl5

Supplementary material 6

The accession number or ID of the parsing dataset of COI, 16S, and PEPCK sequences for *BEAST analysis

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Sequence ID (word document)

Link: https://doi.org/10.3897/jhr.96.104715.suppl6

Supplementary material 7

Ancestral area reconstruction model selection, estimated in BioGeoBEARS

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Model test (word document)

Link: https://doi.org/10.3897/jhr.96.104715.suppl7

Supplementary material 8

List of specimens, including species, collection, specimen ID, origin country and latitude group, and measurement of intertegular distance (ID), head width (HW), median ocelli width (MOW) in millimetres (mm)

Authors: Chawatat Thanoosing, Michael C. Orr, Natapot Warrit, Alfried P. Vogler, Paul H. Williams

Data type: Morphological (word document)

Explanation note: List of specimens, including species, collection (CUNHM = Chulalongkorn University Natural History Museum, Bangkok, Thailand; KKIC = Kasetsart Kamphaeng Saen Insect Collection, Kasetsart University Kamphaeng Saen Campus, Nakhon Pathom, Thailand; NHMUK = Natural History Museum, London, UK; NMNL = Naturalis Biodiversity Center, Leiden, the Netherlands; PHW = Paul H. Williams research collection, UK), specimen ID, origin country and latitude group (Low = 0°–20°N; High = > 20°N), and measurement of intertegular distance (ID), head width (HW), median ocelli width (MOW) in millimetres (mm) (available at the NHM Data Portal: https://doi.org/10.5519/wknn9sd2).

Link: https://doi.org/10.3897/jhr.96.104715.suppl8