ZooKeys 1053: 1–42 (2021)
doi: 10.3897/zookeys.1053.65324
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Seek and ye shall find: new species and new records of *Microporella* (Bryozoa, Cheilostomatida) in the Mediterranean

Emanuela Di Martino[1], Antonietta Rosso[2,3]

1 *Natural History Museum, University of Oslo – Blindern, P.O. Box 1172, Oslo 0318, Norway* **2** *Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Catania – Corso Italia 57, 95129, Catania, Italy* **3** *CoNISMa – Consorzio Interuniversitario per le Scienze del Mare – Piazzale Flaminio, 9, 00196, Roma, Italy*

Corresponding author: Emanuela Di Martino (e.d.martino@nhm.uio.no)

Academic editor: Pavel Stoev | Received 1 March 2021 | Accepted 20 May 2021 | Published 2 August 2021

http://zoobank.org/E67F6F86-686D-44AC-9105-37FF58BC2183

Citation: Di Martino E, Rosso A (2021) Seek and ye shall find: new species and new records of *Microporella* (Bryozoa, Cheilostomatida) in the Mediterranean. ZooKeys 1053: 1–42. https://doi.org/10.3897/zookeys.1053.65324

Abstract

The Mediterranean specimens of the genus *Microporella* collected from shallow water habitats during several surveys and cruises undertaken mostly off the Italian coast are revised. As a result of the disentanglement of the *M. ciliata* complex and the examination of new material, three new species, *M. bicollaris* **sp. nov.,** *M. ichnusae* **sp. nov.,** and *M. pachyspina* **sp. nov.,** are described from submarine caves or associated with seagrasses and algae. An additional species *Microporella* sp. A, distinct by its finely reticulate ascopore, is described but left in open nomenclature owing to the limitations of a single infertile fragment. After examination of all available material, based on their identical zooidal morphology, the genus *Diporula* is regarded as junior synonym of *Microporella* and the combination *Microporella verrucosa* is resurrected as first suggested by Neviani in 1896. *Fenestrulina joannae* is also reassigned to *Microporella*. The availability of a large number of colonies of the above-mentioned and other species already well known from the area (i.e., *M. appendiculata*, *M. ciliata*, and *M. modesta*), allowed the assessment of their high intraspecific variability as well as the observation, for the first time, of some morphological characters including ancestrulae, early astogeny, and kenozooids. Finally, *M. modesta*, in spite of *M. ciliata* as defined by the neotype selected by Kukliński & Taylor in 2008, appears to be the commonest species in the basin.

Keywords

Biodiversity, cryptic species, detritic bottoms, *Diporula*, Infralittoral Algae Biocoenosis, Ionian Sea, marine protected areas, submarine caves

Introduction

The genus *Microporella* Hincks, 1877 is one of the most distinctive bryozoan genera (Taylor and Mawatari 2005), both cosmopolitan and species-rich, currently including 34 fossil and 115 Recent species (Bock 2020). These numbers are constantly increasing, with new species of *Microporella* continuously being described worldwide, both fossil (e.g., Di Martino et al. 2017, 2019, 2020a) and Recent (e.g., Almeida et al. 2017; Figuerola et al. 2018; Dick et al. 2020; Di Martino et al. 2020a; Ramalho et al. 2020).

In the Mediterranean, *Microporella* is represented to date by nine species (Rosso and Di Martino 2016; Di Martino et al. 2020a), and knowledge of the diversity of the genus in the basin has been stable during the last decade. The last thorough revision was by Harmelin et al. (2011), but was limited to the south-eastern sectors of the Mediterranean along the coast of Lebanon. This work increased the number of *Microporella* species recorded from the Mediterranean, but also showed how the stock of *Microporella* species found in this area was composed only of tropical alien species.

Here, we examine large volumes of material, collected along the Italian coast in several shallow water habitats, to assess the diversity of the genus in these sectors of the Mediterranean, the morphological intraspecific variability of the *Microporella* species found, as well as their distribution and commonness. We also describe three new species and, for those previously known, illustrate for the first time some key morphological features. An additional species is described and left unnamed. Although some of its morphological features are distinct from other congeners (e.g., ascopore), the lack of some diagnostic characters, such as ovicells, and the scarcity of material available prevents the description of a new species.

Materials and methods

This study is based on material collected during the last 40 years in several biodiversity surveys carried out under the umbrella of different projects summarised in Table 1, which also provides collection data for each described species. The studied area with the distribution of species is shown in Fig. 1. Further details for some cruises can be found in the following papers: PS/81: Piattaforma Siciliana cruise (Rosso 1989; 1996a; 1996b); N/96: Noto cruise (Cantone 1997); Mazzere and Granchi caves, Plemmirio Marine Protected Area (MPA) (Rosso et al. 2013a); LCT: Gulf of Catania cruise (Poluzzi and Rosso 1988; Rosso 1989); CI: Ciclopi 2000 cruise (Rosso 2001); SM: Ciclopi Islands MPA (Rosso et al. 2019a); AM: Amendolara Bank cruise (Di Geronimo et al. 1998); CL: Calvì cruise (Rosso 1989); Bari Canyon (D'Onghia et al. 2015); Lesvos Island, Agios Vasilios cave (Rosso et al. 2019b).

Scanning electron microscopy (SEM) was conducted on uncoated specimens using a TESCAN VEGA 2 LMU in backscattered-electron/low-vacuum mode at the Microscopical Laboratory of the University of Catania. Measurements were taken from SEM micrographs using the image processing program ImageJ (available from https://

Table 1. *Microporella* species studied in this paper with related sampling information and number of specimens found in each sample; numbers in brackets refer to dead specimens. Abbreviations for samples: PS/81, Piattaforma Siciliana cruise; N/96, Noto cruise; MZ and GR, Mazzere and Granchi caves from Plemmirio MPA; Cast. beach., Castelluccio beached; LCT, Gulf of Catania cruise; CI, Ciclopi 2000 cruise; AC and SM, Ciclopi Islands MPA samples; AM, Amendolara Bank cruise on board of Urania; PC, Porto Cesareo; Ta I, Taccio I; Ma, Madonna; Sc, Scoglio di Fora; ECE and EBE, Marettimo; CL, Calvì cruise of the University of Nice; AV, Agios Vasilios; c., cave; cn., Canyon; Isl., Island. Abbreviations for Biocoenoses: DC, Coastal Detritic Bottoms; DL, Offshore Detritic Bottoms; C, Coralligenous; VTC, Terrigenous Muddy Bottoms; DE, Muddy Detritic Bottoms; GSO, Semi-Obscure caves; IA, Infralittoral Algae; HP, Posidonia Meadow; GO, Obscure Caves; CB, Cold-Water Corals; na, not applicable; f, fragment.

Sea/ Locality	Sample	Depth	Biocoenosis	*appendiculata*	*bicollaris* sp. nov.	*ciliata*	*ichnusae* sp. nov.	*modesta*	*pachyspina* sp. nov.	sp. A	*verrucosa*
Ionian/ Gulf of Noto	PS/81 CR1	45	DC	27(8)				16(12)			
	PS/81 2B	65	DC								(2)
	PS/81 2C	83–74	DC								1(44)
	PS/81 2XA	128	DL								(4)
	PS/81 2XB	120	DL					(1)			(28)
	PS/81 4C	95–86	DL					(1)			(32)
	PS/81 4C1	89–84	DL								(44)
	PS/81 4X	102–93	DL					(1)			1(33)
	PS/81 6D	98–96	DL								(87)
	PS/81 9B	44	DC	(1)				(1)			
	PS/81 9C	60	DC					(1)			(3)
	PS/81 9D	78	DC					(12)			10(24)
	PS/81 10C	60	DC	(1)				(1)			(1)
	PS/81 11E	98	DL					(2)			(13)
	N/96 3C	20	C					11			
	N/96 5E	40	C-DC					1			
	N/96 6C	45	VTC	2							
	N/96 7E	35	C					12			
	N/96 8I	77	DE								1
	N/96 9E	50	DC	1							
	N/96 10G	82	DE					1			6
	N/96 10H	80	DE-DL								4
	N/96 10 I	107	DL					(1)			
	N/96 WP	90	DL			(1)		(24)			
Ionian/ Plemmirio caves	MZ1	≈23	GSO		(1)						
	GR E	≈19	C					3(1)			
Ionian/ Gulf of Catania	Cast. beac.	0	na					15			
	LCT69	90	DL					(2)			(18)
	Ognina	4	plastic					2			
	CI 2G	87.5	DE-DL					(4)			1(3)
	CI 3H	71	DC								(1)
	CI 4E	52	DC	1							(1)
	CI 6H	75	DC?								1(2)
	CI 8F	79	DC								(1)
	CI 8H	92.5	DE-DL								(1)
	CI 8I	95	DE-DL					(3)			(1)
	CI 9G	63	DC					(10)			(30)f
	CI 10G	85	DC-DE								(1)
	CI 12E	62	DC					(7)			(2)
	CI 12F	70	DC					(1)			(2)
	CI 12G	83	DE-DL					(5)			(1)
	CI 13H	105	DL								10(32) f
	CI 14G	90	DL	1							(1)
	AC/L	50	C								(16)
	AC/1B	110	DL								11(18) f
	SM1Z25	25	IA					1			

Sea/ Locality	Sample	Depth	Biocoenosis	*appendiculata*	*bicollaris* sp. nov.	*ciliata*	*ichnusae* sp. nov.	*modesta*	*pachyspina* sp. nov.	sp. A	*verrucosa*
Ionian	Messina Strait	65	no data								2
Ionian/ Gulf of Taranto	AM 1D	30–40	DC					1			(3)
	AM 5D	40	DC					1			(1)
	PCI 10	5–15	C		2(1)						
Sicily Strait/ Pelagian Island	Ta I cave	10–20	C-GSO					1(1)			
	Ma cave	15	GSO					1			
	Sc cave	10	GSO					2(2)			
Sicily Strait/ Egadi Island	ECE 5	8	IA; IA-HP					ca.100	3		
	EBE/EBI	19							15		
Tyrrhenian	Palinuro c.	46	GO							(1)	
	Ustica Isl.	60	C					6(2)			(77)
Iberian-Provençal basin/ Sardinia, Capo Caccia, and Asinara	Falco 1	7	GSO	2							
	Falco 2	4					3				
	Bisbe 1	8		2			1				
	Bisbe 2	8		1			4				
	Galatea 1	8					1				
	Galatea 2	6					1				
	PSE/PSI	5–15	IA					7			
W Corsica	CL 74	150–110	DL	(11)							(50)
Adriatic	Bari cn. 1B1	280	CB					(1)			
Aegean/ Lesvos Island	AV1	30	GSO	(1)							(1)
	AV2	30	GO								(3)

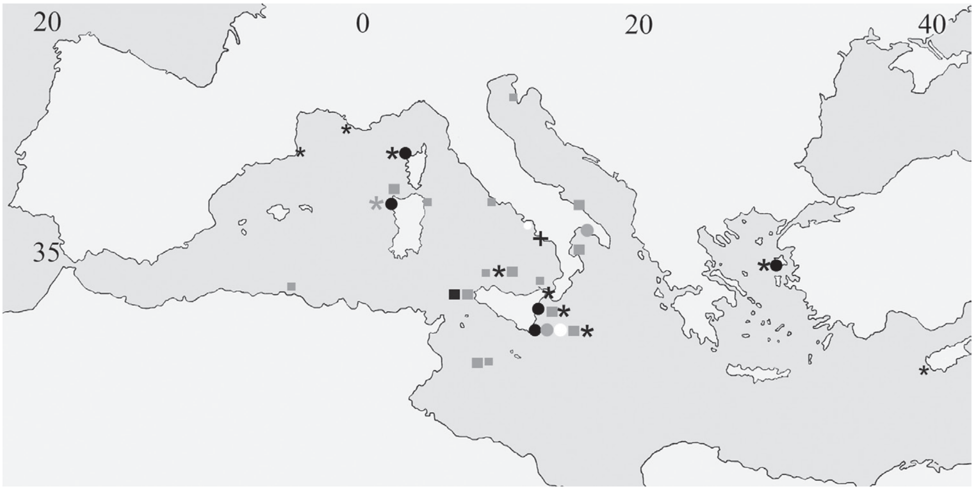

Figure 1. Geographical distribution of the Mediterranean species of *Microporella* studied in this paper, either based on examined material (larger symbols) or on data from the literature (Kukliński and Taylor 2008 for *M. ciliata*; Hayward and McKinney 2002; Chimenz Gusso et al. 2014 and Di Martino et al. 2020a for *M. modesta*; André et al. 2014 and Achilleos et al. 2020 for *M. verrucosa*) that include SEM images (smaller symbols). Black circles: *M. appendiculata*; grey circles: *M. bicollaris* sp. nov.; white circles: *M. ciliata*; grey asterisk: *M. ichnusae* sp. nov.; grey squares: *M. modesta*; black squares: *M. pachyspina* sp. nov.; black cross: *Microporella* sp. A; black asterisks: *M. verrucosa*.

imagej.nih.gov/) and are given in the species descriptions and/or in the remarks as ranges and, in parentheses, mean ± standard deviation plus the number of zooids measured (N). Abbreviations for the measurements are:

AvL	avicularium length;	**OvL**	ovicell length;
AvW	avicularium width;	**OvW**	ovicell width;
OL	orifice length;	**ZL**	autozooid length;
OW	orifice width;	**ZW**	autozooid width.

Type material of the new species and figured specimens form part of the Rosso Collection deposited at the Museum of Palaeontology of the University of Catania (**PMC**) under the catalogue numbers reported for each species.

Note that we follow Harmelin et al. (2011) for the authorships of *Microporella coronata* (Audouin & Savigny, 1826) and *M. genisii* (Audouin & Savigny, 1826).

Taxonomic treatments

Phylum Bryozoa Ehrenberg, 1831
Class Gymnolaemata Allman, 1856
Order Cheilostomatida Busk, 1852
Superfamily Schizoporelloidea Jullien, 1883
Family Microporellidae Hincks, 1879

Genus *Microporella* Hincks, 1877

Type species. *Eschara ciliata* Pallas, 1766

Microporella appendiculata (Heller, 1867)

Fig. 2

Lepralia appendiculata Heller, 1867: 107, pl. 2, fig. 8.
?*Microporella coronata* (Audouin & Savigny, 1826): Gautier 1962: 173.
Microporella coronata (Audouin & Savigny): Zabala 1986: 513, fig. 180.
Microporella marsupiata (Busk, 1860): Zabala 1986: 514, fig. 181, pl. 15D.
Microporella pseudomarsupiata Arístegui, 1984: 325, pl. 24, fig. 6; Zabala and Maluquer 1988: 141, fig. 335, pl. 19C; Di Geronimo et al. 1993a: table 1; Di Geronimo et al. 1997: table 2; Chimenz and Faraglia 1995: 40, table 1, pl. 2C; Rosso 1996a: table 2.
Microporella appendiculata (Heller): Hayward and Ryland 1999: 294, figs 134A, B, 135 (cum syn.); Chimenz Gusso et al. 2014: 187, fig. 100a–e.

Examined material. Italy • 2 living colonies; Ionian Sea, E Sicily, Ciclopi Island MPA; samples Ciclopi 2000 4E and 14G; 37°32'28"–37°34'30"N, 15°8'59"–15°11'1"E; 52 and 90 m; 16 Jul. 2000; A. Rosso leg.; dredging; DC and DL Biocoenoses; PMC Rosso-Collection I. H. B.84a. Italy • 27 living and 10 dead colonies/fragments; Ionian Sea, SE Sicily, Gulf of Noto; 36°41'45"–36°57'48"N, 15°8'35"–15°20'0"E; PS/81 cruise; samples CR1, 9B and 10C; 45, 44 and 60 m; Jul. 1981; I. Di Geronimo leg.; dredging; DC Biocoenoses; and 3 living colonies; Noto 1996 cruise; samples 6C and 9E; 45–50 m; 1996; E. Mollica leg.; dredging; VTC and DC Biocoenoses; PMC Rosso-collection I. H. B84c. Italy • 5 living colonies; Iberian-Provençal Basin, NW Sardinia, Capo Caccia-Punta Giglio MPA; samples Bisbe 1, Bisbe 2 and Falco 1; 40°35'40"N, 8°11'39"E; 7–8 m; Jun. 2009; V. Di Martino leg.; submarine cave; scuba diving; PMC Rosso-Collection I. H. B.84b. France • 11 dead colonies; Iberian-Provençal Basin, Corsica, off Calvì; sample CL 74; 42°47'31"N, 9°8'10"E; 150–110 m; G. Fredj leg.; dredging; DL Biocoenosis; PMC Rosso-collection Fr. H. B84d. Greece • 1 dead colony; NE Aegean Sea, Lesvos Island, Agios Vasilios cave; sample AV1; 38°58'9"N, 26°32'28"E; ca. 30 m, V. Gerovasileiou leg.; submarine cave; scuba diving; PMC Rosso-collection Gr. H. B84e.

Description. Colony encrusting multiserial, unilaminar, forming subcircular patches; interzooidal communications typically via two proximolateral, two distolateral and three distal pore-chamber windows, 48–122 (71±25, N = 10) × 16–26 μm (20±3, N = 10) along lateral walls.

Autozooids polygonal, 529–742 (644±66, N = 14) × 347–582 (458±66, N = 14) μm (mean L/W = 1.41), distinct, the boundaries marked by narrow grooves between the slightly raised vertical walls (Fig. 2D, E). Frontal shield flat to slightly convex, coarsely, densely and evenly granular; 5–8 marginal areolae only occasionally distinguishable from pseudopores; pseudopores circular to elliptical (6–16 μm in diameter), numbering 30–42 (fewer in periancestrular zooids), placed in the proximal half of the zooid (Fig. 2E); area between orifice and ascopore imperforate.

Primary orifice transversely D-shaped, 100–110 (105±7, N = 2) × 129–141 μm (135±8, N = 2) (mean OL/OW = 0.78; mean ZL/OL = 6.14); hinge-line straight or concave, smooth, without condyles and denticles. Five, occasionally six, articulated oral spines, 170–310 μm long (diameter of the base 25–42 μm), the proximalmost pair bi- to trifurcated, the tips sometimes curved towards the centre of the orifice (Fig. 2A, B); joints brown.

Ascopore field an area of smooth, gymnocystal calcification, placed 50–80 μm below the orifice, transversely elliptical, 48–122 × 61–110 μm, narrow distally, more extensive proximally and developing a prominent, pointed mucro not concealing the ascopore; ascopore subcircular, 22–43 μm in diameter, with a dozen of radial spines (Fig. 2F, G).

Avicularia paired, 72–170 (103±29, N = 37) × 46–103 (67±13, N = 37) μm (mean AvL/AvW = 1.53), located distolaterally, the complete crossbar at the same level of the orifice hinge-line (Fig. 2D, E); rostrum short, arched or truncated distally and open-ended, distally directed. Mandible brown, 387–659 μm long, setiform, typically curved, lying on the distal zooid (Fig. 2A).

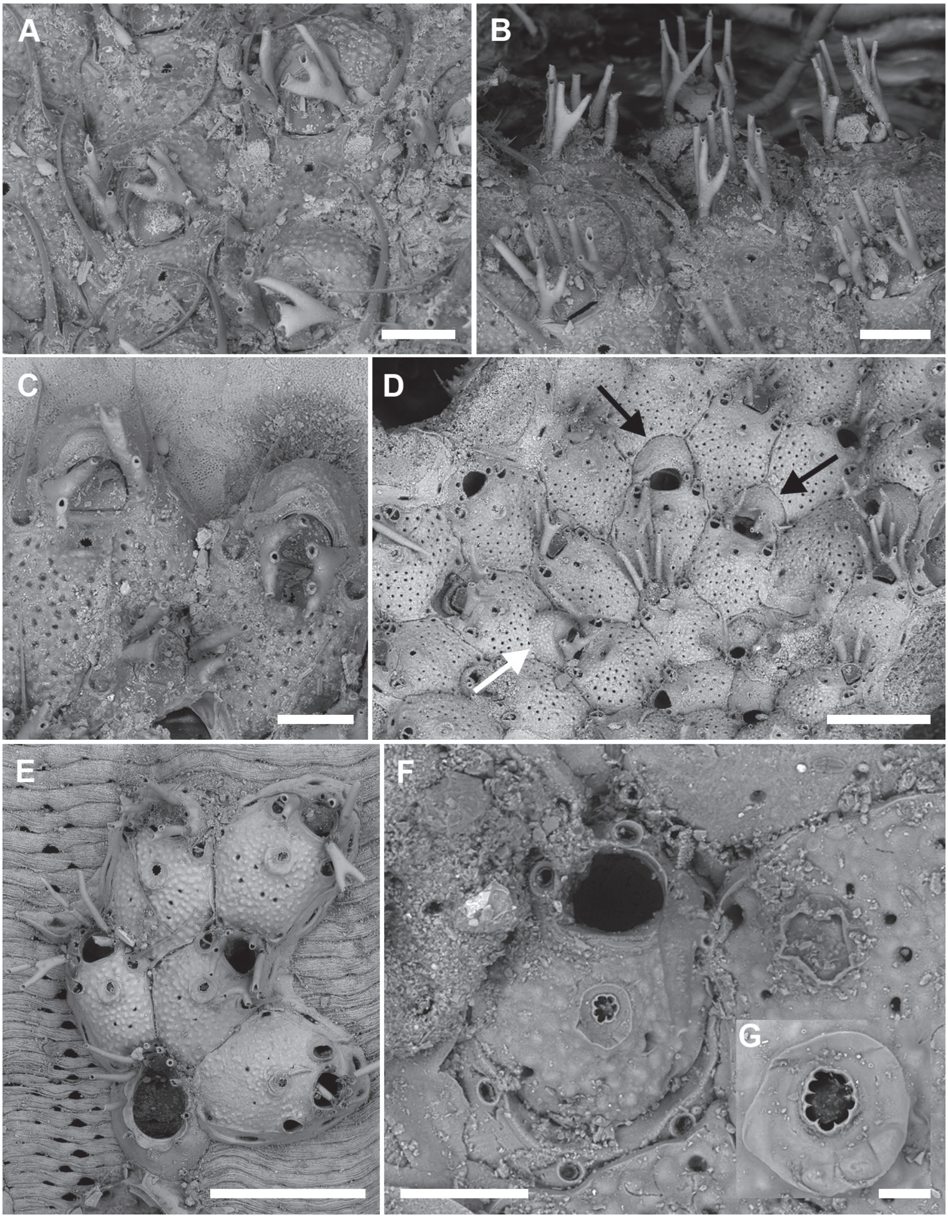

Figure 2. *Microporella appendiculata* (Heller, 1867) from the Iberian-Provençal Basin **A, B** Bisbe cave **E** Falco Cave, PMC Rosso-Collection I. H. B.84b **C, D, F, G** Ionian Sea, Ciclopi 2000, PMC Rosso-Collection I. H. B.84a **A** unbleached autozooids with trifurcate proximal oral spines and long, setiform avicularian mandibles **B** unbleached autozooids with bifurcate proximal oral spines. Note the vertical arrangement of the unbranched distal spines forming a sort of fence around the orifice **C** two kenozooidal ovicells developed on marginal autozooids **D** colony portion showing the co-occurrence of kenozooidal ovicells (black arrows) and ovicells formed by the distal autozooid (white arrow). Note the occurrence of bifurcate and trifurcate proximal spines **E** young colony showing the tatiform ancestrula and first budded autozooids with bifurcate proximal spines **F** ancestrula regenerated as a miniaturised autozooid **G** close-up of the ascopore. Scale bars: 200 μm (**A–D**); 500 μm (**E**); 100 μm (**F**); 30 μm (**G**).

Ovicell subglobular and semi-immersed, 143–235 (195±29, N = 15) × 262–378 (329±38, N = 15) µm (mean OvL/OvW = 0.59), non-personate, not obscuring the proximal part of the orifice, closed by the operculum during brooding (Fig. 2A, C, D), in the same colony either kenozooidal (Fig. 2C, D black arrows) or produced by the distal autozooid (Fig. 2D white arrow); surface finely granular, imperforate; a proximal rim of gymnocystal calcification occupying about one-third of the ooecium length, forming a raised visor-like rim; proximalmost pair of spines (branched) visible in ovicellate zooids.

Ancestrula tatiform (Fig. 2E), oval (424 × 324 µm), gymnocyst more extensive proximally than laterally, about 150 µm wide; opesia pyriform (270 × 180 µm), surrounded by a smooth, flared cryptocyst with the undulate marginal rim indented by ten gymnocystal spines (six distal, two median, three proximal). Ancestrula budding two distolateral autozooids, often regenerated as a small autozooid lacking avicularia (Fig. 2F).

Remarks. Originally described from the Adriatic by Heller (1867), *Microporella appendiculata* has often been recorded as *Microporella marsupiata* Busk, 1860 or as *M. pseudomarsupiata* Arístegui, 1984 (see Hayward and Ryland 1999 and references therein; Rosso et al. 2010; Chimenz Gusso et al. 2014). With the exception of Hayward and Ryland (1999) and recent online material such as the catalogue of the Museu de Ciènces Natural de Barcelona (https://zoologiaenlinia.museuciencies.cat/detall/zoologia_general/N1064271/) and the website of the program DORIS (https://doris.ffessm.fr/Especes/Microporella-pseudomarsupiata-Microporelle-ciliee-noire-1695), a comprehensive description and illustration of this species is absent in the literature.

Microporella flabelligera Levinsen, 1909 described from the vicinity of Siracusa, at depths (28–46 m) comparable to those of the PS/81 sites in the Gulf of Noto, is likely to be conspecific with *M. appendiculata* based on the original drawings (Levinsen 1909: 331, pl. 24 cited as 23 in the text, fig. 6A–C). However, a formal synonymy requires the examination of the type specimen.

Microporella appendiculata differs from other Mediterranean congeners in having paired avicularia, a character shared only with *M. coronata* (Audouin & Savigny, 1826). However, in *M. coronata* the avicularia are located proximally to the ascopore, the ovicell is personate, the oral spines are greater in number (6–8) and unbranched.

Here, we document the regeneration of the ancestrula as an autozooid for the first time (Fig. 2F). Trifurcated proximal spines have already been figured on some zooids, though not described as such by Zabala (1986: fig. 181B, as *M. marsupiata*) and by Chimenz and Faraglia (1995: pl. 2C, as *M. pseudomarsupiata*). Gautier (1962) also recorded autozooids with up to seven oral spines.

Size differences were observed between specimens from Sicily and those from Sardinia, with Sardinian colonies showing longer autozooids (Sicily: mean 604±56 × 458±71 µm, N = 8, L/W 1.32; Sardinia: 698±30 × 458±64 µm, N = 6, L/W 1.53), slender avicularia (Sicily: mean 135±7 × 105±8 µm, N = 25, L/W 1.38; Sardinia: 142±14 × 80±14 µm, N = 12, L/W 1.78), and larger ovicells (Sicily: mean 173±20 × 280±14 µm, N = 5, L/W 0.78; Sardinia: 206±27 × 354±13 µm, N = 10, L/W 0.58), as well as trifurcated proximalmost spines.

Distribution and ecology. In the Mediterranean, *M. appendiculata* has been reported from several localities and usually in shelf habitats, associated with coarse detritic bottoms, often encrusting shells and calcareous algae (Gautier 1962; Rosso 1996a, b; Madurell et al. 2013; Chimenz Gusso et al. 2014), as well as from shadowed microhabitats associated with *Cystoseira* s. l. communities (e.g., Campisi 1973; Rosso et al. 2019a). It also occurs in submarine caves of NW Sardinia (Fraschetti et al. 2010) and near Monaco (J.-G. Harmelin, pers. comm., May 2021) in the Iberian-Provençal basin, at the transition between coralligenous and semi-dark cave habitats. *Microporella appendiculata* has been also collected in dark sectors of Agios Vasilios cave in Lesvos, Greece (Rosso et al. 2019b) and (as *M. umbracula*) in the Mitigliano cave in the Sorrento peninsula, Italy (Balduzzi et al. 1989; Balduzzi and Rosso 2003).

Microporella bicollaris sp. nov.

http://zoobank.org/1C5E0C9C-D08C-48B5-8E7D-8DFB6D6F480D
Fig. 3

Microporella sp. C Rosso et al. 2013a: table 17.1; Rosso et al. 2013b: table 1.

Type material. ***Holotype*****:** Italy • The largest of 2 living colonies on the basal part of a thallus of *Halimeda tuna* (Ellis & Solander) Lamoroux, including the ancestrula and several ovicellate zooids; northern Ionian Sea, Gulf of Taranto, Porto Cesareo MPA; sample PCE10; 40°15'54"N, 17°52'38"E; 5–15 m; 2008; A. Sinagra leg.; scuba diving; C Biocoenosis; ***Paratypes*****:** Italy • 1 dead colony fragment consisting of about a dozen zooids, some fertile; sample PCI10; same details as the holotype; PMC. B29b1. 20.11.2020; 1 dead colony fragment consisting of 9 zooids, 3 of which fertile; Ionian Sea, SE Sicily, Plemmirio MPA, Mazzere submarine cave; sample MZ1 (sediment); 37°00'18"N, 15°18'36"E; 23 m; 14 Sep. 2009; V. Di Martino leg.; scuba diving; C and GSO Biocoenoses; PMC. B29b2. 20.11.2020.

Diagnosis. Colony encrusting, multiserial. Autozooid frontal shield densely pustulose and centrally pseudoporous. Orifice transversely D-shaped; hinge-line smooth with rectangular condyles at corners; five or six oral spines, two visible in ovicellate zooids. Ascopore field circular to elliptical; ascopore opening bean-shaped, with small tongue and radial spines. Avicularium single, located at half zooidal length, directed laterally or slightly disto-laterally; crossbar complete; rostrum lanceolate, channelled. Ovicell produced by the distal zooid, personate with collar enclosing the ascopore and forming a bridge between the orifice and the ascopore, producing two secondary openings.

Description. Colony encrusting, multiserial, unilaminar (Fig. 3A); interzooidal communications through four elliptical, lateral (two proximo- and two disto-lateral), and two rounded, distal pore chamber windows (38–67 × 16–21 µm).

Autozooids hexagonal, 460–522 (494±31, N = 3) × 411–476 (433±37, N = 3) µm (mean L/W = 1.16), boundaries marked by narrow, sinuous grooves and/or a raised rim. Frontal shield slightly convex, densely and evenly pustulose, with 11–25 circular

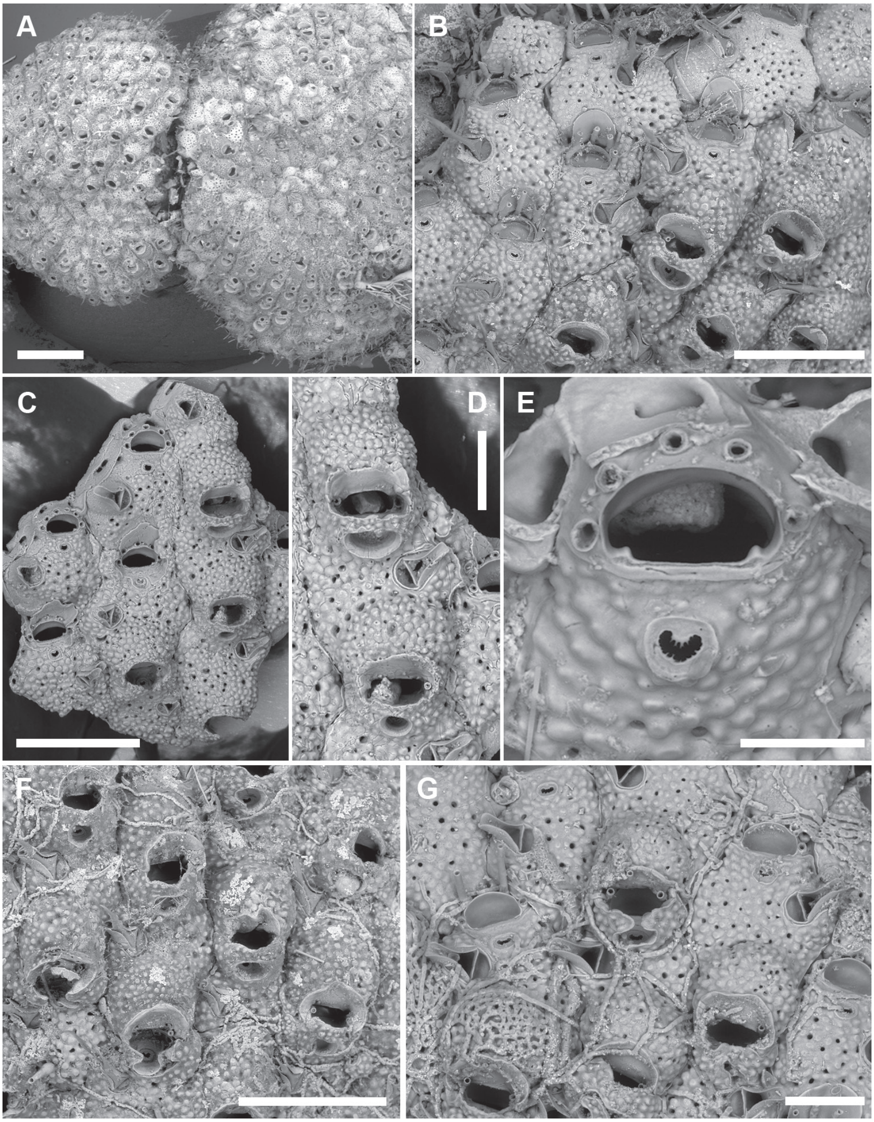

Figure 3. *Microporella bicollaris* sp. nov. from the Ionian Sea **A, B, F** Gulf of Taranto, Porto Cesareo MPA, sample PCE 10 Holotype, PMC. B29a. 20.11.2020 **C, D** SE Sicily, Plemmirio MPA, Mazzere cave, Paratype PMC. B29b2. 20.11.2020 **E, G** Gulf of Taranto, Porto Cesareo MPA, sample PCI 10, Paratype, PMC. B29b1. 20.11.2020 **A** two colonies nearly completely covering subsequent segments of the green alga *Halimeda tuna* **B** peripheral colony portion, showing the transition from the older autozooids (ovicellate, bottom right) to younger autozooids (non-ovicellate, top left) **C** group of autozooids, one with six oral spine bases (centre left) **D** close-up of two ovicellate zooids with the typical personate ovicell forming a collar bridge between the orifice and the ascopore **E** close-up of the orifice with five spine bases and smooth hinge-line with two rectangular condyles at corners **F** unbleached group of ovicellate autozooids with well-developed collars and avicularian mandibles **G** group of bleached autozooids, some ovicellate, fouled by algae. Note the collar developing from converging lateral lappets, the vizor-like band of gymnocystal calcification leaving visible the proximalmost pair of oral spines. Scale bars: 1 mm (**A**); 500 µm (**B, C, F**); 200 µm (**D, G**); 100 µm (**E**).

(diameter 5–20 µm) pseudopores, irregularly distributed centrally; 3–6 marginal areolae, often indistinguishable from pseudopores (Fig. 3C, D).

Orifice transversely D-shaped, 83–95 (89±5, N = 6) × 141–170 (150±11, N = 6) µm (mean OL/OW = 0.60; mean ZL/OL = 5.47), outlined by a thin, raised (relative to the surrounding frontal shield) rim; hinge-line straight, smooth, with a pair of rectangular condyles at corners (Fig. 3E). Oral spines five or six (diameter of the base 18–27 µm), evenly spaced (Fig. 3C, E); proximalmost pair of spines sometimes visible in ovicellate autozooids, embedded between the proximal margin of the ooecium and the personate collar (Fig. 3D, G).

Ascopore field a very narrow, subcircular area of gymnocystal calcification, 35–42 × 46–70 µm, located 35–47 µm below the orifice, at the same level as the orifice but slightly raised relative to the adjacent frontal shield; opening bean-shaped, 32–37 × 9–19 µm, with a small, subcircular tongue projecting from distal edge and tiny radial denticles (Fig. 3E).

Avicularium single, relatively large, 134–190 (165±18, N = 10) × 86–109 (97±9, N = 10) µm (mean AvL/AvW = 1.70), located laterally, on either side, at about half zooidal length (Fig. 3B–D, G); crossbar complete, thin; rostrum long, lanceolate, channelled and open-ended, directed laterally or distolaterally, often raised distally on a smooth, gymnocystal cystid. Mandible lanceolate, 220–245 µm long, slightly longer than the rostrum (Fig. 3B, F).

Ovicell subglobular and slightly prominent, 147–239 (187±34, N = 8) × 262–343 (309±33, N = 8) µm (mean OvL/OvW = 0.60), produced by and continuous with frontal shield of distal zooid, personate, obscuring distal half of the orifice; calcification fabric similar to frontal shield but with smaller pseudopores (diameter 3–8 µm); distal boundary marked by a row of larger pseudopores; proximal margin of gymnocystal calcification forming a raised visor-like band (e.g., Fig. 3B–D). Personate structure of the ovicell with a collar enclosing the ascopore and forming a bridge of two fused flaps between the orifice and the ascopore, producing two secondary openings (Fig. 3D, F, G); secondary orifice transversely elliptical, 71–137 × 180–218 µm; secondary opening over the ascopore trumpet-like (38–52 × 83–145 µm).

Ancestrula tatiform partially overgrown (four spines still visible) and regenerated as an autozooid without avicularium.

Etymology. From the Latin prefix *bi-*, two/double, and the adjective *collaris*, pertaining to the neck, referring to the bridging structure between the orifice and the ascopore appearing as a double collar.

Remarks. Four species with personate ovicells are known to date from the Mediterranean. *Microporella coronata* (Audouin & Savigny, 1826) differs from the new species in having paired avicularia and a greater number of oral spines, always hidden in ovicellate zooids. *Microporella browni* Harmelin, Ostrovsky, Cáceres-Chamizo & Sanner, 2011, *M. genisii* (Audouin & Savigny, 1826), and *M. orientalis* Harmer, 1957 differ in having personate ovicell structures not enclosing the ascopore, and by the denticulation either on the distal or the proximal margin of the orifice.

Among all *Microporella* species known worldwide, the most similar to *M. bicollaris* sp. nov. is the eastern Pacific *M. pontifica* Osburn, 1952 reported from Clarion Island, Galapagos and the Gulf of California. Unfortunately, SEM images are not available for this species, but the original drawing (Osburn 1952: pl. 44, fig. 5) shows the same personate structure of the ovicell observed in *M. bicollaris* sp. nov. However, the new species differs in having a larger avicularium placed more terminally relative to the lateral margin of the zooid, and by the presence of condyles in the orifice. The specimen drawn in Hayward and Ryland (1999: fig. 136D) as *Microporella ciliata* "personate" form of Hincks (1880), also appears similar to *M. bicollaris* sp. nov. However, the illustration in Hincks (1880) appears different, but it is unclear whether Hayward and Ryland (1999) examined any additional material. The north-eastern Atlantic specimens need to be revised to assess their conspecificity with the Mediterranean colonies.

Distribution and ecology. *Microporella bicollaris* sp. nov. is presently known only from Porto Cesareo MPA (Gulf of Taranto, southwestern Apulia, NE Ionian Sea), and the Mazzere submarine cave in the Plemmirio MPA (western Ionian Sea). All colonies are from shallow waters, collected in photophilic algae or found in a semi-dark submarine cave.

***Microporella ciliata* (Pallas, 1766)**

Fig. 4

Eschara ciliata Pallas, 1766: 38.
Microporella ciliata (Pallas): Kukliński and Taylor 2008: 1895, fig. 1a–i.
Non *Microporella ciliata* (Pallas): Hayward and McKinney 2002: 83, fig. 37e–j.

Examined material. Italy • 1 dead colony; Ionian Sea, SE Sicily, Gulf of Noto; sample WP120; 36°44'26"N, 15°10'3"E; 50 m; 1996; E. Mollica leg.; dredging; PMC Rosso-Collection I. H. B.85a.

Remarks. The neotype chosen by Kukliński and Taylor (2008) was selected from material collected in 1984 and 2005 at Penta Palummo Bank, a submerged volcanic edifice in the Bay of Naples rising up to about 40 m depth from the surrounding 80 m shelf. Kukliński and Taylor (2008) already suggested that the Mediterranean material overall assigned to *M. ciliata*, might actually correspond to more than one closely related species. This was observed, for instance, in SEM images of north Adriatic specimens in Hayward and McKinney (2002), which differ from the neotype. Following Kukliński and Taylor (2008), Rosso et al. (2010), Chimenz Gusso et al. (2014), and Rosso and Di Martino (2016) remarked on the need for a revision of the material assigned to this species, whose accorded great variability (e.g., Gautier 1962; Hayward and Ryland 1999) is very likely to correspond to a species complex. The effort to disentangle the *ciliata* complex began with the recent description of *Microporella modesta* Di Martino, Taylor & Gordon, 2020, and is pursued in the present paper with the description of two new species sharing with *M. ciliata* the general appearance and the presence of a single, lateral avicularium as well as non-personate ovicells. Examination of all material available to us, as well as images available in the literature, suggest that

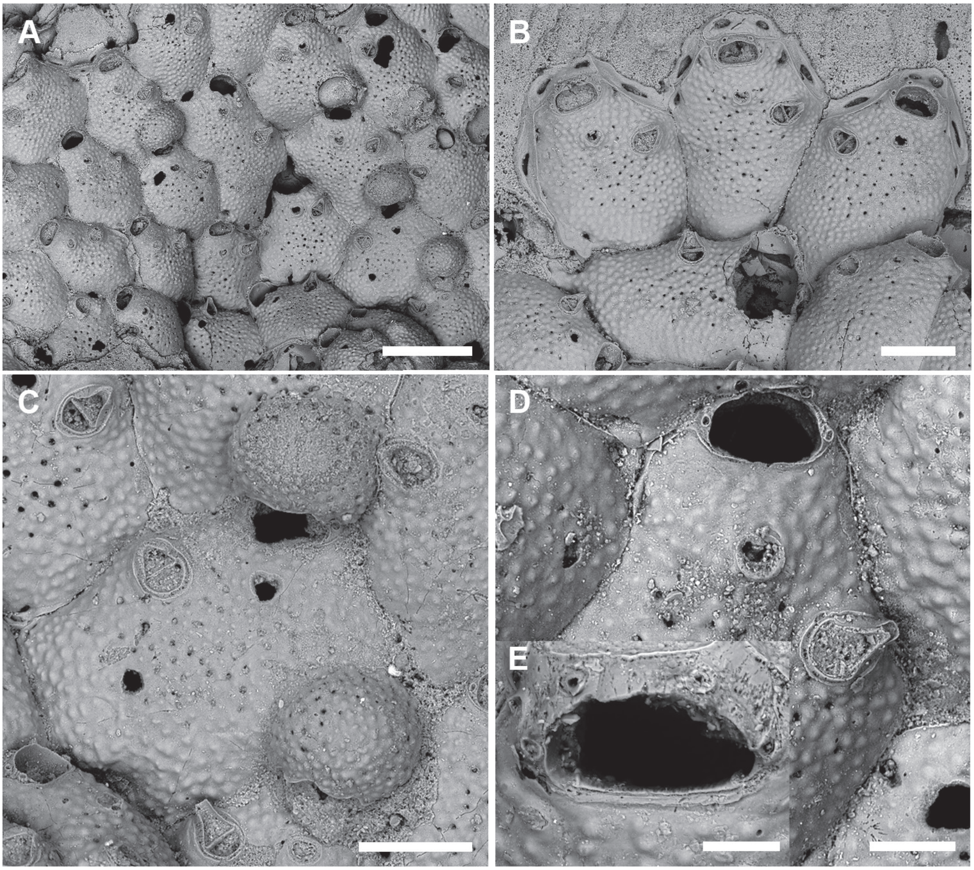

Figure 4. *Microporella ciliata* (Pallas, 1766) from the Ionian Sea, Gulf of Noto, PMC Rosso-Collection I. H. B.85a **A** general view of the colony **B** autozooids at the colony margin showing distal and distolateral pore chamber windows **C** ovicellate autozooids **D** autozooid with the characteristic four, thin, oral spine bases. Note how commonly avicularia regenerate **E** close-up of the orifice showing a series of median denticles and two lateral condyles. Scale bars: 500 µm (**A**); 250 µm (**B**); 200 µm (**C**); 100 µm (**D**); 50 µm (**E**).

M. ciliata, as defined by the neotype, is possibly a rare species in the Mediterranean Sea, or at least a species with a very restricted geographical and/or ecological distribution. A similar conclusion was reached by Chimenz Gusso et al. (2014) after revising their material identified as *M.* cf. *ciliata*, found associated to *Posidonia* and algae between 5 and 88 m depth in several localities of the Tyrrhenian Sea (i.e., off Latium; Spargiotto Island, NE Sardinia; Ustica and Volcano Islands) and the Sicily Strait (Lampedusa Island). The revision of all specimens originally assigned to *M. ciliata* or *M.* gr. *ciliata* in the collections of one of us (AR), originating from several regions and habitats of the Mediterranean Sea, led to the detection of only one colony corresponding with the neotype (Fig. 4). Although the type locality is unknown, it is likely that the original material described by Pallas (1766) was collected in shallow waters from easily accessible substrates, which is not the case for the selected neotype. Colonies of *M. ciliata* recorded from different western Mediterranean localities (Gautier 1962; Zabala 1986, and references therein), Greece (Harmelin 1969) and Turkey (Ünsal 1975), all show great variability and need to be revised to ascertain their identity.

Distribution. Awaiting a general revision of specimens reported from all over the world, focusing on the Mediterranean Sea, the occurrence of *Microporella ciliata* to date is only confirmed in the Gulf of Naples (SE Tyrrhenian Sea) and the Gulf of Noto (W Ionian Sea).

Microporella ichnusae sp. nov.

http://zoobank.org/01CCC2A6-8D65-49F0-8AA9-732ADA5A2ED9
Figs 5, 6

Microporella sp. A Fraschetti et al. 2010: table 27.

Type material. ***Holotype*:** Italy • 1 living colony consisting of more than 100 zooids, including some complete and some broken ovicells; Iberian-Provençal Basin, NW Sardinia, Capo Caccia–Isola Piana MPA, Bisbe submarine cave; sample Bisbe 2; 40°34'15"N, 8°12'55"E; 8 m; 2009; V. Di Martino leg.; scuba diving; GSO Biocoenosis; PMC. B30a. 20.11.2020. ***Paratypes*:** Italy • 9 living colonies, each consisting of a dozen zooids; Iberian-Provençal Basin, NW Sardinia, Capo Caccia–Isola Piana MPA, Bisbe, Falco and Galatea caves; samples Bisbe 1, Bisbe 2, Falco 2, Galatea 1 and Galatea 2; Bisbe, same details as the holotype; Falco: 40°34'09"N, 8°13'14"E; Galatea: 40°34'09"N, 8°13'54"E; 4–8 m; 2008; V. Di Martino leg.; scuba diving; GSO Biocoenosis; PMC. B30b. 20.11.2020.

Diagnosis. Colony encrusting, multiserial. Autozooid frontal shield densely pustulose and sparsely pseudoporous. Orifice transversely D-shaped; hinge-line smooth with blunt condyles close to corners; four thin oral spines, hidden in ovicellate zooids. Ascopore field semi-elliptical; ascopore opening an arched fissure marked by a distal tongue with radial spines. Avicularium usually single, same level as or proximal to the ascopore, occasionally paired, directed distolaterally; crossbar complete; rostrum lanceolate, channelled. Ovicell non-personate.

Description. Colony encrusting multiserial, unilaminar (Fig. 5C, D) with zooids arranged in alternate rows often disrupted on particularly irregular substrata; interzooidal communications through 6–8 elliptical pore chamber windows (40–65 × 18–26 µm).

Autozooids usually hexagonal to rhomboidal but sometimes irregularly shaped, 307–587 (434±73, N = 20) × 284–439 (357±59, N = 20 µm) (mean L/W = 1.21), boundaries marked by narrow grooves and raised rims of lateral walls (Figs 5F, 6B, G). Frontal shield slightly convex with polygonal and flat-topped pustules giving a tessellate appearance, and pierced by circular (diameter 6–12 µm), irregularly distributed pseudopores, usually numbering 10–30 but more numerous in some colonies; 2–4 marginal areolae, elliptical to fissure-like, barely visible or distinguishable from pseudopores (Figs 5F, 6B).

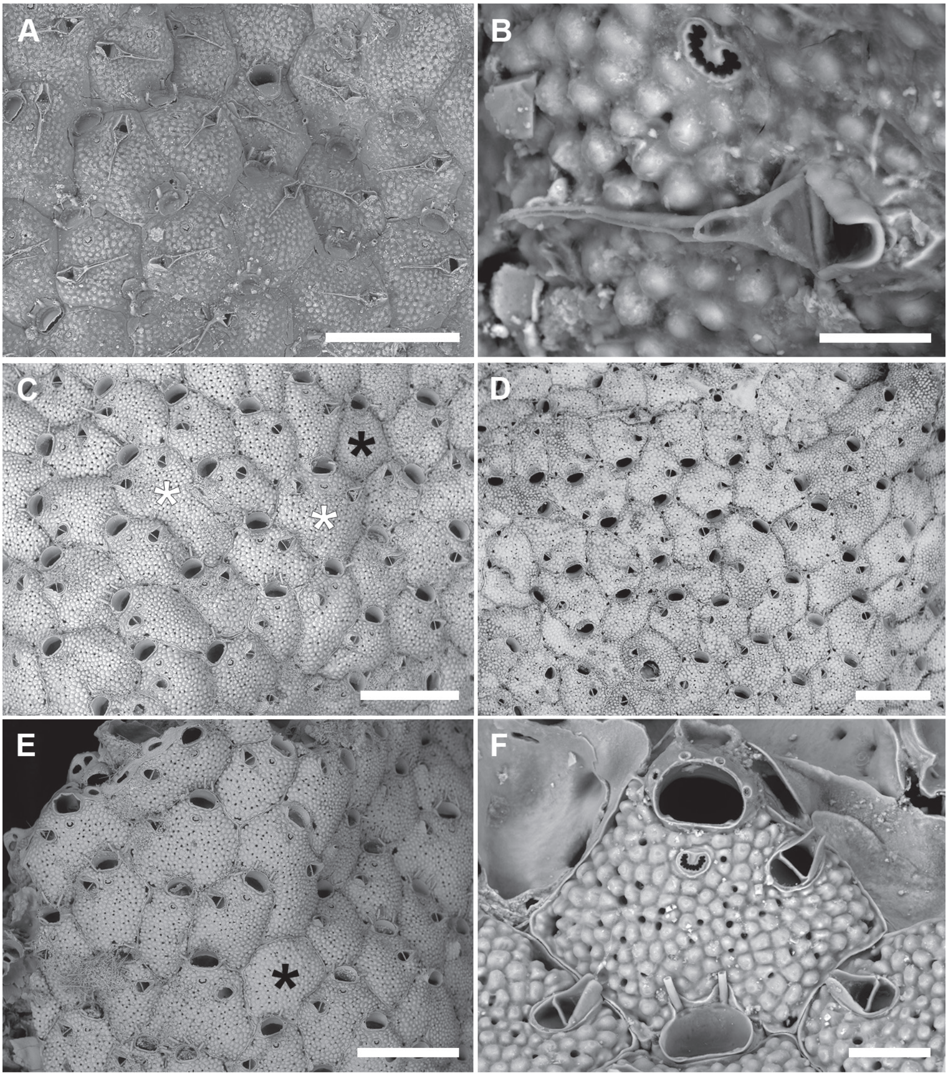

Figure 5. *Microporella ichnusae* sp. nov. from the Iberian-Provençal Basin, NW Sardinia, Capo Caccia-Isola Piana MPA, Falco Cave, Paratype PMC. B30b. 20.11.2020 **A** unbleached colony **B** avicularium with open mandible, showing the channelled rostrum. The straight, short, setiform mandible has a hook at about one-third of its length which clamps it to the rostrum tip **C** bleached autozooids showing size and shape variability. Note that the majority of autozooids has a single avicularium, while few autozooids have paired avicularia (white asterisks) or none (black asterisks) **D** irregularly-shaped autozooids and kenozooids along the contact zone of lobes **E** autozooids and kenozooid (asterisk) near the colony margin with pore-chamber windows visible along exposed lateral walls **F** autozooid at the growing edge showing the morphology of the orifice and four, thin spine bases. Scale bars: 500 µm (**A, C, D, E**); 50 µm (**B**); 100 µm (**F**).

Orifice transversely D-shaped, 75–94 (81±5, N = 20) × 109–145 (122±10, N = 20) µm (mean OL/OW = 0.67; mean ZL/OL = 5.33), outlined by a thin, slightly raised rim; hinge-line straight, smooth, with a pair of small triangular, blunt condyles close to corners (Fig. 5F). Oral spines four, occasionally five or six (diameter of the bases 10–14 μm), evenly spaced, the proximal pair located at orifice mid-length; spines hidden in ovicellate autozooids (Fig. 6B, E).

Ascopore field a small and very narrow, transversely semi-elliptical area marked by a thin raised gymnocystal rim, 28–36 × 30–50 μm, located 25–50 μm below the orifice, at the same level as the frontal shield; opening transversely C-shaped, 20–30 × 6–10 μm, with a subcircular tongue projecting from distal edge, and relatively few, tiny, radial denticles.

Avicularium most often single (Figs 5E, F, 6B, D), occasionally paired (Fig. 5C) or absent (Figs 5C, E, 6C), relatively large, 75–120 (98±13, N = 20) × 55–91 (71±11, N = 20) μm (mean AvL/AvW = 1.39), located laterally, on either side, in the distal zooidal half, same level as or proximally to the ascopore (Figs 5B, F, 6B, E) but on irregularly shaped zooids occasionally placed in the proximal part; crossbar complete, thin; rostrum triangular, channelled and open-ended, directed laterally or distolaterally, often distally raised on a smooth, gymnocystal cystid (Fig. 5F). Mandible 160–180 μm long, setiform, with a hook at about one-third of its length that clamps it to the rostrum tip, crossing the whole zooid when open (Fig. 5A, B).

Ovicell subglobular and prominent, 185–241 (214±25, N = 4) × 290–314 (297±11, N = 4) μm (mean OvL/OvW = 0.72), produced by and continuous with frontal shield of distal zooid, obscuring distal part of the orifice; calcification fabric similar to frontal shield but with smaller and more prominent pustules; pseudopores small (diameter 5–10 μm), densely packed at the periphery, absent centrally (Fig. 6B, E).

Kenozooids smaller than or nearly as large as autozooids, lacking openings such as orifices and ascopores but sometimes equipped with avicularium (Fig. 6A, F).

Ancestrula not observed.

Etymology. From *Ichnusa* the Latinized form of the ancient Greek name for Sardinia.

Remarks. Size and shape of autozooids vary remarkably within and between colonies, including dwarf-like autozooids, about half the size of the more regular ones, as well as extremely large and irregularly shaped autozooids, appearing as the result of the fusion of contiguous autozooids (Fig. 5C, E). In this latter case the avicularium can be placed much more proximally than in regular autozooids. Irregularly-shaped autozooids also occur in *M. browni* (Harmelin et al. 2011: fig. 3b). These unusual autozooids and the kenozooids observed in this species seem to be particularly common in zones of contact between colonies or lobes of the same colony, and in damaged areas, also associated with evidences of reparation (Figs 5D, 6A, D), such as regeneration of broken autozooids, patches of calcification to close holes in the frontal shield, or orifices of presumably not functional autozooids (Fig. 6G). Intrazooidal budding, a feature that is common in bryozoans from submarine caves (e.g., Rosso et al. 2020a, 2020b), has been more commonly observed in avicularia (Fig. 6C, D) than autozooids (Fig. 6F, G). The occurrence of ovicells seems rare, observed only on the colony selected as the holotype.

The general appearance of this new species is very similar to *M. ciliata*. However, the orifice in *M. ciliata*, although of comparable size (0.06–0.08 mm long by 0.11–0.15 mm wide), is proportionately shorter, the hinge-line shows a series of median denticles

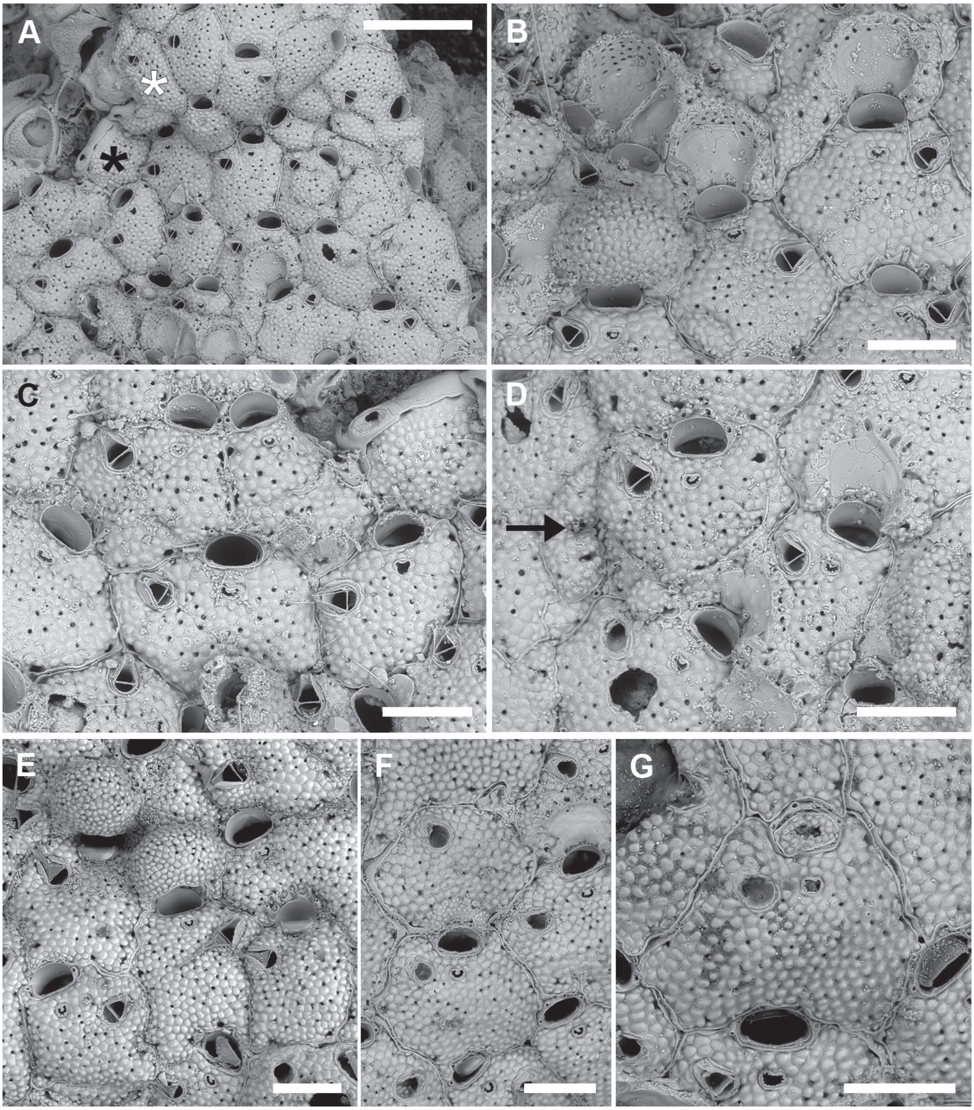

Figure 6. *Microporella ichnusae* sp. nov. from the Iberian-Provençal Basin, NW Sardinia, Capo Caccia-Isola Piana MPA, Bisbe Cave, Holotype PMC. B30a. 20.11.2020 **A** colony portion with broken ovicells, autozooids showing evidences of reparation, and kenozooids with (white asterisk) and without (black asterisk) avicularia **B** autozooids with complete or broken ovicells **C** paired autozooids, seemingly repaired, one lacking avicularium **D** close-up of a colony portion with evidence of zooidal repair. Note the occluded orifice indicated by the partly protruding spines (see arrow) **E** group of zooids (two ovicellate), some with open or closed mandibles and one lacking an avicularium **F** close-up of two zooids. Owing to the absence of an ascopore, which is usually placed at the same level as the avicularium, the upper one is more likely to be a kenozooid equipped with an avicularium than an autozooid with obliterated orifice. Note also the different frontal shield texture of its proximal margin, likely due to ovicell resorption **G** close-up of an autozooid with sealed orifice (central zooid), and an orifice with a thin secondary rim, indicating intramural budding presumably as a result of predation. Scale bars: 500 µm (**A**); 200 µm (**B–G**).

and the two lateral condyles are more prominent and more laterally placed (Fig. 4E; see also Kukliński and Taylor 2008: fig. 1G). The type and position of the oral spines are similar but the number of spines is 4–6 (more commonly four) in *M. ichnusae* sp. nov. and 1–4 (and occasionally lacking in the zone of astogenetic repetition) in *M. ciliata* (Kukliński and Taylor 2008). In *M. ciliata* the frontal avicularium is constantly single, only lacking in the first autozooid budded from the ancestrula, and no kenozooids were reported (Kukliński and Taylor 2008). Furthermore, the ovicells in *M. ciliata* have length comparable with those of *M. ichnusae* sp. nov. but are much narrower.

Distribution and ecology. *Microporella ichnusae* sp. nov. is presently known only from submarine caves in the Capo Caccia-Isola Piana MPA, in NW Sardinia. However, it is possible that some previous records of *M. ciliata*, to date the only *Microporella* species with a single avicularium considered as widespread in the Mediterranean, belong to this species.

Microporella modesta Di Martino, Taylor & Gordon, 2020

Fig. 7

Microporella modesta Di Martino et al. 2020a: 23, fig. 11, table 8.
Microporella orientalis Harmer, 1957: Rosso 1996a: table 2.
Microporella ciliata (Pallas): Rosso 1989: tables 3, 4, 6; Di Geronimo et al. 1990: table 1; Di Geronimo et al. 1993b: table 3; Rosso 1996a: table 2; Rosso 1996b: table 1; Hayward and McKinney 2002: 83, fig. 37e–j.
Microporella cf. *ciliata* (Pallas): Chimenz Gusso et al. 2014: 189, fig. 101a–f.
Microporella gr. *ciliata* (Pallas): Rosso et al. 2019a: table 1.

Examined material. Italy • 30 dead colony fragments, 8 of which bilaminar, 1 pseudovinculariform and the majority encrusting on *Cellaria* internodes; Ionian Sea, E Sicily, Ciclopi Islands MPA; Ciclopi 2000 cruise; sample 2G, 8I, 9G, 12E, 12F, 12G; 37°34'4"N, 15°10'51"E; 63–95 m; Jul. 2000; DC, DE–DL, DL Biocoenoses; A. Rosso leg.; dredging; PMC Rosso-Collection I. H. B.86a. Italy • 1 living colony, Ionian Sea, E Sicily, Ciclopi Islands MPA; sample SM1Z25; 37°38'17"N, 15°10'53"E; 25 m; Jun. 2015; R. Leonardi leg.; scuba diving; IA Biocoenosis; PMC Rosso-Collection I. H. B.86a1. Italy • 2 living colonies fouling on a plastic bag; Ionian Sea, E Sicily, Gulf of Ognina, North of Catania; 37°31'52"N, 15°6'59"E; 4 m; 11 Feb. 2012; V. Grado leg.; scuba diving; PMC Rosso-Collection I. H. B.86b. Italy • 15 living colonies on *Posidonia* leaves; Ionian Sea, E Sicily, S of the Gulf of Catania, Castelluccio; 37°18'32"N, 15°7'59"E; beached; 6 Feb. 2019; A. Rosso leg.; hand-collected; PMC Rosso-Collection I. H. B.86c. Italy • 3 living and 1 dead colony fragments; Ionian Sea, SE Sicily, Plemmirio MPA, Granchi submarine cave; sample GR1; 37°00'18"N, 15°18'35"E; 23 m; 14 Sep. 2009; V. Di Martino leg.; scuba diving; C and GSO Biocoenoses; PMC Rosso-Collection I. H. B.86d. Italy • 16 living and 32 dead colony fragments, nearly all on *Cellaria* internodes, Ionian Sea, SE Sicily, Gulf of Noto; 36°41'45"–36°57'47"N, 15°8'35"–15°20'00"E; PS/81 cruise; samples

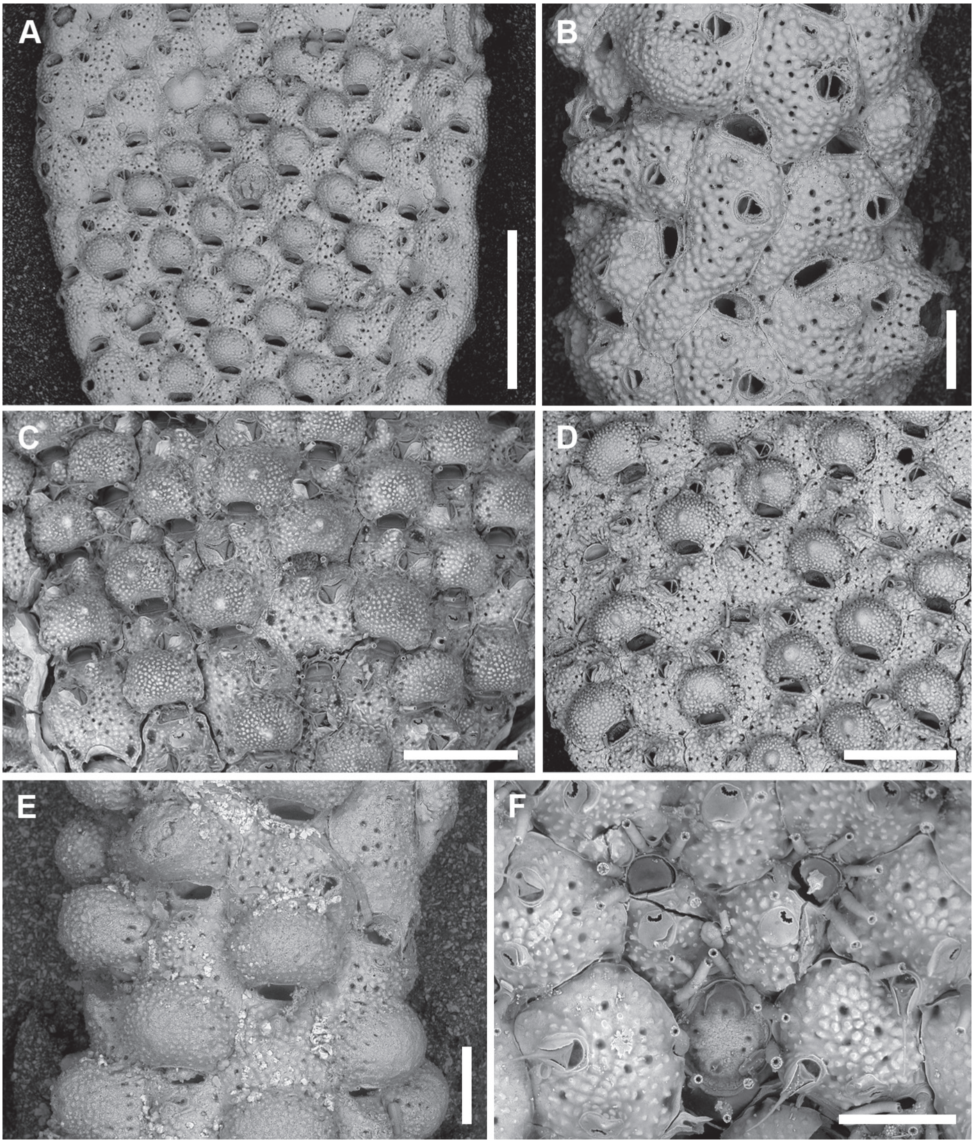

Figure 7. *Microporella modesta* Di Martino, Taylor & Gordon, 2020 from several localities **A** Ionian Sea, Ciclopi 2000, PMC Rosso-Collection I. H. B.86a **B** Ionian Sea, Gulf of Noto, PMC Rosso-Collection I. H. B.86e **C** Sicily Strait, Egadi Islands, PMC Rosso-Collection I. H. B.86h **D** Ionian Sea, Castelluccio, PMC Rosso-Collection I. H. B.86c **F** Iberian-Provençal Basin, Asinara MPA, PMC Rosso-Collection I. H. B.86j **A** bilaminar branch with elongate autozooids along branch edge and a cluster of ovicells **B** apparently cylindrical branch resulting from a colony encrusting an internode of *Cellaria*. Note the formation of irregularly elongate autozooids **C** unbleached colony encrusting a soft algal frond. Prominent avicularian rostra and mucros associated with ascopore contribute to the spiky appearance of the colony. Note the co-occurrence of ovicells with and without frontal tubercles **D** bleached colony on algae with ovicells with different degrees of frontal tubercle development **E** ovicellate zooids of a tubular "pseudovinculariiform" colony originally developed on a thin ephemeral substratum **F** originally tatiform ancestrula regenerated as a kenozooid, budding two distolateral autozooids lacking avicularia. Scale bars: 1 mm (**A**); 200 µm (**B, E, F**); 500 µm (**C, D**).

CR1, 2XB, 4C, 4X, 9B, 9C, 9D, 10C, 11E; 45 m (living), 44–120 m (dead); I. Di Geronimo leg.; dredging; and 25 living and 25 dead colony fragments, nearly all on *Cellaria* internodes; Noto 1996 cruise; samples 3C, 5E, 7E, 10G, 10I, WP120; 20–82 m (living), 90–107 m (dead); 1996; E. Mollica leg.; dredging; C, DC, DE and DL Biocoenoses; PMC Rosso-Collection I. H. B.86e. Italy • 2 living colonies, Ionian Sea, Gulf of Taranto, Amendolara Bank; samples 1D and 5D; 39°51'42"–39°52'54"N, 16°42'00"–16°43'24"E; 30–40 m; Jun. 1991; R. Sanfilippo leg.; dredging; DC Biocoenosis; PMC Rosso-Collection I. H. B.86f. Italy • 4 living and 3 dead colonies; Sicily Strait, Pelagie Islands MPA, Lampedusa Island; submarine caves: Taccio Vecchio I, 35°31'29"N, 12°35'58"E, 20 m; Grotta della Madonna, 35°30'2"N, 12°33'25"E, 15 m; Grotta dello Scoglio di Fora, 35°30'25"N, 12°33'33"E, 10 m; Jun. 2009; V. Di Martino leg.; scuba diving; C and GSO Biocoenoses; PMC Rosso-Collection I. H. B.86g. Italy • about 100 living colonies, mostly on *Posidonia* leaves, soft algae, light calcified *Peissonnelia* spp. and calcified thin-branched geniculate corallines; Sicily Strait, Egadi Islands, Marettimo Island; sample ECE5; 37°56'59"N, 12°3'56"E; 8 m; summer 2007; A. Sinagra leg.; IA and HP Biocoenoses; scuba diving; PMC Rosso-Collection I. H. B.86h. Italy • 6 living and 2 dead colony fragments, 2 of which bilaminar; southern Tyrrhenian Sea, SW Ustica, Apollo Bank; 38°42'19"N, 13°7'58"E; 60 m; Jun. 1986, dredging and scuba diving; *Laminaria rodriguezii* Bornet, 1888 seagrass and associated DC; PMC Rosso-Collection I. H. B.86i. Italy • 7 living colonies; Iberian-Provençal Basin, Asinara MPA; samples PSE and PSI1; 41°6'59"N, 8°18'6"E; 5–15 m; A. Sinagra leg.; scuba diving; IA Biocoenosis; PMC Rosso-Collection I. H. B.86j. Italy • 1 dead colony, southern Adriatic Sea, off Apulia, Bari canyon; sample 1B1; 41°17'29"N, 17°9'14"E; 280 m; 29 May 2012; F. Mastrototaro leg.; dredging; PMC Rosso-Collection I. H. B.86k.

Remarks. *Microporella modesta* has been recently established (Di Martino et al. 2020a) for some Mediterranean specimens collected off Algeria and growing as erect, narrow, bilaminar fronds. However, SEM images in Hayward and McKinney (2002) and Chimenz Gusso et al. (2014) reveal that a large part of the figured Mediterranean specimens seem to be conspecific with *M. modesta*, although none of them has been described as erect bilaminar. This is also the case for most colonies and colony fragments in the collection of one us (AR), mostly previously assigned to *M. ciliata*, which allowed us to assess the intraspecific variability of *M. modesta*.

Strap-like branches including up to 11 or 12 longitudinal series of zooids occur only occasionally (Fig. 7A), while bilaminar arched fronds narrowing proximally are rare, and encrusting sheets are the most common. Branches are always broken off so that the way they form from the putative encrusting base remains unknown. Lateral edges often consist of extremely elongate autozooids covering the length of three regular autozooids, with the proximal two thirds about half the width of the distal part (Fig. 7A). Apparently cylindrical branches result from colonies encrusting thin, cylindrical substrata (Fig. 7B, E), either mineralised and persistent (mostly internodes of *Cellaria* in deep-water samples, and geniculate coralline algae in shallow-water samples), or organic and ephemeral. In this latter case, the resulting pseudovinculariiform colonies are found in the sediment as hollow tubular fragments after substratum decay. A great number of colonies were observed encrusting soft algae, small *Peissonnelia* spp., and leaves of *Posidonia oceanica* (Linnaeus) Delile 1813, usually developing relatively small colonies, occasionally reaching 1–2 cm^2.

In addition to colony morphology, variability includes also autozooidal characters. The orificial condyles were less prominent and more laterally placed in specimens from the Apollo Bank; the number of spines is usually five in encrusting colonies from the Ionian Sea (e.g., Amendolara and Ognina), but up to six or seven on some autozooids in colonies from the Sicily Strait (e.g., Madonna cave); spines also tend to be thicker, and the proximal pair more visible on ovicellate autozooids (e.g., in colonies from caves of the Ionian Sea and Sicily Strait) than in the holotype; a prominent central umbo can develop on the ovicell of some zooids (Fig. 7C, D). As in *Microporella ichnusae* sp. nov., irregularly shaped elongated autozooids develop when lobes of a colony join, mostly in colonies on cylindrical substrata (Fig. 7B). Intrazooidal budding frequently occurs in avicularia, while repair of autozooids was rarely observed.

The ancestrula was observed for the first time only in two colonies (sample PSI1 and ECE5), seemingly because it is soon overgrown. It is tatiform, with 10–12 spines surrounding a very thin, raised rim without apparent cryptocyst. It is rebudded as a kenozooid with a row of at least eight pores in one case (Fig. 7F). A comparable structure was figured in Kukliński and Taylor (2008) for *M. ciliata* and can be also observed in *M. browni* from the Maldive Islands (https://www.univie.ac.at/Palaeontologie/Sammlung/Bryozoa/Maldive_Islands/Cheilostomata/Microporellidae/Microporella/Microporella-browni.html). The ancestrula buds two distolateral autozooids with 5–7 oral spines.

Ovicells are very numerous in this species, occurring in the majority of autozooids in some colonies (Fig. 7A, C, E). Ovicell tubercles when developed, along with the mucro associated to the ascopore, and the raised rostrum of the avicularium give to the colony a characteristic knobby or spiky appearance.

The majority of specimens recorded from the Mediterranean previously assigned to *M. ciliata*, as well as some isolated colony fragments attributed to *M. orientalis* seem to belong to *M. modesta*.

Distribution and ecology. *Microporella modesta* was previously reported exclusively from off Algeria (Di Martino et al. 2020a), but the material studied here as well as specimens figured in recent literature (Hayward and McKinney 2002; Chimenz Gusso et al. 2014) widen its geographical distribution. The species appears to be widely distributed in the Mediterranean where it occurs in the Iberian-Provençal basin, the Tyrrhenian, Ionian, and Adriatic seas as well as in the Sicily Strait. The species seems widely distributed in shallow shelf habitats with preference for the vegetate bottoms of the infralittoral zone and the Coralligenous Biocoenosis, with the possibility to extend into semi-dark caves. Findings from deeper (mid-shelf) particulate bottoms are largely represented by dead colonies/fragments possibly indicating a displacement.

Microporella pachyspina **sp. nov.**

http://zoobank.org/01E293A7-7645-4D29-B3D3-70905E995CE8

Fig. 8

Type material. *Holotype*: Italy • 1 living colony consisting of about 50 zooids, several fertile; Sicily Strait, Egadi Islands, Marettimo Island; 37°56'59"N, 12°3'56"E; sample ECE5; 8 m; summer 2007; A. Sinagra leg.; IA and HP Biocoenoses; scuba diving; PMC. B31a.3.12.2020. ***Paratypes*:** Italy • ECE5, 2 living, fertile colonies, one including the ancestrula on a *Posidonia oceanica* leaf; same details as the holotype; PMC. B31b. 3.12.2020.

Other material. Italy • a few living colonies, Sicily Strait, Egadi Islands, Marettimo Island; 37°56'43"N, 12°5'3"E; sample EBE4; 19 m; summer 2007; A. Sinagra leg.; IA-HP Biocoenoses; scuba diving; PMC Rosso Collection I. H. B.87a.

Diagnosis. Colony encrusting, multiserial. Autozooid frontal shield granular and centrally pseudoporous. Orifice transversely D-shaped; hinge-line smooth with rectangular condyles at corners; five (more commonly) to eight oral spines, the proximalmost pair placed slightly below the orifice hinge-line and very large in diameter. Ascopore field reniform to elliptical, developing a mucro proximally; ascopore opening transversely C-shaped, with tongue and radial spines. Avicularium single, located at half zooidal length, directed distolaterally; crossbar complete; rostrum triangular, channelled. Ovicell produced by distal autozooid, non-personate.

Description. Colony encrusting, multiserial, unilaminar, forming subcircular patches less than 1 cm in diameter, consisting of several tens of zooids, typically on *Posidonia* leaves; interzooidal communications through pore chamber windows along lateral walls (44–99 × 12–20 μm), two elliptical pairs placed proximolaterally and distolaterally, and a single distal one more rounded.

Autozooids hexagonal, 374–510 (442±50, N = 24) × 257–346 (290±31, N = 24) μm (mean L/W = 1.52), distinct with interzooidal boundaries marked by deep grooves between salient vertical walls (Fig. 8A), often exposing the smooth, lateral gymnocyst. Frontal shield nearly flat proximally, slightly convex disto-centrally, finely to coarsely granular and pseudoporous (Fig. 8C, D); granules 5–10 μm in diameter, irregularly spaced; 6–18 pseudopores, circular (7–25 μm in diameter), irregularly arranged, mostly centrally in the proximal half of the zooid; 3–6 marginal areolae, usually visible at zooidal corners, those placed proximally and laterally fissure-like (up to 90 μm long), the single or paired distal ones rounded (20 μm in diameter).

Orifice transversely D-shaped, 75–93 (84±6, N = 15) × 89–127 μm (108±12, N = 15) (mean OL/OW = 0.78; mean ZL/OL = 5.17), outlined by a thin and smooth raised rim; hinge-line straight, smooth, with a pair of rectangular condyles at corners (Fig. 8B). Five (Fig. 8B) (occasionally 6–8: Fig. 8G) oral spines; the proximalmost pair robust, the base 36–51 μm in diameter, horn-shaped, terminally tapering and bending, placed slightly below the level of the orifice hinge-line, persisting in ovicellate autozooids (Fig. 8E); the three (occasionally 4–6) distal spines thinner (base diameter 13–32 μm).

Ascopore field a reniform to elliptical area of smooth gymnocystal calcification (39–78 × 45–102 μm), more extensive proximally, developing a pointed, upward directed mucro not concealing the ascopore opening, placed 30–60 μm below the orifice, slightly depressed

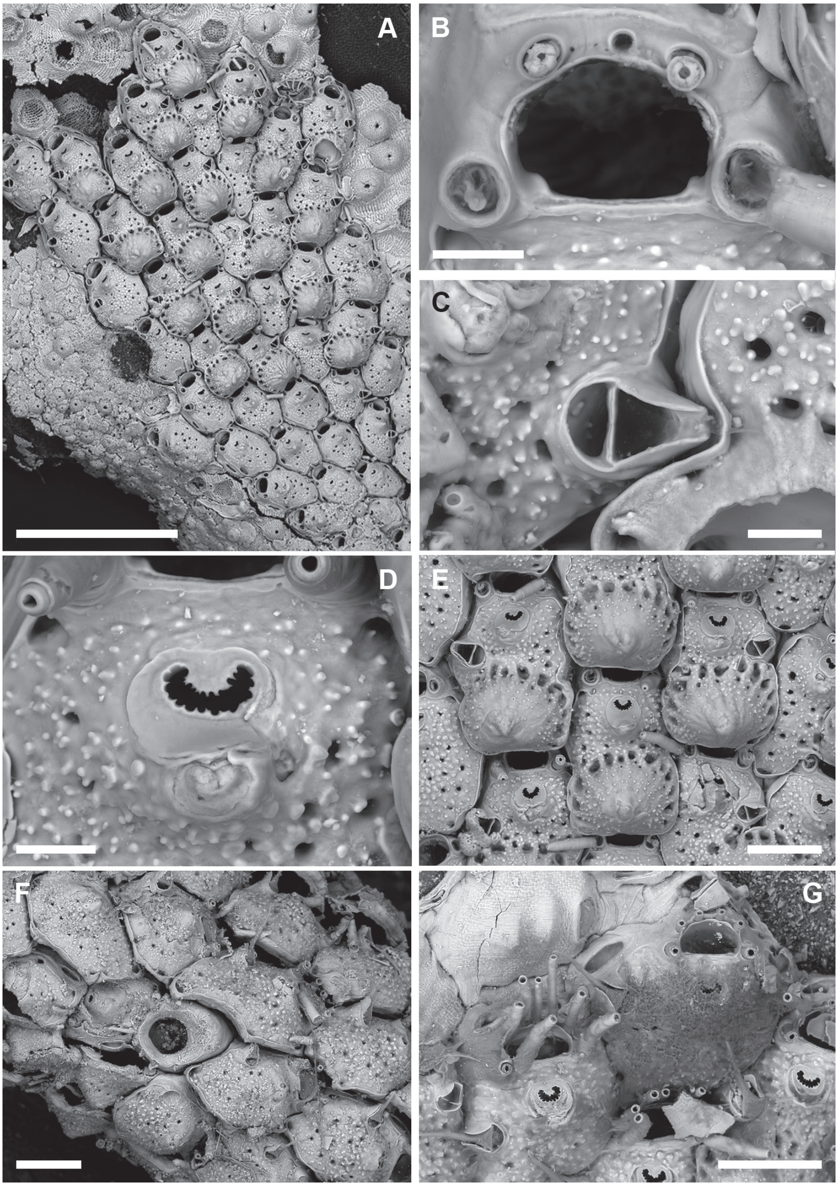

Figure 8. *Microporella pachyspina* sp. nov. from Sicily Strait, Egadi Islands **A–E** holotype PMC. B31a.3.12.2020 **F, G** paratype PMC. B31b. 3.12.2020 **A** colony general view **B** close-up of orifice with proximolateral rectangular condyles, smooth hinge-line, and five oral spine bases. Note the giant proximolateral pair of spine bases located at hinge-line level and at some distance from the thinner, distal ones **C** close-up of avicularium with truncated, channelled rostrum projecting laterally outside its edge affecting the shape of the adjacent zooid margin **D** close-up of ascopore with proximal mucro **E** ovicells smooth and imperforate centrally, finely granular and with a row of large pores peripherally. Radial buttresses between marginal pores converge towards the median umbo **F** Ancestrula budding one distal and two distolateral autozooids. Two larger, proximolateral, curved autozooids complete the periancestrular region **G** autozooids from the colony growing margin with six or seven oral spines. Scale bars: 1 mm (**A**); 50 µm (**B–D**); 200 µm (**E–G**).

relative to the adjacent frontal shield (Fig. 8D); opening transversely C-shaped, 32–64 × 7–18 µm, with subcircular tongue projecting from distal edge and radial, tiny denticles.

Avicularium single, often absent (e.g., 40% of zooids without avicularium in a colony of 42 zooids), moderately large, 76–115 (94±10, N = 33) × 48–78 µm (63±9, N = 33) (mean AvL/AvW = 1.50), located laterally, on either side, at about half zooidal length; crossbar complete; rostrum short, rounded triangular, channelled, directed distolaterally, often raised distally on a smooth, gymnocystal cystid (Fig. 8C). Mandible 143–224 µm long, pointed, with a hook at about one-third of its length that clamps it to the rostrum tip, lying proximally to ascopore when open (Fig. 8G).

Ovicell non-personate, subglobular, prominent, 216–320 (251±23, N = 20) × 241–312 (288±22, N = 20) µm (mean OvL/OvW = 0.87), obscuring half to two-thirds of the zooidal orifice, formed by and continuous with frontal shield of distal zooid (Fig. 8E) (occasionally of two zooids), lateral gymnocystal margins raised, exceeding boundaries of the autozooid on which it lies; calcification fabric similar to frontal shield but with smaller and more widely-spaced granules, sometimes completely smooth centrally and with a rounded mucro (Fig. 8A, E); imperforate except for 12–18 large pseudopores aligned in a peripheral row, closely and evenly spaced, separated by radial ridges, rounded quadrangular, 17–42 µm in diameter, plus an additional, discontinuous inner row of 4–6 smaller, circular pseudopores (5–10 µm).

Ancestrula tatiform, oval (300 × 218 µm), gymnocyst moderately developed, more extensive proximally (Fig. 8F); opesia subcircular, surrounded by a well-developed, smooth cryptocyst, more extensive proximally, narrowing distally, outlined by a thin elevated rim indented by ten gymnocystal spines (six distal, two median, two proximal). Ancestrula budding two distolateral autozooids, followed by two lateral and two proximolateral ones.

Etymology. From the Greek *pachys*, meaning thick, and the Latin *spina* meaning spine, referring to the robust proximalmost pair of oral spines.

Remarks. The main diagnostic character of *Microporella pachyspina* sp. nov. is the great size of the proximalmost pair of oral spines, as well as their position, halfway below the level of the orifice hinge-line. Among *Microporella* species known worldwide, *M. alaskana* Dick & Ross, 1988 from the eastern Pacific, *M. echinata* Androsova, 1958, and *M. trigonellata* Suwa & Mawatari, 1998, both from off Japan, share similar features. In *M. alaskana* the proximalmost pair of spines are larger in diameter compared to the remaining spines but they are placed more distally compared to the new species, approximately at orifice mid-length (Dick and Ross 1988); in addition, this species has paired avicularia, the ascopore is placed very close to the orifice hinge-line, and there is a prominent umbo centrally on the frontal shield (Dick and Ross 1988). *Microporella echinata* differs in having an evenly pseudoporous frontal shield, with pseudopores visibly larger, and tubercular (Mawatari et al. 1991). *Microporella trigonellata* shows the same number, relative size, arrangement and position of spines but differs from the new species in having the avicularium placed distolaterally, directed distally, with a pointed, non-channelled rostrum; also, the ridges and grooves on the ovicells are distinctly defined and more marked, and the ancestrula has a narrower proximal gymnocyst (Suwa and Mawatari 1998).

The general appearance of those zooids lacking avicularia in *M. pachyspina* sp. nov. reminds those of *Fenestrulina joannae* (Calvet, 1902), which are also similar in having the proximalmost pair of spines long, robust and rounded, non-stellate pseudopores sparse on the frontal shield, centrally smooth ovicells, sometimes with peripheral radial ridges, developing a mucro (Chimenz Gusso et al. 2014: 165, fig. 82a–c). This latter species, originally described as *Microporella* by Calvet (1902), was reassigned to *Fenestrulina* by Gautier (1962: 171) apparently based on a suggestion made by Hastings without any supporting statement, instead highlighting the different type of pseudopores (non-stellate) compared with those of the type species of the genus *Fenestrulina malusii* Audouin, 1826. Subsequent authors followed Gautier (1962). *Fenestrulina* species have large, stellate pseudopores mostly occupying the area of the frontal shield between the ascopore and the orifice, a sector that is usually imperforate in *Microporella*. Based on these observations, *Fenestrulina joannae* seems to have more affinities with *Microporella* and here we suggest its displacement.

Dry specimens on organic substrates (i.e., *Posidonia* leaves) appear with the zooids disconnected or almost disconnected, giving to the colony a slightly disjunct appearance because the zooids were less packed hence exposing a more extensive, smooth gymnocyst laterally (Fig. 8F). This loose packing is a common adaptation in species growing on flexible substrates to reduce the potential breakage of the zooidal skeletons.

Distribution and ecology. Presently known only from shallow waters off Egadi Islands, at the western limit of the Sicily Strait in the Mediterranean Sea, associated with *Posidonia* meadows and the Infralittoral Algae Biocoenosis.

Microporella sp. A

Fig. 9

Examined material. Italy • 1 dead colony fragment consisting of ca. 14 zooids (some incomplete), none fertile; Tyrrhenian Sea, Palinuro Cape, Scaletta submarine cave; sediment sample; 40°1'35"N, 15°16'7"E; 46 m; 14 Sep. 2009; R. Leonardi leg.; scuba diving; PMC Rosso Collection I. H. B.88a.

Description. Colony encrusting, multiserial, unilaminar.

Autozooids irregularly polygonal, rounded, 435–676 (510±80, N = 7) × 255–427 µm (342±68, N = 7) (mean L/W = 1.49), distinct, with interzooidal boundaries marked by a narrow, raised, gymnocystal rim (Fig. 9A). Frontal shield nearly flat to slightly convex, densely and coarsely granular and irregularly pseudoporous; granules 5–25 µm in diameter; 20–30 pseudopores, circular (5–12 µm in diameter), sparse in the proximal two-thirds of the zooid; 4–6 marginal areolae, usually visible at zooidal corners, circular to elliptical (10–40 µm long).

Orifice transversely D-shaped, 90–107 (94±5, N = 10) × 118–143 (132±9, N = 10) µm (mean OL/OW = 0.71; mean ZL/OL = 5.43); hinge-line straight, smooth to slightly crenulated; in each corner a short, blunt, triangular condyle directed distally (Fig. 9B). Oral spine bases four or five, 10–18 µm in diameter, evenly spaced, the proximalmost pair at about one-third of orifice length (Fig. 9B).

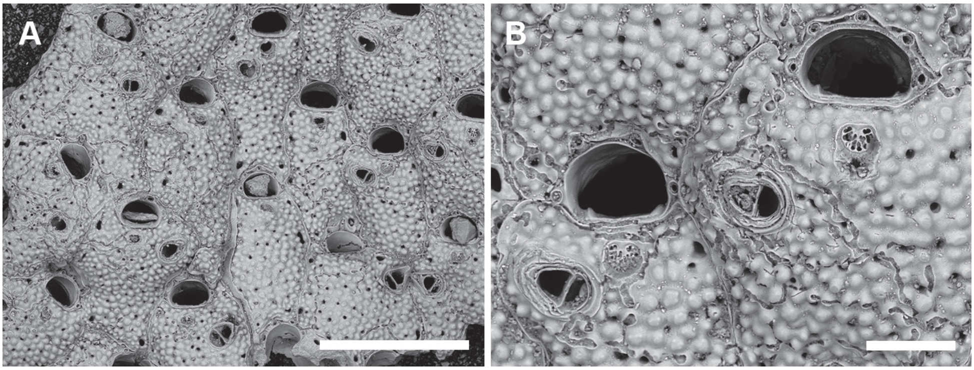

Figure 9. *Microporella* sp. A from Palinuro Cape, Scaletta cave PMC Rosso Collection I. H. B.88a **A** irregularly shaped autozooids with inconstant avicularia **B** close-up of two zooids with details of the orifice, the lateral condyles on the hinge-line, four or five thin oral spines and the ascopore divided by thin radial septa. Scale bars: 500 µm (**A**); 100 µm (**B**).

Ascopore field a narrow, elliptical area of smooth gymnocystal calcification (33–44 × 39–55 µm), placed 22–30 µm below the orifice, slightly depressed relative to the adjacent frontal shield; ascopore opening divided by thin radial septa, usually with a distinct tongue extending proximally from the distal edge (Fig. 9B).

Avicularium single, sometimes absent (two out of 14 zooids without avicularium in the fragment available), 93–123 (107±12, N = 9) × 70–87 (79±6, N = 9) µm (mean AvL/AvW = 1.36), located distolaterally, on either side; crossbar complete; rostrum short, triangular, not channelled, directed distolaterally, sometimes slightly raised distally (Fig. 9A, B). Mandible, ovicells and ancestrula not observed. Subsequent intramural budding observed in avicularia.

Remarks. This species differs from its Mediterranean congeners in having a finely reticulate ascopore but it is left in open nomenclature owing to the availability of a single, infertile colony fragment. Similar ascopores can be found in *M. arctica* Norman, 1903 from Norway, *M. ketchikanensis* Dick, Grischenko & Mawatari, 2005 from Alaska, *M. santabarbarensis* Soule, Chaney & Morris, 2004 from southern California, and *M. stellata* (Verril, 1879) from Maine, USA. *Microporella arctica* differs from *Microporella* sp. A in having a finely granular frontal shield pierced by a greater number of marginal areolae that are always very distinct from pseudopores, in the lack of oral spines, and in having a smooth gymnocystal area laterally and proximally to the orifice that is continuous with the gymnocyst of the ascopore field (Kukliński and Taylor 2008). The ascopores of both *M. ketchikanensis* and *M. santabarbarensis* have a similar, delicate cribrate aspect but lack the distal tongue extending from the distal edge (Dick et al. 2005; Soule et al. 2004). *Microporella stellata* differs in having only two oral spines and a proximal orifice margin with broad, rectangular condyles (Winston et al. 2000).

Distribution and ecology. Presently known only from the Palinuro Peninsula, along the Tyrrhenian coast of Campania (southern Italy). A dead colony was collected from the biogenic muddy sediment covering the floor of a completely dark sector of the Scaletta submarine cave, at 46 m depth where the colony presumably lived.

Microporella verrucosa (Peach, 1868)

Figs 10, 11

Eschara verrucosa Peach, 1868: 116.

Diporula verrucosa (Peach): Hincks, 1880: 220, pl. 31, figs 1, 2; Gautier, 1962: 176; Zabala, 1986: 501, fig. 174, pl. 15A, B; Hayward and Ryland, 1979: 226, fig. 97; Hayward and Ryland, 1999: 302, figs 138C, D, 139; André et al. 2014: 225, 5 figs; Rosso et al. 2014: table 2, fig. 3A–C.

Microporella (*Diporula*) *verrucosa* (Peach): Neviani, 1896a: 105; 1896b: 24.

Examined material. Italy • 2 colonies and 10 fragments (living), 17 colonies and 62 fragments (dead), some very large, some regenerated and twisted; Ionian Sea, SE Sicily, Ciclopi Islands MPA; Ciclopi 2000 cruise; samples 2G, 3H, 4E, 6H, 8F, 8H, 8I, 9G, 10G, 12E, 12F, 12G, 13H, 14G; 37°32'39"–37°34'31"N, 15°8'58"–15°11'1"E; 63–92.5 m; Jul. 2000; A. Rosso leg.; dredging; C, DC, DE, and DL Biocoenoses; PMC. Rosso Collection I.H. B-17a. Italy • 11 living and 33 dead colonies/large fragments, 1 dead colony including the base; off Acitrezza; sample AC/L, AC/1B; coordinates unknown; 50 and 110 m; 1980; I. Di Geronimo leg.; dredging; pre-Coralligenous and DL Biocoenoses; PMC. Rosso Collection I.H. B-17a1. Italy • 12 living and 315 dead colonies/fragments; Ionian Sea, Gulf of Noto; 36°41'45"–36°57'47"N, 15°8'35"–15°20'00"E; PS/81 cruise; samples 2C, 4X, 9D (living) and samples 2B, 2C, 2XA, 2XB, 4C, 4C1, 4X, 6D, 9C, 9D, 10C, 11E (dead); Jul. 1981; I. Di Geronimo leg.; dredging; DC and DL Biocoenoses; and 11 living colonies; Noto 1996 cruise; samples 8I, 10G, 10H; 77–82 m; 1996; E. Mollica leg.; dredging; DE and DL Biocoenoses; PMC. Rosso Collection I.H. B-17b. Italy • 18 dead colonies; Ionian Sea, Gulf of Catania; sample LCT69; 37°18'42"N, 15°14'24"E; 90 m; Jul. 1980; I. Di Geronimo leg.; dredging; DL Biocoenosis; PMC. Rosso Collection I.H. B-17c. Italy • 4 dead colonies; Ionian Sea, Gulf of Taranto, Amendolara Bank; samples 1D and 5D; 39°51'42"–39°52'54"N, 16°42'00"–16°43'24"E; 30–40 m; Jun. 1991; R. Sanfilippo leg.; dredging; DC Biocoenosis; PMC. Rosso Collection I.H. B-17g. Italy • 77 dead colonies and fragments; southern Tyrrhenian Sea, SW Ustica, Apollo Bank; 38°42'19"N, 13°7'58"E; 60 m; Jun. 1986, dredging; *Laminaria rodriguezii* Bornet, 1888 seagrass and associated DC Biocoenosis; PMC. Rosso Collection I.H. B-17d. Italy • 2 living colonies; Messina Strait; coordinates unknown; 65 m; 1990; S. Giacobbe leg.; dredging; no Biocoenosis information; PMC. Rosso Collection I.H. B-17g. France • 50 dead colonies; Iberian-Provençal Basin, Corsica, off Calvì; sample CL74; 42°47'31"N, 9°8'10"E; 150–110 m; G. Fredj leg.; dredging; DL Biocoenosis; PMC. Rosso Collection F.H. B-17e. Greece • 4 dead colonies, Aegean Sea, Lesvos Island, Agios Vasilios cave; samples AV1 and AV2; 38°58'8"N, 26°32'28"E; 30 m; V. Gerovasileiou leg.; scuba diving; GSO and GO Biocoenoses; PMC. Rosso Collection GR.H. B-17f.

Description. Colony erect, rigid, branched, with a limited number of relatively spaced-out bifurcations, a few cm long, raising from an encrusting basal portion (Fig. 10A), extending up to 3 mm around the main stem.

Branches cylindrical, often flattened at bifurcations (Fig. 10C, E), consisting of 9–16 longitudinal rows of zooids, alternating very regularly to simulate an helicoidal

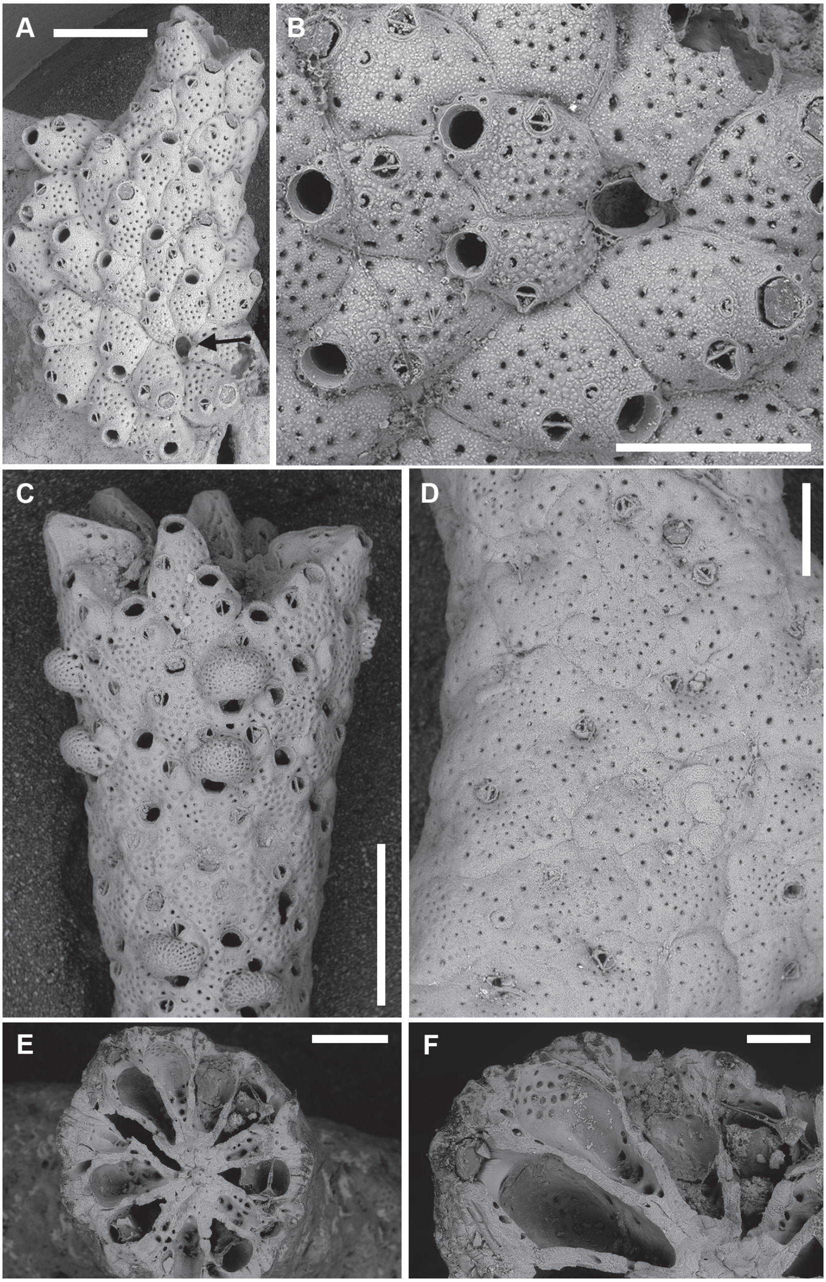

Figure 10. *Microporella verrucosa* (Peach, 1868) from the Ionian Sea, Ciclopi Islands MPA **A, B** PMC. Rosso Collection I.H. B-17a **C–F** PMC. Rosso Collection I.H. B-17a1 **A** young colony showing the encrusting portion with ancestrula (arrow) and starting developing branch (top right) **B** partly overgrown ancestrula and periancestrular autozooids **C** growing tip of a distally enlarging branch **D** old (proximal) branch portion showing secondary calcification obliterating orifices, sometimes only frontal avicularia are still visible **E** transverse section of a branch showing the thick walls converging towards the centre of the branch **F** close-up of wedge-shaped polypide cavities visible in transverse section. Scale bars: 500 µm (**A, B, D, E**); 1 mm (**C**); 200 µm (**F**).

pattern; branch diameter 10–15 mm (exceptionally up to 20 mm), becoming thicker and stouter in older portions of the colony, near the encrusting base, owing to secondary calcification.

Encrusting base unilaminar, multiserial (Fig. 10A), formed by autozooids similar to those of the erect branches (Fig. 10B) but with a greater number of oral spines (5–7, commonly six) and, subordinately, autozooids with occluded orifices (not functional) and/or kenozooids, often bearing an adventitious avicularium as those associated with autozooids. Interzooidal communications via basal pore-chambers in the encrusting portion (see Rosso et al. 2014: fig. 3A) and via multiporous septula in the erect branches (Fig. 10C).

Autozooids rounded hexagonal to lozenge-shaped, 477–779 (661±93, N = 18) × 389–615 (493±68, N = 18) µm (mean L/W = 1.34), distinct, interzooidal boundaries marked by narrow, shallow, locally undulate grooves (Fig. 11A, B, D). Frontal shield nearly flat, finely granular, and pseudoporous; about 10 marginal areolae distinguishable from frontal pseudopores only in early ontogeny because larger, subcircular to elongate elliptical, 25–65 µm long; 19–26 subcircular pseudopores, 20–30 µm in diameter, placed centrally on the frontal (Fig. 11A, B, D). Transverse section of the branch showing thick frontal and vertical walls, converging towards the centre of the branch, forming wedge-like polypide cavities (Fig. 10E, F).

Primary orifice approximately semi-circular to horseshoe-shaped, 130–151 (143±6, N = 10) × 145–177 (161±10, N = 10) µm (mean OL/OW = 0.89; mean ZL/OL = 4.63), outlined by a thin and smooth raised rim (Fig. 11C); hinge-line smooth, straight to slightly concave with two short, blunt lateral condyles and a smooth, proximal shelf sloping outwards; distal margin of the orifice corrugated because of a deeply placed, drawstring-like, arched rim seemingly functioning as support for the closed operculum. Oral spines four, occasionally five, thin (base diameter 15–20 µm), relatively short (60–90 µm), placed distally, often detached (Fig. 11A, B, D).

Ascopore field a narrow, reniform to U-shaped rim of smooth gymnocystal calcification, 50–60 × 57–80 µm, placed 65–80 µm below the orifice, same level as the orifice and the adjacent frontal shield; ascopore opening transversely C-shaped, 40–63 × 5–12 µm, with a massive, upside-down mushroom-shaped tongue projecting from distal edge with radial spines (Fig. 11A, B).

A single, constant, large avicularium, 121–156 (142±9, N = 20) × 119–139 (130±7, N = 20) µm (mean AvL/AvW = 1.09), located laterally, on either side, at about half zooidal length (Figs 10B, C, 11A, B, D, F); crossbar complete; rostrum short, rounded triangular, channelled, directed laterally or less often distolaterally and slightly upward. Mandible 142–273 µm long, with a pointed, hooked tip, toothed at the level of the rostrum tip, lining proximally to the ascopore when open (Fig. 11F).

Ovicell non-personate, subglobular, prominent, large, 250–327 (286±36, N = 4) × 384–430 (402±20, N = 4) µm (mean OvL/OvW = 0.71), formed by the distal autozooid, obscuring half of the zooidal orifice; calcification fabric similar to frontal shield but with larger and more prominent tubercles, and smaller (15–20 µm in diameter), more closely spaced pseudopores, seemingly radially aligned with rows separated by raised ridges; a discontinuous, peripheral row of larger pseudopores sometimes present (Figs 10C, 11B, E).

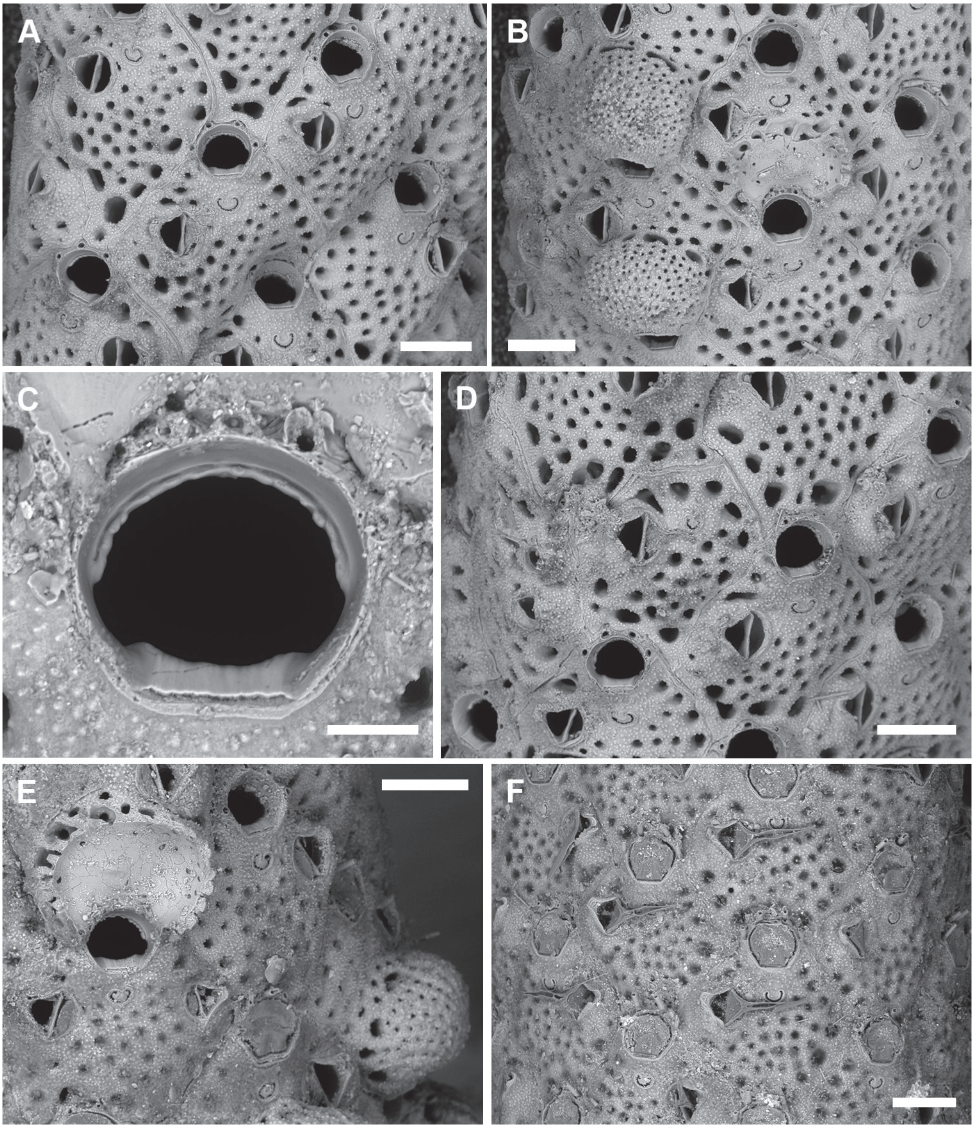

Figure 11. *Microporella verrucosa* (Peach, 1868) from the Ionian Sea, Ciclopi Islands MPA, PMC. Rosso Collection I.H. B-17a **A** typical rhomboidal autozooids with large avicularia, transversely C-shaped fissure-like ascopore at the same level as the frontal shield, large pseudopores and larger marginal areolae, and thin oral spines surrounding the distal half of the orifice **B** autozooids, two of which have ovicells pierced by small, evenly distributed pseudopores, and outlined by a row of few, large, elongate pores **C** horseshoe-shaped orifice with blunt lateral condyles and slightly corrugated proximal border at the end of a smooth proximal shelf. Note the distal rim of calcification **D** a possibly abutted autozooid lacking the orifice **E** autozooids, one exceptionally developing paired avicularia **F** unbleached colony portion with opercula and open mandibles. Scale bars: 200 µm (**A, B, D–F**); 50 µm (**C**).

Ancestrula tatiform (Fig. 10A, B), oval (220 × 150 μm), gymnocyst concealed, cryptocyst smooth, narrowing distally; opesia oval (160 × 110 μm); only four, distal spines visible on the single ancestrula observed. Ancestrula budding two distolateral autozooids, and subsequently surrounded by two lateral and one proximal autozooids.

Older colony parts thickly calcified owing to secondary calcification progressively obliterating zooidal openings including orifices, ascopores and avicularia (Fig. 10D), making difficult the distinction between old autozooids and genuine kenozooids that probably also develop.

Remarks. First assigned to *Eschara* (Peach 1868), *Eschara verrucosa* served as the type species of the genus *Diporula* Hincks, 1879 in which it has been included since then with the exception of Neviani (1896a, b). Characters used to distinguish *Diporula* from *Microporella* included the "dendroid zoarium with cylindrical branches" and the morphology of the orifice described as "expanded above, contracted below, and slightly constricted by lateral projections (horseshoe-shaped)" (Hincks 1880: 220; and similar description in Gautier 1962: 176). However, both characters seem feeble to justify the distinction between the two genera. At least nine species of *Microporella* possess erect colony-growth, starting with a more or less developed encrusting portion as does *Diporula*. Also the shape of the orifice in *Microporella* species is highly variable (Di Martino et al. 2020a), with several examples of species having orifices with the proximal margins narrower than the orifice maximum width [e.g., *Microporella curta* Almeida, Souza, Mengola & Vieira, 2017 from Brazil, *Microporella franklini* (Soule, Chaney & Morris, 2003) from California, the Mediterranean *Microporella genisii* (Audouin & Savigny, 1826), *Microporella hastingsae* Harmelin, Ostrovsky, Cáceres-Chamizo & Sanner, 2011 from the Red Sea, and the Arctic *Microporella klugei* Kukliński & Taylor, 2008].

Further differences between *Microporella* and *Diporula* were highlighted by Hayward and Ryland (1999: 292, 312), including interzooidal communications via basal pore-chambers in the former genus and multiporous septula in the latter, and the presence of pseudopores in the ovicells of *Diporula*. However, multiporous septula were observed, for example, in *Microporella ordo* (see Di Martino et al. 2020a: fig. 7D), and basal pore-chambers were observed in the encrusting portions of *M. verrucosa*, while pseudopores occur in the ooecium of many *Microporella* species including the type *M. ciliata* (see Kukliński and Taylor 2008: fig. 1c). A further presumed difference relates to the ooecium porosity, with *Diporula* reported as having a fully perforated endooecium and *Microporella* species usually described as having only pits in the endooecium (Harmelin et al. 2011: 2; Ostrovsky 2013: figs 2.43B–D, 2.44A). However, pores clearly perforate the endooecium also in *Microporella* as seen in broken ooecia of *M. ichnusae* sp. nov. (Fig. 6B)

Based on these observations, here we propose *Diporula* as junior synonym of *Microporella* and resurrect the combination *Microporella verrucosa* first proposed by Neviani (1896a, b). Specimens of a second species of *Diporula*, *D. coronula* Ortmann, 1890 need re-examination. Based on the original description and illustration (Ortmann 1890: 39, pl. 3, fig. 7), this species has a lepralioid orifice with condyles at about one-third of the orifice length, a single avicularium with spathulate mandible, and up to two frontal foramina, characters reminiscent of other cheilostome genera such as, for example, *Poricella* Canu, 1904.

Specimens originally described as *Eschara lunaris* Waters, 1878, from Pleistocene sediment of eastern Sicily and synonymised with *M. verrucosa* by Hincks (1880) need to be re-examined as well to confirm their conspecificity, but this is out of the scope of the present paper.

The rugose appearance observed by Peach (1868) and Hincks (1880), which inspired the species name, was not observed in our material, although secondary calcification is always very common in older parts of the colony. Intramural budding is rare and restricted to avicularia, while branch regeneration is common, apparently following breakage as indicated by broken autozooids with sharp edges. We also observed zooids with reverse polarity, sometimes budded from old stems with autozooids obliterated by secondary calcification. However, in these instances few whorls of autozooids usually develop from the regeneration surface, with only few tips appearing actively growing. Colony fragments longer than 2 cm can appear twisted, a morphology observed in some cyclostomes (Harmelin 1976) and other erect cheilostomes from the Gulf of Noto and the Ciclopi MPA area (Rosso 1989). This twisted branch morphology and the ability to regenerate after breakage might represent the adaptation of this species to colonize soft sediment bottoms. Basal, encrusting colony portions are relatively common in our samples and show that the ancestrulae settled on clasts ranging from a few mm to 1–2 cm in size. The ability of this species to encrust small particles, in addition to large substrates in rocky habitats, was suggested by Gautier (1962) after finding only colony fragments in dredges from sandy-muddy bottoms.

The diagnostic characters of this species seem constant in the Mediterranean specimens, except for the size of the ascopore related to the development of the distal tongue sometimes leaving only a fissure-like opening. Paired avicularia were observed only in one autozooid (Fig. 11E). Higher variability is observed when comparing the Mediterranean specimens with those from the Atlantic (e.g., Hayward and Ryland 1999: 302, figs 138C, D, 139A, B; unpublished SEM images provided by P.D. Taylor from Mauritania and Madeira) related to the ascopore shape, the size of the spines, and the distribution and size of pseudopores on the frontal shield, suggesting the existence of a species complex.

Distribution and ecology. *Microporella verrucosa* is a warm-temperate species with Atlanto-Mediterranean distribution. In the Atlantic, it has been reported from West Africa to the southwest of the British Isles (Hayward and Ryland 1999); in the Mediterranean, it occurs preferentially in mid- and outer-shelf habitats below 50–60 m depth, with an optimum at 70–120 m (Gautier 1962; Zabala 1986; Rosso 1989, 1996a; Rosso and Di Martino 2016), but it was also observed at shallower depths (20 m) in a shadowed open cave in Catalonia (André et al. 2014). It is associated with shadowed rocky habitats, including the Coralligenous and Semi-Dark and Dark Cave Biocoenoses, and detritic habitats, such as the Coastal Detritic and the Offshore Detritic Biocoenoses (Table 1; Gautier 1962; Harmelin 1969, 1976; Zabala 1986; Rosso 1989, 1996a, 1996b; Di Geronimo et al. 1990; Madurell et al. 2013; Rosso et al. 2014,

Table 2. Main diagnostic characters of Mediterranean *Microporella* species. Abbreviations are as follows. ; Colony form: E, encrusting; EC, erect cylindrical; EB, erect bilaminar. Ascopore: C, C-shaped; O, circular lacking distal denticle; R, reticulate. Ovicell: NP, non-personate; Pe, personate, ascopore not included; PA, personate, ascopore included; RI, visor-like proximal rim; ov, peristome arching on the ascopore. Pseudopores: ev perf, evenly perforate; centr, centrally; margin, marginally. Others: P, present; n.o., not observed; NO, not occurring. Numbers in brackets indicate formulas that are observed less commonly.

Species	Colony form	Ascopore	Frontal mucro	Avicularia	Ovicell	Pseudopores		Areolae	Oral spines		Orifice margin		Kenozooids
						Ovicell	Frontal		not ovicellate	ovicellate	Proximal	Distal	
appendiculata	E	O	P	2	NP; RI	absent	30–42	barely visible	5(6) first pair tri- or bifid	2	smooth	smooth	
bicollaris sp. nov.	E	C		1	PA; RI	1 row margin	11–25	3–6	5(6)	2	condyles at corners	smooth	
browni	E	C		1	Pe; RI	ev perf	31–98	barely visible	4–5 (3–7)	hidden	condyles, corrugated	beaded	
ciliata	E	C		1	NP	margin	30, central	4–5	1–4(0)	2	condyles laterally	smooth	
coronata	E	C	?	2	PA; RI	ev perf	50–60	1–3	7 (6–8)	2	condyles at corners	smooth	
genisii	E	C		1	Pe, ov; RI	less centr	18–30	barely visible	4 (3–6)	1–2	beaded	smooth	
ichnusae sp. nov.	E	C		1 (0–2)	NP	margin	10–30	2–4	4 (5–6)	hidden	condyles laterally	smooth	P
harmeri	E	C		1	P; RI	distal	45–90	5–9	3 (2–5)	hidden	11–20 teeth	smooth	
modesta	E, EB	C	P	1	NP	margin	50	6	5 (6–7)	2	condyles laterally	smooth	
orientalis	E	C		1	Pe	ev perf	?	?	0–5	hidden	condyles	beaded	
pachyspina sp. nov.	E	C	P	1	NP	1 row	6–18	3–6	5 (6–8)	2	condyles at corners	smooth	
sp. A	E	R		1	n.o.	n.o.	20–30	4–6	4–5	n.o.	condyles laterally	smooth	
verrucosa	EC	C		1 (0–2)	NP	small, large margin	19–26	10	4(5)	NO	sloping shelf; low condyles	corrugated	P

2019b; Gerovasileiou and Rosso 2016). However, it is never very common or dominant at sample or habitat scale, occurring only with a few colonies per sample and/or in one out of four or five sampling stations (Table 1; see also Harmelin 1976: tables 1, 3).

Discussion

The present study increases the number of *Microporella* species known from the Mediterranean from nine (Rosso and Di Martino 2016; Di Martino et al. 2020a) to 14 (see Table 2 for a summary of species characters). The presence of *M. orientalis* and *M. coronata* remains based only on the records of Hayward (1974) from Chios and Harmelin et al. (2011) from Lebanon. Based on the description and illustrations of the ovicell as globose but non-personate (e.g., Zabala 1986: 513, fig. 180), further records of these two species are more likely to correspond to *M. appendiculata*. *Microporella marsupiata*, although listed in Rosso and Di Martino (2016), can be considered restricted to the Atlantic. Mediterranean specimens identified as *M. marsupiata* (Zabala 1986) belong to *M. appendiculata*. This also applies to some specimens in our collection.

Modifications to genus and species diversity in the Mediterranean include the resurrection of the combinations *M. verrucosa* and *M. joannae*, and three new species described here (i.e., *M. bicollaris* sp. nov., *M. ichnusae* sp. nov. and *M. pachyspina* sp. nov.), as well as a potential additional species left in open nomenclature as *Microporella* sp. A. This is the result either of the re-examination of previously studied material assigned to the *M. ciliata* species complex or the examination of new material. *Microporella bicollaris* sp. nov. is clearly distinct from *M. ciliata*, given the presence of a personate ovicell. *Microporella ichnusae* sp. nov., *M. pachyspina* sp. nov., and the recently described *M. modesta*, on the other hand, have major affinities and share a certain number of features with *M. ciliata*. Furthermore, these species show high intracolonial and intraspecific variability common to other *Microporella* species and groups of species (e.g., Harmelin et al. 2011).

Most often, variability concerns the number of oral spines (e.g., 4–6 in *M. ichnusae* sp. nov.), 5–7 in *M. modesta*, 5–8 in *M. pachyspina* sp. nov., and 0–4 in *M. ciliata*), and the development of a tubercle on ovicells with the co-occurrence of tuberculate and non-tuberculate ooecia as in *M. modesta*. In this latter species, the mucro associated with the ascopore, considered as a diagnostic character by Di Martino et al. (2020a), also varies remarkably in the encrusting colonies examined here. In contrast, the size, density and distribution pattern of pseudopores on both autozooids and ovicells, as well as characters of the orifice, including the shape and size of condyles and denticulation of the hinge-line, are more stable. Harmelin et al. (2011) considered the variability of the denticulation of the orifice hinge-line in *M. harmeri* Hayward, 1988 (associated with differences in the morphology of the ascopore and in the shape of the avicularium and its mandible) as the indication that this widespread species, actually corresponds to a species complex. Periancestrular autozooids can lack avicularia in some species (e.g., *M. luellae* Grischenko, Dick & Mawatari, 2007, see Grischenko et al. 2007: fig. 34F), but the number of avicularia also seems constant within species, although sporadically autozooids may lack avicularia (as in *M. ichnusae* sp. nov.) or bear a second avicularium (as in *M. ichnusae* sp. nov. and *M. verrucosa*). Paired avicularia were also described in "*M. ciliata*" by Zabala (1986) and appear in *Microporella ketchikanensis* Dick, Grischenko & Mawatari, 2005 (Dick et al. 2005: fig. 20F) and *M. stellata* (Winston et al. 2000: fig. 19). Autozooids lacking avicularia have been occasionally reported in *Microporella* species, such as the Pliocene *Microporella sarasotaensis* Di Martino, Taylor & Portell, 2019 from Florida (Di Martino et al. 2019: fig. 37), the Pleistocene *M. rusti* from New Zealand (Di Martino et al. 2017: fig. 4), and the present-day *M. maldiviensis* Harmelin, Ostrovsky, Cáceres-Chamizo & Sanner, 2011 from the Maldive Islands (Harmelin et al. 2011: fig. 12I), and *M. ketchikanensis* (Dick et al. 2005: fig. 20A). The three latter species also show autozooids developing paired avicularia, thus paralleling *M. ichnusae* sp. nov. for the co-occurrence of autozooids with 0, 1, or 2 avicularia.

Kenozooids, with or without an avicularium, are here mentioned for the first time for Mediterranean species. Kenozooids were observed in *M. ichnusae* sp. nov., *M. modesta* and *M. verrucosa*, often along the contact zone between two different colonies or lobes of the same colony, as already seen in fossil species of *Microporella* involved in competitive interactions (Di Martino et al. 2020b).

Of the Mediterranean *Microporella* species examined here, *M. verrucosa* and *M. modesta* are the most frequently recorded (Fig. 1). *Microporella verrucosa* is also the only Mediterranean erect species with cylindrical branches forming relatively large colonies, therefore easily recognisable. The identical zooidal morphology of erect species of *Microporella* (*M. hastigera*, see Di Martino et al. 2020a) with those originally assigned to *Diporula*, such as *M. verrucosa*, led to the suggested synonymy between these two genera. The main difference between the two genera related to the porosity of the ooecium does not hold (see also Remarks for *M. verrucosa*): *Microporella* species can have either evenly pseudoporous ooecia with pores penetrating the endooecium (e.g., *M. ichnusae* sp. nov., Fig. 6B), or ooecia with a single row of marginal pores imperforate centrally (e.g., *M. pachyspina* sp. nov., Fig. 8E), as well as imperforate ooecia (e.g., *M. appendiculata*, Fig. 2E). The lack of pseudopores in the ooecium is also a feature of the Langhian *M. berningi* Zagorsek, 2010 from the Czech Republic, which also shares with *M. appendiculata* the formation of ooecia by kenozooids that are therefore independent of the distal autozooids, which is likely the reason for the lack of peripheral areolar pores (Fig. 2C, D). Although based on a single species, "*M. ciliata*", the ooecia in *Microporella* have been defined as microporelliform (i.e., an outgrowth of the proximal part of the frontal shield of the distal autozooid) (Ostrovsky 2013: 141, fig. 2.43A–D), which does, therefore, not apply to at least some of the species.

Another *Microporella*-like genus, *Flustramorpha* Gray, 1872, recorded off the coast of South Africa, is likely to be also indistinguishable from *Microporella*. However, species assigned to *Flustramorpha* need to be revised before the synonymy can be considered.

Microporella modesta has high growth plasticity and, although first described as erect bifoliate, encrusting colonies are more common. No habitat information is available for the type locality off the coast of Algeria, while colonies studied here are from shelf habitats. At shallow depths, *M. modesta* preferentially lives as an epibiont of soft and ephemeral substrates such as seagrasses and algae, and also on geniculate corallines, while in deeper environments it is mainly associated with other bryozoans. Despite the large number of colonies examined, no evidence was found of bilaminar branches starting from the encrusting base. The revision of large bryozoan collections from the Mediterranean (i.e., Rosso's collection, this study; Chimenz Gusso's collection in Chimenz Gusso et al. 2014), has shown that those species, including *M. ciliata*, previously considered widespread in the Mediterranean, are instead restricted to some specific areas and habitats. For instance, *Microporella ichnusae* sp. nov. and *M.* sp. A were found only in submarine cave habitats, with the former species inhabiting relatively lit caves of NW Sardinia (E Iberian-Provençal basin) shallower than 10 m, and the latter species collected dead at 46 m depth in a completely dark cave of the Palinuro Peninsula (E Tyrrhenian Sea). *Microporella bicollaris* sp. nov. and *M. pachyspina* sp. nov. seem to be southern species, inhabiting shallow-water habitats from the Sicily Strait, mostly associated with the Infralittoral Algae and the *Posidonia* meadow Biocoenoses.

In summary, based on the above discussion, some characters were observed for the first time in *Microporella*: tatiform ancestrula regenerated as an autozooid or kenozooid; presence of kenozooids; interzooidal communication through basal pore chamber windows in encrusting species or encrusting base of erect species and multiporous septula in erect branches; ovicells of kenozooidal origin; erect species with cylindrical branches (owing to the displacement of *M. verrucosa*).

Conclusions

With the description of three new species (i.e., *M. bicollaris* sp. nov., *M. ichnusae* sp. nov., *M. pachyspina* sp. nov.), and the inclusion of *M. verrucosa* and *M. joannae*, this study confirms *Microporella* as one of the most species-rich genera of the Mediterranean, after *Schizomavella* and *Reteporella*, with 22 and 15 known species, respectively (see Rosso and Di Martino 2016). Three or even four *Microporella* species, such as those recorded or described from the Mediterranean eastern sectors, are considered non-indigenous and possibly introduced in recent times, mostly via the Suez Canal (Harmelin et al. 2011) as suggested by the fact that they are all shallow-water species (3–43 m depth) found in harbours, marinas, and nearby natural environments. For the new species described here, their status as native or alien species cannot be assessed with certainty, although two of them, *M. bicollaris* sp. nov., *M. pachyspina* sp. nov., but also *M.* sp. A, show their highest affinities with extra-Mediterranean species, specifically with species from the Pacific Ocean, including the Galapagos Islands and the Arctic, areas that are geographically distant and characterised by decidedly different environmental parameters. An anthropogenically-mediated transport might be hypothesised for the first two species that have a shallow-water distribution, often in association with algal fronds. However, a similar widely disjunct distribution was observed for the calescharid species *Tretosina arculifera* (Canu & Bassler, 1927), previously only known from deep-waters of Hawaii and recently discovered in submarine caves from Lesvos Island (Rosso et al. 2020b). To date, there is no evidence of the occurrence of *Microporella* species in highly human-impacted areas (Ferrario et al. 2018), with the only exception of colonies of *M. modesta* found on plastic at Ognina marina, north of Catania.

Like for some other genera (e.g., *Setosella* Hincks, 1877; see Rosso et al. 2020a), the description of such a significant number of new species shows how incomplete our knowledge of the bryozoan biodiversity in the Mediterranean basin still is, despite being one of the most investigated areas during the past few centuries (see Rosso and Di Martino 2016, and references therein).

Acknowledgements

EDM has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 724324 to L.H. Liow) and the Research Council of Norway (grant 314499 to E. Di Martino). AR has received funding from the University of Catania through "PiaCeRi–Piano Incentivi per la Ricerca di Ateneo 2020–22 linea di intervento 2". Examined material was sampled in the framework of the following projects: Ciclopi

2000 project funded by the Italian Ministry of Environment and Capitaneria di Porto di Catania (PI A. Rosso); the CoNISMa projects MATTM 3AMP "Study of submarine cave environments–CODICE HABITAT 8330– in the Marine Protected Areas of Pelagie, Plemmirio and Capo Caccia-Isola Piana" (PI S. Fraschetti) and MATTM 4AMP "Analisi e valutazione dello stato degli ecosistemi marini delle zone A e B in 4 Aree Marine Protette anche al fine di valutare l'efficacia delle misure di gestione delle stesse"; the projects Noto 1996 and Piattaforma Siciliana (PS) funded by the Regione Sicilia and led by I. Di Geronimo and G. Cantone (University of Catania), respectively; the ENEA-CNR Minerva cruise 1996 at Amendolara Bank, Gulf of Taranto. The following people provided samples of species studied in the present paper: I. Di Geronimo (formerly at the University of Catania, Italy), G. Fredj (formerly at the University of Nice, France), V. Gerovasileiou (Hellenic Centre for Marine Research, Heraklion, Greece), F. Mastrototaro (University of Bari), S. Giacobbe (University of Messina), V. Grado (graduated from the University of Catania), A. Sinagra (temporary staff, 2007, University of Catania), V. Di Martino (Istituto per i Sistemi Agricoli e Forestali del Mediterraneo, Consiglio Nazionale delle Ricerche, Italy), and R. Sanfilippo and R. Leonardi (University of Catania, Italy). We thank J.-G. Harmelin (Station Marine d'Endoume, France), P.D. Taylor (Natural History Museum, London, UK), and B. Berning (Oberösterreichisches Landesmuseum, Leonding, Austria) for useful discussions and for providing photographs of several species for comparison. B. Berning, D.P. Gordon (NIWA, Wellington, New Zealand), and J.-G. Harmelin, with their careful reviews, considerably improved the original submitted manuscript. This is Catania Paleontological Research Group: contribution n. 475.

References

Achilleos K, Jimenez C, Berning B, Petrou A (2020) Bryozoan diversity of Cyprus (eastern Mediterranean Sea): first results from census surveys (2011–2018). Mediterranean Marine Science 21(1): 228–237. https://doi.org/10.12681/mms.21201

André JP, Corolla B, Lanza B, Rochefort G (2014) Bryozoaires d'Europe. Les carnets du plongeur. Edition Neptune Plonges, Audry & Schaffer, Marseille, 255 pp.

Almeida ACS, Souza FBC, Menegola CMS, Vieira LM (2017) Diversity of marine bryozoans inhabiting demosponges in northeastern Brazil. Zootaxa 4290(2): 281–323. https://doi.org/10.11646/zootaxa.4290.2.3

Arístegui Ruiz J (1984) Briozoos quilostomados (Ectoprocta, Cheilostomata) de Canarias: estudio sistematico, faunistico y biogeografico. Tesis Doctoral, Facultad de Biologia, Universidad de La Laguna, Las Palmas, 524 pp.

Balduzzi A, Rosso A (2003) Briozoi. In: Cicogna F, Bianchi NC, Ferrari G, Forti P (Eds) Grotte marine: cinquant'anni di ricerca in Italia, CLEM-ONLUS, Ministero dell'Ambiente e della Tutela del Territorio: 195–202.

Balduzzi A, Bianchi C, Boero F, Cattaneo Vietti R, Pansini M, Sarà M (1989) The suspension-feeder communities of a Mediterranean sea cave. In: Ros JD (Ed.) Topics in Marine Biology. Scientia Marina 53: 387–395.

Bock PE (2020) Recent and Fossil Bryozoa. http://bryozoan.net/index.html [accessed 26 Feb 2021]

Calvet L (1902) Bryozoaires marins des côtes de Corse (récoltés par M. Caziot). Travaux de l'institut de zoologie de l'Université de Montpellier et de la station zoologique de Cette 12: 1–52.

Campisi MR (1973) Briozoi dell'Isola Lachea (Golfo di Catania) – Nota preliminare. Bollettino Accademia Gioenia di Scienze Naturali, Catania (Serie 4) 11: 135–156.

Cantone G (1997) Cartografia delle biocenosi bentoniche e dei sedimenti della piattaforma continentale del Golfo di Noto tra Capo Murro di Porco e Capo Passero. Regione siciliana, Assessorato Cooperazione, Commercio, Artigianato e Pesca. Convenzione L.R. n° 26/87, art. 6: 1–306.

Chimenz C, Faraglia E (1995) Some faunistic and ecological observations on the Bryozoa Gymnolaelata assemblages from the coast of Puglia (Italy). Atti della Società Toscana di Scienze Naturali, Memorie, ser. B 102: 37–47.

Chimenz Gusso C, Nicoletti L, Bondanese C (2014) Briozoi. Biologia Marina Mediterranea 20 (Suppl. 1): 1–336.

Dick MH, Grischenko AV, Mawatari SF (2005) Intertidal Bryozoa (Cheilostomata) of Ketchikan, Alaska. Journal of Natural History 39(43): 3687–3784. https://doi.org/10.1080/00222930500415195

Dick MH, Ross JRP (1988) Intertidal Bryozoa (Cheilostomata) of the Kodiak vicinity, Alaska. Western Washington University, Bellingham, 133 pp. [Centre for Pacific Northwest Studies occasional paper: 23.]

Dick MH, Ngai ND, Doan HD (2020) Taxonomy and diversity of coelobite bryozoans from drift coral cobbles on Co To Island, northern Vietnam. Zootaxa 4747(2): 201–252. https://doi.org/10.11646/zootaxa.4747.2.1

Di Geronimo I, Allegri L, Improta S, La Perna R, Rosso A, Sanfilippo R (1997) Spatial and temporal aspects of Recent benthic thanatocoenoses in a Mediterranean Infralittoral cave. Rivista Italiana di Paleontologia e Stratigrafia 103(1): 15–28.

Di Geronimo I, Giacobbe S, Rosso A, Sanfilippo R (1990) Popolamenti e tanatocenosi del Banco Apollo (Ustica, Mar Tirreno meridionale). Bollettino del Museo Regionale di Scienze Naturali Torino vol. spec.: 697–729.

Di Geronimo I, La Perna R, Rosso A, Sanfilippo R (1993a) Popolamento e tanatocenosi bentonica della Grotta dell'Accademia (Ustica, Mar Tirreno meridionale), Naturalista Siciliano (Serie 4) 17(1–2): 45–63.

Di Geronimo I, La Perna R, Rosso A, Sanfilippo R (1998) Notes on two upper-circalittoral assemblages from the Amendolara Bank (Northern Ionian Sea). Bollettino Accademia Gioenia di Scienze Naturali, Catania 30(353): 243–262.

Di Geronimo I, Rosso A, Sanfilippo R (1993b) The *Corallium rubrum* fossiliferous banks off Sciacca (Strait of Sicily). In: Cicogna F, Cattaneo-Vietti R (Eds) Red coral in the Mediterranean Sea: Art, History and Science. Ministero Risorse Agricole, Alimentari e Forestali, Roma: 75–107.

Di Martino E, Taylor PD, Gordon DP, Liow LH (2017) New bryozoan species from the Pleistocene of the Wanganui Basin, North Island, New Zealand. European Journal of Taxonomy 345: 1–15. https://doi.org/10.5852/ejt.2017.345

Di Martino E, Taylor PD, Portell RW (2019) *Anomia*-associated bryozoans from the upper Pliocene (Piacenzian) lower Tamiami Formation of Florida, USA. Palaeontologia Electronica 22.1.11A 1–65. https://doi.org/10.26879/920

Di Martino E, Taylor PD, Gordon DP (2020a) Erect bifoliate species of *Microporella* (Bryozoa Cheilostomata), fossil and modern. European Journal of Taxonomy 678: 1–31. https://doi.org/10.5852/ejt.2020.678

Di Martino E, Liow LH, Perkins T, Portell RW, Taylor PD (2020b) Sneaking up on 'enemies': alleviating inherent disadvantages in competitive outcomes in a nearly 3-million-year old palaeocommunity from Florida, USA. Lethaia 53: 553–562. https://doi.org/10.1111/let.12376

D'Onghia G, Capezzuto F, Cardone F, Carlucci R, Carluccio A, Chimienti G, Corriero G, Longo C, Maiorano P, Mastrototaro F, Panetta P, Rosso A, Sanfilippo R, Sion L, Tursi A (2015) Macro- and megafauna recorded in the submarine Bari Canyon (southern Adriatic, Mediterranean Sea) using different tools. Mediterranean Marine Science 16(1): 180–196. https://doi.org/10.12681/mms.1082

Ferrario J, Rosso A, Marchini A, Occhipinti-Ambrogi A (2018) Mediterranean non-indigenous bryozoans: an update and knowledge gaps. Biodiversity and Conservation 27: 2783–2794. https://doi.org/10.1007/s10531-018-1566-2

Figuerola B, Gordon DP, Cristobo J (2018) New deep Cheilostomata (Bryozoa) species from the Southwestern Atlantic: shedding light in the dark. Zootaxa 4375(2): 211–249. https://doi.org/10.11646/zootaxa.4375.2.3

Fraschetti S, Boero F, Guarnieri G, Terlizzi A, Guidetti P, Bussotti S, Piraino S, De Vito D, Cormaci M, Furnari G, Catra M, Alongi G, Rosso A, Di Martino E, Ceccherelli G, Manconi R, Ledda F, Cattaneo-Vietti R, Cerrano C, Pantaleo U, Scinto A, Bavestrello G, Di Camillo CG, Betti F, Chemello R, Milazzo M, Graziano M, Di Franco A, Marchini A, Russo GF, Di Stefano F, Cimmino P (2010) Studio degli ambienti di grotte marine sommerse (Cod. 8330) nelle aree marine protette di Capo Caccia, Plemmirio e Isole Pelagie. Relazione finale. CoNISMa-Ministero dell'Ambiente e della Tutela del Territorio e del Mare, 337 pp.

Gautier YV (1962) Recherches ecologiques sur les Bryozoaires Chilostomes en Méditerranée occidentale. Recueillis des Travaux de la Station Marine d'Endoume 38: 1–435.

Gerovasileiou V, Rosso A (2016) Marine Bryozoa of Greece: an annotated checklist. Biodiversity Data Journal 4: e10672. https://doi.org/10.3897/BDJ.4.e10672

Grischenko AV, Dick MH, Mawatari SF (2007) Diversity and taxonomy of intertidal Bryozoa (Cheilostomata) at Akkeshi Bay, Hokkaido, Japan. Journal of Natural History 41(17–20): 1047–1161. https://doi.org/10.1080/00222930701391773

Harmelin J-G (1969) Bryozoaires des grottes sous-marines obscures de la région Marseillaise: faunistique et écologie. Téthys 1: 793–806.

Harmelin J-G (1976) Le sous-ordre des Tubuliporina (Bryozoaires Cyclostomes) en Méditerranée. Écologie et systématique. Mémoires de l'Institut océanographique 10: 1–326.

Harmelin J-G, Ostrovsky AN, Cáceres-Chamizo JP, Sanner J (2011) Bryodiversity in the tropics: taxonomy of *Microporella* species (Bryozoa, Cheilostomata) with personate maternal zooids from Indian Ocean, Red Sea and southeast Mediterranean. Zootaxa 2798: 1–30. https://doi.org/10.11646/zootaxa.2798.1.1

Hayward PJ (1974) Studies on the cheilostome bryozoan fauna of the Aegean island of Chios. Journal of Natural History 8(4): 369–402. https://doi.org/10.1080/00222937400770321

Hayward PJ, McKinney FK (2002) Northern Adriatic Bryozoa from the vicinity of Rovinj, Croatia. Bulletin of the American Museum of Natural History 270: 1–139. https://doi.org/10.1206/0003-0090(2002)270<0001:NABFTV>2.0.CO;2

Hayward PJ, Ryland JS (1979) *British ascophoran bryozoans*. In: Kermack DM, Barnes RSK (Eds) Synopses of the British fauna (n.s.), Academic Press for the Linnaean Society, London 14: 1–312.

Hayward PJ, Ryland JS (1999) *Cheilostomatous Bryozoa. Part 2. Hippothoidea – Celleporoidea.* Barnes RSK, Crothers JH (Eds) Synopses of the British Fauna (New Series) Field Studies Council, Shrewsbury 14: 1–416.

Heller C (1867) Die Bryozoen des adriatischen Meeres. Verhandlungen der zoologisch-botanischen Gesellschaft in Wien 17: 77–136.

Hincks T (1880) A history of the British Marine Polyzoa. Van Voorst, London, 601 pp. [83 pls.] https://www.biodiversitylibrary.org/page/23373713

Kukliński P, Taylor PD (2008) Arctic species of the cheilostome bryozoan *Microporella*, with a redescription of the type species. Journal of Natural History 42(27–28): 1893–1906. https://doi.org/10.1080/00222930802126904

Levinsen GMR (1909) Morphological and Systematic Studies on the Cheilostomatous Bryozoa. Nationale Forfatterers Forlag, Copenhagen, 431 pp. https://www.biodiversitylibrary.org/page/4713708

Madurell T, Zabala M, Dominguez-Carrió C, Gili JM (2013) Bryozoan faunal composition and community structure from the continental shelf off Cap de Creus (Northwestern Mediterranean). Journal of Sea Research 83: 123–126. https://doi.org/10.1016/j.seares.2013.04.013

Mawatari SF, Kaneko N, Gordon DP (1991) Redescription of *Microporella echinata* Androsova, 1958 (Bryozoa: Cheilostomata) from Hokkaido, with special reference to its astogeny. Memoirs of the National Science Museum, Tokyo 24: 61–66.

Neviani A (1896a) Briozoi fossili della Farnesina e di Monte Mario presso Roma. Paleontographia Italica 1: 77–140.

Neviani A (1896b) Briozoi postpliocenici di Spilinga (Calabria). Atti Accademia Gioenia di Scienze Naturali in Catania 9, ser. 4: 1–66.

Ortmann A (1890) Die Japanische Bryozoenfauna. Bericht über die von Herrn Dr.L.Döderlein in Jahre 1880–81, gemachten Sammlungen. Archiv für Naturgeschichte 56: 1–74.

Osburn RC (1952) Bryozoa of the Pacific coast of America, part 2, Cheilostomata-Ascophora. Report of the Allan Hancock Pacific Expeditions 14: 271–611.

Ostrovsky AN (2013) Evolution of sexual reproduction in marine invertebrates. Example of Gymnolaemate bryozoans. Springer, Dordrecht, 356 pp. https://doi.org/10.1007/978-94-007-7146-8

Pallas PS (1766) Elenchus zoophytorum sistens generum adumbrationes generaliores et speciarum cognitarum succintas descriptiones cum selectis auctorus synonymis. Pterum van Cleef, Hagae-Comitum, 451 pp. https://www.biodiversitylibrary.org/page/6019462

Peach CW (1868) On a new British *Eschara*, and the occurrence, in Cornwall, of *Sphenotrochus Wrightii*, of Gosse. Journal of the Royal Institution of Cornwall 3: 116–117.

Poluzzi A, Rosso A (1988) I tipi zoariali di un'associazione a briozoi del Mare Ionio. Acta Naturalia de l'Ateneo Parmense 24(1): 83–108.

Ramalho LV, López-Fé CM, Mateo-Ramírez A, Rueda JL (2020) Bryozoa from deep-sea habitats of the northern Gulf of Cádiz (Northeastern Atlantic). Zootaxa 4768(4): 451–478. https://doi.org/10.11646/zootaxa.4768.4.1

Rosso A (1989) Contributo alla conoscenza di alcuni popolamenti, tanatocenosi e tafocenosi a briozoi di alcuni fondi mobili circalitorali. PhD thesis, University of Messina.

Rosso A (1996a) Popolamenti e tanatocenosi a Briozoi di fondi mobili circalitorali del Golfo di Noto (Sicilia SE). Naturalista Siciliano (Serie 4) 20(3–4): 189–225.

Rosso A (1996b) Valutazione della biodiversità in Mediterraneo: l'esempio dei popolamenti a briozoi della Biocenosi del Detritico Costiero. Biologia Marina Mediterranea 3(1): 58–65.

Rosso A (2001) Cartografia topografica e biocenotica dei fondali mobili della Riserva Marina "Isole Ciclopi". Ministero dell'Ambiente – Capitaneria di Porto – Università degli Studi di Catania, 119 pp. [con 1 Carta dei Sedimenti e 1 Carta delle Biocenosi.]

Rosso A, Chimenz Gusso C, Balduzzi A (2010) Bryozoa. In: Relini G (Ed.) Checklist della flora e della fauna dei mari italiani (parte II). Biologia Marina Mediterranea 17(Suppl.): 589–615.

Rosso A, Di Martino E (2016) Bryozoan diversity in the Mediterranean Sea: an up-date. Mediterranean Marine Science 17(2): 567–607. https://doi.org/10.12681/mms.1706

Rosso A, Di Martino E, Gerovasileiou V (2020a) Revision of the genus *Setosella* (Bryozoa: Cheilostomata) with description of new species from deep-waters and submarine caves of the Mediterranean. Zootaxa 4728(4): 401–442. https://doi.org/10.11646/zootaxa.4728.4.1

Rosso A, Di Martino E, Sanfilippo R, Di Martino V (2013a) Bryozoan Communities and Thanatocoenoses from Submarine Caves in the Plemmirio Marine Protected Area (SE Sicily). In: Ernst A, Schäfer P, Scholz J (Eds) Bryozoan Studies 2010. Proceedings of the 15th IBA Conference, 2010 Kiel, Germany. Springer, Berlin, Heidelberg. Lecture Notes in Earth System Sciences 143: 251–269. https://doi.org/10.1007/978-3-642-16411-8_17

Rosso A, Gerovasileiou V, Di Martino E (2020b) Really onychocellids? Revisions and new findings increase the astonishing bryozoan diversity of the Mediterranean Sea. In: Crocetta F (Ed.) Benthic Biodiversity in the Northeastern Atlantic and the Mediterranean Sea, Journal of Marine Science and Engineering, sec. Marine Biology 8(11): e904. https://doi.org/10.3390/jmse8110904

Rosso A, Gerovasileiou V, Sanfilippo R, Guido A (2019b) Bryozoans assemblages from two submarine caves in the Aegean Sea (Eastern Mediterranean). Marine Biodiversity 49(2): 707–726. https://doi.org/10.1007/s12526-018-0846-0

Rosso A, Sanfilippo R, Sciuto F (2014) Open shelf soft bottom bryozoan communities from the Ciclopi Marine Protected Area (E Sicily, Mediterranean). In: Rosso A, Wyse Jackson PN, Porter J (Eds) Bryozoan Studies 2013. Proceedings of the 16th Conference of the International Bryozoological Association, Catania, Italy. Studi Trentini di Scienze Naturali 94: 195–207.

Rosso A, Sanfilippo R, Sciuto F, Serio D, Catra M, Alongi G, Viola A, Leonardi R (2019a) Preliminary information on bryozoans associated with selected *Cystoseira* communities from Sicily (Mediterranean). In: Schmidt R, Reid C, Gordon DP, Walker-Smith G, Martin S, Percival I (Eds) Bryozoan Studies 2016. Proceedings of the 17th International Bryozoology Association Conference, Melbourne, Australia. Memoirs of the Australasian Association of Palaeontologists 52: 115–129.

Rosso A, Sanfilippo R, Taddei Ruggiero E, Di Martino E (2013b) Faunas and ecological groups of Serpuloidea, Bryozoa and Brachiopoda from submarine caves in Sicily (Mediterranean Sea). Bollettino della Società Paleontologica Italiana 52(3): 167–176.

Soule DF, Chaney HW, Morris PA (2004) Additional new species of *Microporelloides* from southern California and American Samoa. Irene McCulloch Foundation Monograph series 6A: 1–14.

Suwa T, Mawatari SF (1998) Revision of seven species of *Microporella* (Bryozoa, Cheilostomatida) from Hokkaido, Japan, using new taxonomic characters. Journal of Natural History 32: 895–922. https://doi.org/10.1080/00222939800770461

Taylor PD, Mawatari SF (2005) Preliminary overview of the cheilostome bryozoan *Microporella*. In: Moyano GHI, Cancino JM, Wyse-Jackson PN (Eds) Bryozoan Studies 2004. AA Balkema Publishers, Leiden, London, New York, Philadelphia, Singapore: 329–339. https://doi.org/10.1201/9780203970799.ch31

Ünsal I (1975) Bryozoaires marins de Turquie. Istanbul Üniversitesi Fen Fakültesi Mecmuasi, Serie B 40: 37–54.

Winston JE, Hayward PJ, Craig SF (2000) Marine bryozoans of the northeast coast of the United States: new and problem species. In: Herrera Cubilla A, Jackson JBC (Eds) Proceedings of the 11th International Bryozoology Association Conference, Republic of Panama, January 26–31, 1998. Smithsonian Tropical Research Institute, Balboa Republic of Panama: 412–420.

Zabala M (1986) Fauna dels bryozous dels Països Catalans. Barcelona. Institut D'estudis Catalans Secció de Ciències 84: 1–836.

Zabala M, Maluquer P (1988) Illustrated keys for the classification of Mediterranean Bryozoa. Treballs del Museu de Zoologia, Barcelona 4: 1–294.

ZooKeys 1053: 43–105 (2021)
doi: 10.3897/zookeys.1053.67288
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Contribution to the knowledge of the bee fauna (Hymenoptera, Apoidea, Anthophila) in Serbia

Sonja Mudri-Stojnić[1], Andrijana Andrić[2], Zlata Markov-Ristić[1],
Aleksandar Đukić[3], Ante Vujić[1]

1 *University of Novi Sad, Faculty of Sciences, Department of Biology and Ecology, Trg Dositeja Obradovića 2, 21000 Novi Sad, Serbia* **2** *University of Novi Sad, BioSense Institute, Dr Zorana Đinđića 1, 21000 Novi Sad, Serbia* **3** *Scientific Research Society of Biology and Ecology Students "Josif Pančić", Trg Dositeja Obradovića 2, 21000 Novi Sad, Serbia*

Corresponding author: Sonja Mudri-Stojnić (sonja.mudri-stojnic@dbe.uns.ac.rs)

Academic editor: Thorleif Dörfel | Received 13 April 2021 | Accepted 1 June 2021 | Published 2 August 2021

http://zoobank.org/88717A86-19ED-4E8A-8F1E-9BF0EE60959B

Citation: Mudri-Stojnić S, Andrić A, Markov-Ristić Z, Đukić A, Vujić A (2021) Contribution to the knowledge of the bee fauna (Hymenoptera, Apoidea, Anthophila) in Serbia. ZooKeys 1053: 43–105. https://doi.org/10.3897/zookeys.1053.67288

Abstract

The current work represents summarised data on the bee fauna in Serbia from previous publications, collections, and field data in the period from 1890 to 2020. A total of 706 species from all six of the globally widespread bee families is recorded; of the total number of recorded species, 314 have been confirmed by determination, while 392 species are from published data. Fourteen species, collected in the last three years, are the first published records of these taxa from Serbia: *Andrena barbareae* (Panzer, 1805), *A. clarkella* (Kirby, 1802), *A. fulvicornis* (Schenck, 1853), *A. intermedia* (Thomson, 1870), *A. lapponica* (Zetterstedt, 1838), *A. pandellei* (Pérez, 1895), *A. paucisquama* (Noskiewicz, 1924), *A. simillima* (Smith, 1851), *Panurginus herzi* (Morawitz, 1892), *Epeoloides coecutiens* (Fabricius, 1775), *Nomada leucophthalma* (Kirby, 1802), *Chelostoma nasutum* (Pérez, 1895), *Hoplitis claviventris* (Thomson, 1872), and *Dasypoda pyrotrichia* (Förster, 1855). Almost all the species recorded so far in Serbia belong to the West-Palaearctic biogeographical region, except *Megachile sculpturalis* (Smith, 1853), which is an alien invasive species native to East Asia. According to the European Red List of bees, 221 species listed in this paper were assessed as Data Deficient; threatened species mostly belong to the families Apidae with 13 species, Colletidae with eight species, and Halictidae with five species. This study contributes to the knowledge of the distribution of bee species in Europe. The present work provides a baseline for future research of wild bee diversity in Serbia and neighbouring regions at the local and regional levels, and a basis for their conservation.

Keywords

diversity, fauna, Serbia, wild bees

Introduction

The first available data on the faunistic research of Hymenoptera: Apoidea: Anthophila in the Balkan countries derives from the late 19th century, from the period of the Austro-Hungarian Empire. At that time, scientists were collecting data on the wild bee fauna while travelling through the area of today's Balkan countries, or they researched parts of the countries where they lived. The borders and names of the Balkan countries have changed several times since then. Therefore, in the present paper, the localities are shown within the current borders of the Republic of Serbia.

The earliest publication, which provided the data on the bee fauna of Serbia is by Korlević (1890), who recorded 15 bee species in the Pannonian Region of the country. Six years later, Apfelbeck (1896) collected specimens of 101 wild bee species in southeast Serbia during his travels through Balkan countries. Soon after that, Mocsáry (1897) published "Fauna Regni Hungarie". This publication contains significant data from Deliblato Sands in today's Serbia, where 199 wild bee species were recorded. Vorgin (1918) provided data on the bee fauna from Fruška Gora Mountain and several sites on the margins of the Danube, where 97 bee species were recorded, and for the first time from all families of Apoidea. The most reliable and comprehensive publication on the bee fauna of Serbia was published by Lebedev (1931). Bee specimens were collected across several Balkan countries by more than ten experts and encompassed 258 bee species from former Yugoslavia, among which 203 were from Serbia. Most of these bees belong to Central European species and the whole fauna was very similar to that of Hungary and Romania (Lebedev 1931). Vorgin (1955) published contributions to the fauna Hymenoptera: Apoidea: Anthophila of Yugoslavia, including new data on bee fauna and sites for 114 bee species, which were recorded in Serbia. Rafajlović and Seleši (1958) presented data from Alfred Taubert's collection, who collected insects for 35 years (1909–1944) in the territory of former Yugoslavia. In Serbia, 267 bee species were recorded mostly in the Vojvodina province, in the vicinity of the city of Subotica and Deliblato Sands. The value of the collection lies in the fact that Taubert collected twice as many species as Mocsáry (1897) in the same area (Rafajlović and Seleši 1958).

After World War II, many authors mainly focused their research on studying the ecology or life history and biology of some species, or the bee diversity of certain regions. Grozdanić studied the life history and ecology of *Lasioglossum marginatum* (Brullé, 1832) (as *Halictus marginatus* Brullé, 1832), *L. interruptum* (Panzer, 1798) (as *H. interruptus* (Panzer, 1798)), *L. malachurum* (Kirby, 1802) (as *H. malachurus* (Kirby, 1802)), *H. sajoi* (Blüthgen, 1923), *H. maculatus* (Smith, 1848), *H. asperulus* (Pérez, 1895), *Seladonia kessleri* (Bramson, 1879) (as *H. kessleri* Bramson, 1879), *Osmia bicornis* Linnaeus, 1758, *O. bicolor* (Schrank, 1781), *O. rufohirta* (Latreille, 1811), *O. bidentata* (Morawitz, 1876), *Xylocopa violacea* (Linnaeus, 1758), *X. valga* (Gerstäcker, 1872), *X. iris* Christ, 1791 (as *X. cyanescens* Brullé, 1832), *Bombus pascuorum* Scopoli, 1763 (as *B. agrorum* (Fabricius, 1787)), *Apis mellifera* (Linnaeus, 1758), *Anthophora plumipes* Pallas, 1772 (as *A. acervorum* (Linnaeus, 1758)), *A. plagiata* Illiger, 1806 (as *A. parietina* (Fabricius, 1793)), *A. salviae* (Panzer, 1804) (as

A. crinipes Smith, 1854), *A. pubescens* (Fabricius, 1781), *Eucera* (*Tetralonia*) *lyncea* (as *Tetralonia lyncea* (Mocsáry, 1879)), *Eucera* (*Tetralonia*) *nana* (as *T. nana* (Morawitz, 1874)), *Systropha planidens* (Giraud, 1861), *S. curvicornis* (Scopoli, 1770), *Eucera excisa* (Mocsáry, 1879), *Megachile ericetorum* (Lepeletier, 1841), and *Ceratina* spp. (Grozdanić 1926, 1928, 1930, 1950a, b, 1956, 1958a, b, 1960, 1961, 1965, 1966, 1968, 1969a–c, 1970, 1971a, b, 1972a, b, 1974; Grozdanić and Čolović 1955a, b; Grozdanić and Stevanović 1959, 1965; Grozdanić and Krunić 1961; Grozdanić and Vasić 1965a, b, 1966a, b, 1967a, b, 1968, 1970; Grozdanić and Mučalica 1966, 1968a, b, 1969, 1973; Grozdanić and Baranov 1963; Grozdanić and Radivojevic 1972). Grozdanić and Vasić (1965c, 1966a) published two papers on their entomological research in the vicinity of Belgrade and their faunistic lists contained 35 bee species. Živojinović (1950) provided a comprehensive monograph on the fauna of insects from eastern Serbia and recorded 112 bee species in the Majdanpek region, on the southern Carpathian Mountain. Petrik (1958) published the results of a two-year study of the insect fauna in the area of Deliblato Sands, where he recorded 58 bee species. Vasić studied the life history and biology of *Lasioglossum marginatum* (as *Halictus marginatus*), *H. quadricinctus* (Fabricius, 1776), *H. scabiosae* (Rossi, 1790), *Megachile albisecta* Klug, 1817 (as *Megachile sericans* Fonscolombe, 1832) (Vasić 1966, 1967, 1968, 1970, 1979a, b). Mučalica, Z. studied the biology and life history of *Halictus fulvipes* (Klug, 1817), *Anthophora plagiata* (as *A. parietina*), and *A. salviae* (as *A. crinipes*) (Mučalica 1968, 1984, 1987a, b, 1990, 1997). Mučalica and Stanivljević (2005) studied the nesting biology of *Megachile willughbiella* (Kirby, 1802). Grozdanić and Mučalica researched the fauna of Hymenoptera across former Yugoslavia; Mučalica collected insects for 33 years (1965–1997) in the area of Serbia and Grozdanić collected insects in the period from 1963 to 1972. Both collections are preserved in the Natural History Museum in Belgrade. The present paper lists 181 bee species recorded in Serbia by the above authors. Krunić studied two important wild bee pollinators of Serbian orchards, namely *Osmia cornuta* (Latreille, 1805) and *O. bicornis* (as *O. rufa* (Linnaeus, 1758)) in all aspects of their life history such as diapause, overwintering, distribution, population management, etc. (Krunić et al. 1989, 1991, 1992a, 1995a, 1996, 1997, 1998, 1999, 2001, 2005; Krunić and Stanisavljević 2006a–d). The other pollinator bee species he studied was *Megachile rotundata* (Fabricius, 1793) (Krunić et al. 1985, 1992b, c, 1995b, 1997). Krunić, Radović and Brajković (1988) published a list of the Megachilide family collected in former Yugoslavia. Krunić also studied the population of honey bees, mostly in the Pannonian region (Krunić 1967, 1986, 1994; Krunić et al. 1994). Stanisavljević continued research into bee pollinators in orchards, mostly *Osmia cornuta* and *O. bicornis* (as *O. rufa*), from the environmental, conservation, morphology, and management aspects (Stanisavljević 1996, 2000, 2009; Stanisavljević et al. 1997a, b, 1999, 2000a, b, 2013). Stanisavljević and Nedić (2008) published a paper on the role of bees in orchard pollination in Serbia. Stanisavljević (2013) published a list of bee species from the Megachilidae family of Fruška Gora. Stanisavljević and Tomović (2006) presented the results of alfalfa seed production with the use of *Megachile rotundata* in Serbian agricultural farms. Mudri-Stojnić studied bee fauna in agro-ecosystems of Vojvodina province from 2011. Markov studied bee fauna in protected areas of Vojvodina province (Markov et al. 2016) and their economic aspect (Markov 2017). Đukić studied the bee fauna of the Vlasina region in southeast Serbia; in two years (2019–2020), he recorded 99 bee species.

The importance of bees in terrestrial ecosystems, as well as their ecosystem role in the process of pollination of agricultural crops and wild plants, is widely known. In many European countries, Red Data Books or Red Lists of bees have been produced at the national level. Some European countries have developed specific national actions in order to enhance bee populations and to arrest decline, introduced legislation with the aim of legally protecting all or some species of bees, and/or produced checklists of bees. For some Balkan countries, such as Serbia, data on the diversity of bees are scarce. Among the reasons for such a situation are an insufficient number of wild bee experts and the absence of proper collections. Up-to-date entomological research programmes of wild bees have not been spatially systematic, so certain areas of Serbia have been studied more, while others less. Although there is clear evidence of a decline in pollinators diversity and abundance across Europe (Potts et al. 2010; Nieto et al. 2014; Goulson et al. 2015), there are no initiatives or activities to protect wild bee species or their habitats in Serbia.

The present study summarises for the first time all the available records of species of wild bees in Serbia. This paper is not intended as a national checklist of bees, since there are undoubtedly more species yet to be found. The aims of this study are: 1) to review the records on the bee fauna, according to bibliographic sources known to the authors, 2) to present some more recent observations, and finally 3) to provide an updated preliminary list of the species of bees occurring in Serbia. The major purpose of this article is to broaden the knowledge of bee diversity in Serbia and pave the way for future research of wild bee fauna at local and regional levels. Another important aim is to improve an understanding of the status and trends of European pollinators.

Materials and methods

Study area

Serbia is situated in central and southeast Europe, mostly in the central Balkan peninsula, while its northern part spreads over the southern belt of the Pannonian Plain. The country's total area is 88,361 km^2 (Spatial Plan RS 2021–2035, Official Gazette of RS No. 48/19). The main geographic units in Serbia are the Pannonian Region in the north, which covers a third of the country, the Peripannonian Region in the central part of the country, which chiefly consists of hills traversed by rivers, and the mountain and basin region which are dominant in the south. The Carpathian Mountains and the Balkan Mountains stretch in the north-south direction through east Serbia. The Dinaric Arc stretches in the west and southwest. The climate of Serbia is under the influences of the landmass of Eurasia, the Atlantic Ocean, and the Mediterranean Sea. It classifies as a warm-humid continental or humid subtropical climate. In the north of the country, the climate is more continental, whereas south and southeast Serbia are influenced by the Mediterranean climate (Stevanović and Stevanović 1995). In the north of Serbia, the Pannonian Plain is a lowland landscape with large rivers (e.g. the Danube, Sava, and Tisa) while to the south hilly or mountainous landscapes are intersected by river valleys. In Vojvodina, there is a large sandy area called Deliblato Sands, which is rare and unusual in inland Europe. The main habitat types are: steppe grasslands and wooded steppe, mesophilic meadows, saline grassland, shrubs, wetland, mainly deciduous southern European forests, coniferous forests, and high-mountain rocky areas and pastures.

Serbia is a country with a number of rich ecosystems, and species diversity of many groups of organisms is high and contributes to a significant part of Europe's biodiversity. According to previous research, in the territory of the Republic of Serbia there are: 39% of the European vascular flora, 74% of the European bird fauna, 67% of the European mammal fauna, 51% of the European fish fauna, and 49% of the European reptile and amphibian fauna (IUCN 2021). Conserved habitats, from lowland grasslands and wetlands, through forests and other higher habitats, to high mountain areas intersected with gorges and major lowland rivers (e.g. the Danube, Sava, and Tisa), all form the basis for its biodiversity. There are 462 protected areas in Serbia on 7.65% of its surface, among which are five National Parks, 18 Nature Parks, 20 Protected Landscapes, 68 Nature Reserves, six Protected Habitats, and 308 Natural Monuments (Spatial Plan RS 2021–2035, Official Gazette of RS No. 48/19). The ecological network that consists of ecologically significant areas and ecological corridors covers 101 nationally and internationally significant areas, comprising 21% of the total area of Serbia. Most areas within the ecological network have an international status based on several aspects: 61 Emerald Areas of Special Conservation Importance – ASCI; 42 Important Bird Areas – IBA; 61 Important Plant Areas – IPA; 40 Prime Butterfly Areas – PBA; ten Ramsar sites. The ecological network also includes other spaces and places that have yet to be spatially identified (Spatial Plan RS 2021–2035, Official Gazette of RS No. 48/19). Agricultural production on annual crops is mostly present in the Pannonian Plain. Serbia produces various agricultural products, mostly grains, fruits, and vegetables. According to the FAOSTAT, Serbia is among the top five world producers of raspberries and plums, which are mainly produced in the southwest. Agricultural landscapes occupy 63.7% of the territory (Spatial Plan RS 2021–2035, Official Gazette of RS No. 48/19).

Methodology

This paper represents a list of bee species in Serbia based on the compiled data known to the authors, gathered from available entomological collections and literature sources between 1890 and 2020, and our own faunistic studies in the decade 2010–2020. Therefore, it includes previously published and unpublished data, supplied by different specialists, as well as some recent records from the authors of this paper. In total, more than 100 publications were examined for relevant records. Additionally, the present list was based on reviewing a database from the online Checklist of Western Palaearctic Bees (Hymenoptera: Apoidea: Anthophila) by Kuhlmann et al. (2020), which provides basic information on bee diversity in the Serbian region.

The following abbreviations are used in the text:

AĐ coll.	Aleksandar Đukić private collection (determined by Zsolt Józan, specialist in Aculeata research in Central Europe; bee specialist Dr Andrej Gogala from the Slovenian Museum of Natural History, Ljubljana, Slovenia; Prof. Denis Michez, Laboratory of Zoology, University of Mons, and PhD student Jelle Devalez, Department of Geography, University of the Aegean);
AZ coll.	Aleksandra Zatezalo collection of the Institute for Nature Conservation of Serbia, Belgrade, Serbia (determined by Zsolt Józan);
FSUNS	Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Novi Sad, Serbia;
SG coll.	Simeun Grozdanić collection of the NHMB (Natural History Museum, Belgrade), Serbia;
ZM coll.	Zoran Mučalica collection of the NHMB, Serbia.

The cited PhD thesis of Stanisavljević (2000) is based on the material collected by the author, data from the available private collections and collections of the NHMB, as well as data from the published literature, which refer to the researched area. PhD theses of Markov (2017) and Mudri-Stojnić (2018) are based on the material from the collection of the FSUNS. The material from the FSUNS entomological collection were determined by Zsolt Józan. The cited Živojinović (1950) and Petrik (1958) collections are not preserved. The paper by Vorgin (1955) was based on data from the collection of the Croatian Natural History Museum, whose data had been collected for ca. 50 years. The data on registered species from the genera *Andrena* (Fabricius, 1775) and *Bombus* (Latreille, 1802) were not published in the paper by Rafajlović and Seleši (1958); the authors had no knowledge of that collection, which at the time was kept in the Zoological Museum of Zagreb; these data were published by Vorgin (1955). The Alfréd Taubert collection was identified by Alfréd Taubert himself with the help of Paul Blüthgen; unfortunately, professional curation of the collection was not provided, and as a consequence, the collection has not been preserved. Lebedev (1931) compiled data from the collection of the Entomological Institute of Belgrade. The collection contained specimens mostly collected by J. Vagnera and A. Matisena from all over Serbia. The species from the material were determined by Lebedev, P. Blüthgen (*Halictus* sensu lato species), and V. Popov (*Bombus* species). This collection was destroyed during World War II. The publication by Vorgin (1918) contains data from the A. Hensch collection and new data collected by Vorgin, as well as bee collections from the Croatian Natural History Museum. The species from the Apfelbeck, V. (1896) material were determined by H. Friese. The species from the Korlević (1890) material were determined by: A. Mocsary, A. Braunis, F. Koh, H. Friese, F.W. Konow,

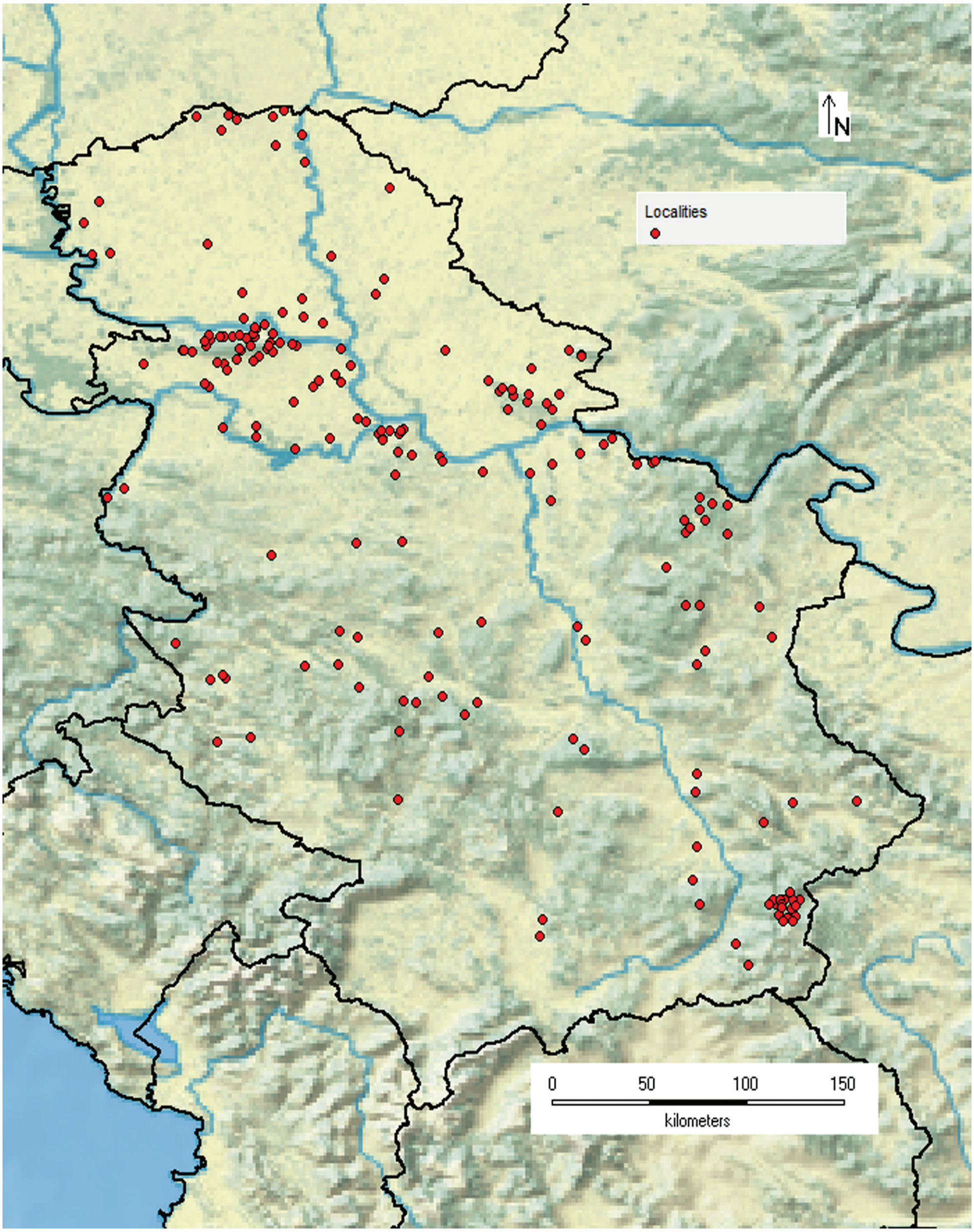

Figure 1. Map of Serbia showing the locations where specimens were collected.

L. Biró, and G. Mayr. The Anton Korlević entomological collection is housed in the Croatian Natural History Museum.

A map of Serbia (Fig. 1) shows the 193 sites where sampling was carried out. The localities were gathered from publications cited in this paper and from data labels in the collections from the Natural History Museum, Belgrade, from the Institute for Nature Conservation of Serbia, and the AĐ collection.

List format

Nieto et al. (2014) were consulted for the nomenclature of the accepted species names, and the nomenclatural and classification changes suggested by Rasmont et al. (2017) and Dorchin et al. (2018) were adopted. Kuhlmann et al. (2020) and Michez et al. (2019) were consulted for classification and the authorities. For clarification of synonyms and other names mentioned in various cited publications, mostly Kuhlmann et al. (2020), but also other sources, were consulted (NBN 2020; Rasmont and Haubruge 2020; Zicha 2020). The valid species' names are shown in bold; families, genera, and species are arranged in alphabetical order. For each species, all references providing records are listed by year; if different from the valid name, the name by which the species is referred to in the original publication is written after "as". Species with no records in Serbia after the 19th century are marked with an asterisk (*). Among the species confirmed by determination of studied material, examined specimens are marked with the double oblique hyphen (⸗) and non-marked species represent records based only on literature data. The black small squares (▪) mark species for which the only source of occurrence in Serbia is the Checklist of the Western Palaearctic Bees (Kuhlmann et al. 2020). At the end of each species paragraph, the IUCN Red List Category (Europe), according to Nieto et al. (2014), is given in square brackets (abbreviations: CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC – Least Concern, DD – Data Deficient). Data about the new material examined are given for the specimens that represent the first published records of species for Serbia.

Results

The list of bees in Serbia presented consists of six families, 58 genera, and 706 species, recorded during the past 130 years. Of the total number of the recorded species, 314 have been confirmed by determination, while 392 species are from literature data. The reported families with the numbers of species (confirmed by determination/based only on literature data) are: Apidae 226 species (91/135), Megachilidae 148 species (62/86), Halictidae 138 species (73/65), Andrenidae 112 species (68/44), Colletidae 69 species (14/55), and Mellitidae 13 species (6/7). The present list includes 14 species with no previously published records for Serbia: *Andrena barbareae* (Panzer, 1805), *A. clarkella* (Kirby, 1802), *A. fulvicornis* (Schenck, 1853), *A. intermedia* (Thomson, 1870), *A. lapponica* (Zetterstedt, 1838), *A. pandellei* (Pérez, 1895), *A. paucisquama* (Noskiewicz, 1924), *A. simillima* (Smith, 1851), *Panurginus herzi* (Morawitz, 1892), *Epeoloides coecutiens* (Fabricius, 1775), *Nomada leucophthalma* (Kirby, 1802), *Chelostoma nasutum* (Pérez, 1895), *Hoplitis claviventris* (Thomson, 1872), and *Dasypoda pyrotrichia* (Förster, 1855).

The diversity and proportional representation of bee families are given in Table 1, and the summary of numbers and proportions of bee species within each category of threat according to the European Red List are presented in Table 2.

Table 1. Diversity and proportional representation of bee families in Serbia, Europe, and the West Palaearctic region (WP).

Family	Serbia				Europe (Nieto et al. 2014 + Rasmont et al. 2017)		WP* (Rasmont et al. 2017)	
	No of genera	% of 58 genera	No of species	% of 706 species	No of species	% of 1,965+86 species	No of species	% of 3,408 species
Andrenidae	6	10.3	112	15.9	465+24	23.8	716	21.0
Apidae	18	31.0	226	32.0	561+16	28.1	926	27.2
Colletidae	2	3.4	69	9.8	146	7.1	270	7.9
Halictidae	12	20.7	138	19.5	314+30	16.8	585	17.2
Megachilidae	17	29.3	148	21.0	442+14	22.2	852	25.0
Mellitidae	3	5.2	13	1.8	37+2	1.9	59	1.7

*area between 26° and 72° latitude north and from 32° longitude west to 62° longitude east.

Table 2. Summary of numbers and proportion of bee species within each category of threat.

The European Red List	Europe (Nieto et al. 2014)		Serbia	
Category	No of species	% of 1,942 species*	No of species	% of 704 species**
Critically Endangered	7	0.4	1	0.1
Endangered	46	2.4	18	2.6
Vulnerable	24	1.2	10	1.4
Near Threatened	101	5.2	64	9.1
Least Concern	663	34.1	390	55.4
Data Deficient	1,101	56.7	221	31.4

*does not include the Not Applicable species in Europe, e.g., species of marginal occurrence (Nieto et al. 2014).
**does not include two species not listed in the European Red List.

Andrenidae (6 genera; 112 species)

Andrena Fabricius, 1775 (104 species)

1. ▪***Andrena aberrans*** Eversmann, 1852 in Kuhlmann et al. (2020). [NT]
2. ⸗***Andrena aeneiventris*** Morawitz, 1872 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Vorgin (1955); Mocsáry (1897). [LC]
3. ****Andrena albopunctata*** (Rossi, 1792) in Mocsáry (1897); as *Andrena funebris* (Panzer, 1798) in Korlević (1890). [LC]
4. ⸗***Andrena alfkenella*** Perkins, 1914 in Mudri-Stojnić (2018); Lebedev (1931). [DD]
5. ***Andrena argentata*** Smith, 1844 in Vorgin (1955); Mocsáry (1897). [DD]
6. ***Andrena atrata*** Friese, 1887 in Vorgin (1918); Mocsáry (1897); as *Andrena bicarinata* (Morawitz, 1876) in Vorgin (1955); Lebedev (1931). [DD]
7. ⸗***Andrena barbareae*** Panzer, 1805 **New material examined:** 1 ♀; Vlasina, Veliki Čemernik; 42.7368°N, 22.2723°E; 25 May 2019; M. Vujić leg.; Andrej Gogala det.; AĐ coll. 1 ♀; Vlasina, Vrtop; 42.7904°N, 22.372°E; 20 Jul. 2019; A. Đukić leg.; Andrej Gogala det.; AĐ coll. [DD]
8. ***Andrena barbilabris*** (Kirby, 1802) as *Andrena sericea* Smith, 1791 in Vorgin (1955); as *Andrena albicrus* (Kirby, 1802) in Mocsáry (1897). [DD]

9. ≠***Andrena bicolor*** Fabricius, 1775 in Kuhlmann et al. (2020); as *Andrena gwynana* (Kirby, 1802) in Živojinović (1950); Lebedev (1931); AĐ coll [LC]
10. ***Andrena bimaculata*** (Kirby, 1802) in Kuhlmann et al. (2020); Živojinović (1950); Lebedev (1931). [DD]
11. ***Andrena brumanensis*** Friese, 1899 in Kuhlmann et al. (2020); as *Andrena clypeata* Brullé, 1832 in Živojinović (1950). [LC]
12. ***Andrena bucephala*** Stephens, 1846 in Kuhlmann et al. (2020); Živojinović (1950); Lebedev (1931). [DD]
13. ≠***Andrena carantonica*** Pérez, 1902 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); ZM coll.; as *Andrena jacobi* Perkins, 1921 in Lebedev (1931). [DD]
14. ≠***Andrena chrysopyga*** Schenck, 1853 in Kuhlmann et al. (2020); Vorgin (1955, 1918); Lebedev (1931); ZM coll. [DD]
15. ▪***Andrena cineraria*** (Linnaeus, 1758) in Kuhlmann et al. (2020). [LC]
16. ≠***Andrena clarkella*** (Kirby, 1802) **New material examined:** 1 ♀; Vlasina Rid; 42.7253°N, 22.3284°E; 21 Jul. 2019; A. Đukić leg.; Andrej Gogala det.; AĐ coll. [DD]
17. ****Andrena coitana*** (Kirby, 1802) as *Andrena shawella* (Kirby, 1802) in Mocsáry (1897). [DD]
18. ***Andrena colletiformis*** Morawitz, 1874 in Kuhlmann et al. (2020); Apfelbeck (1896). [DD]
19. ≠***Andrena combaella*** Warncke, 1966 in Mudri-Stojnić (2018). [DD]
20. ≠***Andrena combinata*** (Christ, 1791) in Kuhlmann et al. (2020); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); ZM coll. [DD]
21. ▪***Andrena comta*** Eversmann, 1852 in Kuhlmann et al. (2020). [EN]
22. ≠***Andrena confinis*** Stöckhert, 1930 in Markov (2017); Markov et al. (2016); Živojinović (1950).
23. ≠***Andrena congruens*** Schmiedeknecht, 1884 in Kuhlmann et al. (2020); AĐ coll. [LC]
24. ≠***Andrena cordialis*** Morawitz, 1877 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016). [DD]
25. ≠***Andrena curvana*** Warncke, 1965 in Markov (2017); Markov et al. (2016). [DD]
26. ▪***Andrena decipiens*** Schenck, 1861 in Kuhlmann et al. (2020). [DD]
27. ***Andrena denticulata*** (Kirby, 1802) in Lebedev (1931). [DD]
28. ≠***Andrena dorsalis*** Brullé, 1832 in Kuhlmann et al. (2020); ZM coll. [DD]
29. ***Andrena dorsata*** (Kirby, 1802) in Kuhlmann et al. (2020); Živojinović (1950); Lebedev (1931); as *Andrena dubitata* Schenck, 1870 in Vorgin (1955); Apfelbeck (1896). [DD]
30. ***Andrena erythrocnemis*** Morawitz, 1870 in Lebedev (1931); Mocsáry (1897). [DD]
31. ****Andrena fimbriata*** Brullé, 1832 in Mocsáry (1897). [DD]

32. ⫽***Andrena flavipes*** Panzer, 1799 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Grozdanić (1971b); Vorgin (1955); Živojinović (1950); Lebedev (1931); AZ coll.; ZM coll.; also as *Andrena extricata* Smith, 1849 in Apfelbeck (1896); as *Andrena extricata* in Mocsáry (1897); Korlević (1890); as *Andrena fulvicrus* Dufour, 1841 in Petrik (1958). [LC]
33. ⫽***Andrena florea*** Fabricius, 1793 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Apfelbeck (1896); as *Andrena rosae* var. *austriaca* Schmied. in Živojinović (1950); as *Andrena austriaca* Panzer, 1798 in Mocsáry (1897). [DD]
34. ⫽***Andrena fulvago*** (Christ, 1791) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Vorgin (1955); Lebedev (1931). [DD]
35. ⫽***Andrena fulvicornis*** Schenck, 1853 **New material examined:** 1 ♀; Beočin, Fruška gora, Časorske livade; 45.1894°N, 19.7451°E; 15 Jun. 2018; S. Mudri-Stojnić leg.; Zsolt Józan det.; FSUNS. [DD]
36. ****Andrena fuscosa*** Erichson, 1835 as *Andrena ephippium* Spinola, 1838 in Mocsáry (1897). [DD]
37. ⫽***Andrena gelriae*** van der Vecht, 1927 in Markov (2017); Markov et al. (2016); AZ coll. [DD]
38. ⫽***Andrena gravida*** Imhoff, 1832 in Kuhlmann et al. (2020); Lebedev (1931); AĐ coll.; AZ coll.; ZM coll. [DD]
39. ***Andrena grozdanici*** Osytshnjuk, 1975 in Kuhlmann et al. (2020); Mučalica (1984). [DD]
40. ⫽***Andrena haemorrhoa*** (Fabricius, 1781) in Kuhlmann et al. (2020); AĐ coll.; AZ coll.; as *Andrena albicans* auct. nec Müller in Živojinović (1950); Lebedev (1931). [LC]
41. ⫽***Andrena hattorfiana*** (Fabricius, 1775) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Lebedev (1931); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896); AĐ coll. [NT]
42. ***Andrena hedikae*** Jaeger, 1934 in Kuhlmann et al. (2020); Vorgin (1955). [DD]
43. ⫽***Andrena humilis*** Imhoff, 1832 in Kuhlmann et al. (2020); Lebedev (1931); in Apfelbeck (1896); AĐ coll.; as *Andrena fulvescens* Smith, 1847 in Vorgin (1955, 1918). [DD]
44. ▪***Andrena hungarica*** Friese, 1887 in Kuhlmann et al. (2020). [DD]
45. ***Andrena hypopolia*** Schmiedeknecht, 1884 in Kuhlmann et al. (2020); Vorgin (1955, 1918); Mocsáry (1897); Korlević (1890). [DD]
46. ⫽***Andrena impunctata*** Pérez, 1895 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016). [LC]
47. ⫽***Andrena intermedia*** Thomson, 1870 **New material examined:** 1 ♀; Vlasina, Veliki Čemernik; 42.7368°N, 22.2723°E; 21 Jul. 2019; M. Vujić leg.; Andrej Gogala det.; AĐ coll. [LC]

48. ⸗***Andrena labialis*** (Kirby, 1802) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Grozdanić (1970); Vorgin (1955, 1918); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); AZ coll.; ZM coll. [DD]
49. ⸗***Andrena labiata*** Fabricius, 1781 in Lebedev (1931); ZM coll. [DD]
50. ▪***Andrena lagopus*** Latreille, 1809 in Kuhlmann et al. (2020). [LC]
51. ⸗***Andrena lapponica*** Zetterstedt, 1838 **New material examined:** 1 ♀; Vlasina, Gadžini; 42.7378°N, 22.3042°E; 25 May 2019; A. Đukić leg.; Andrej Gogala det.; AĐ coll. [LC]
52. ⸗***Andrena lathyri*** Alfken, 1899 in Kuhlmann et al. (2020); Grozdanić (1970); ZM coll. [DD]
53. ⸗***Andrena limata*** Smith, 1853 in Mudri-Stojnić (2018); as *Andrena pectoralis* Schmiedeknecht, 1883 in Vorgin (1955); Mocsáry (1897); Korlević (1890). [DD]
54. ***Andrena limbata*** Eversmann, 1852 in Lebedev (1931). [DD]
55. ***Andrena marginata*** Fabricius, 1776 in Kuhlmann et al. (2020); Lebedev (1931); Mocsáry (1897). [DD]
56. ▪***Andrena mehelyi*** Alfken, 1936 in Kuhlmann et al. (2020). [DD]
57. ⸗***Andrena minutula*** (Kirby, 1802) in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Lebedev (1931); AĐ coll.; as *Andrena parvula* (Kirby, 1802) in Apfelbeck (1896). [DD]
58. ⸗***Andrena minutuloides*** Perkins, 1914 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Lebedev (1931). [DD]
59. ⸗***Andrena mocsaryi*** Schmiedeknecht, 1884 in Markov (2017); Markov et al. (2016). [LC]
60. ***Andrena morio*** Brullé, 1832 in Kuhlmann et al. (2020); Petrik (1958); Vorgin (1955); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [DD]
61. ⸗***Andrena nasuta*** Giraud, 1863 in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Vorgin (1918); Mocsáry (1897). [DD]
62. ***Andrena nigroaenea*** (Kirby, 1802) in Kuhlmann et al. (2020); Vorgin (1955). [LC]
63. ⸗***Andrena nitida*** (Müller, 1776) in Kuhlmann et al. (2020); Vorgin (1955); Mocsáry (1897); AĐ coll. [LC]
64. ⸗***Andrena nitidiuscula*** Schenck, 1853 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov et al. (2016); Mudri-Stojnić et al. (2012); Mocsáry (1897); as *Andrena lucens* Imhoff, 1868 in Vorgin (1955, 1918); Korlević (1890). [LC]
65. ▪***Andrena niveata*** Friese, 1887 in Kuhlmann et al. (2020). [DD]
66. ***Andrena nobilis*** Morawitz, 1874 in Kuhlmann et al. (2020); Vorgin (1955). [DD]
67. ⸗***Andrena oralis*** Morawitz, 1876 in Markov (2017); Markov et al. (2016); Vorgin (1955). [DD]

68. ⸗***Andrena ovatula*** (Kirby, 1802) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Živojinović (1950); AZ coll.; also as *Andrena albofasciata* Thomson, 1871 in Lebedev (1931); as *Andrena afzeliella* (Kirby, 1802) in Petrik (1958). [NT]
69. ⸗***Andrena pandellei*** Pérez, 1895 **New material examined:** 1 ♂; Novi Sad, Kamenički park; 45.2299°N, 19.8518°E; 20 Jun. 2018; A. Đukić leg.; Zsolt Józan det.; AĐ coll. [LC]
70. ⸗***Andrena paucisquama*** Noskiewicz, 1924 **New material examined:** 1 ♀; Fruška gora, Manastir Grgeteg; 45.1383°N, 19.9044°E; 20 May 2018; S. Mudri-Stojnić leg.; Zsolt Józan det.; FSUNS. [DD]
71. ⸗***Andrena pilipes*** Fabricius, 1781 in Kuhlmann et al. (2020); Petrik (1958); Vorgin (1918); Korlević (1890); ZM coll.; as *Andrena carbonaria* (Linnaeus, 1767) in Vorgin (1955); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [LC]
72. ⸗***Andrena polita*** Smith, 1847 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Lebedev (1931). [LC]
73. ⸗***Andrena potentillae*** Panzer, 1809 in ZM coll. [DD]
74. ⸗***Andrena propinqua*** Schenck, 1853 in Kuhlmann et al. (2020); Lebedev (1931); Mocsáry (1897); ZM coll. [DD]
75. ⸗***Andrena proxima*** (Kirby, 1802) in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Vorgin (1955); Živojinović (1950); Lebedev (1931); Apfelbeck (1896). [DD]
76. ****Andrena pyropygia*** Kriechbaumer, 1873 in Mocsáry (1897). [LC]
77. ⸗***Andrena rhenana*** Stoeckhert, 1930 in ZM coll. [DD]
78. ⸗***Andrena rosae*** Panzer, 1801 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Lebedev (1931). [DD]
79. ▪***Andrena rufula*** Schmiedeknecht, 1883 in Kuhlmann et al. (2020). [LC]
80. ▪***Andrena schencki*** Morawitz, 1866 in Kuhlmann et al. (2020). [DD]
81. ▪***Andrena schlettereri*** Friese, 1896 in Kuhlmann et al. (2020). [DD]
82. ***Andrena scita*** Eversmann, 1852 in Kuhlmann et al. (2020); Vorgin (1955, 1918); Mocsáry (1897); Apfelbeck (1896). [DD]
83. ⸗***Andrena seminuda*** Friese, 1896 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); as *Andrena setigera* Alfken, 1911 in Vorgin (1955). [DD]
84. ***Andrena sericata*** Imhoff, 1868 in Kuhlmann et al. (2020); Apfelbeck (1896). [DD]
85. ⸗***Andrena simillima*** Smith, 1851 **New material examined:** 1 ♀; Vlasina, Delnice-Ljote; 42.6933°N, 22.3176°E; 22 Jul. 2019; A. Đukić leg.; Andrej Gogala det.; AĐ coll. [LC]
86. ⸗***Andrena simontornyella*** Noskiewicz, 1939 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016). [LC]
87. ⸗***Andrena subopaca*** Nylander, 1848 in Lebedev (1931); AĐ coll. [LC]
88. ⸗***Andrena suerinensis*** Perkins 1914 in ZM coll. [DD]

89. ⸗***Andrena symphyti*** Schmiedeknecht, 1883 in Markov (2017); Markov et al. (2016); AZ coll.; ZM coll. [DD]
90. ⸗***Andrena taraxaci*** Giraud, 1861 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Schwenninger (2015); Grozdanić (1971b); Grozdanić and Vasić (1965c); Vorgin (1955); Lebedev (1931); ZM coll. [DD]
91. ⸗***Andrena tarsata*** Nylander, 1848 in Vorgin (1918); ZM coll. [DD]
92. ⸗***Andrena thoracica*** (Fabricius, 1775) in Mudri-Stojnić (2018); Vorgin (1955); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [DD]
93. ⸗***Andrena tibialis*** (Kirby, 1802) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Vorgin (1955); Apfelbeck (1896). [LC]
94. ⸗***Andrena trimmerana*** (Kirby, 1802) in Lebedev (1931); ZM coll. [DD]
95. ***Andrena truncatilabris*** Morawitz, 1877 in Kuhlmann et al. (2020); Vorgin (1955, 1918); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [DD]
96. ⸗***Andrena ungeri*** Mavromoustakis, 1952 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Mudri-Stojnić et al. (2012). [LC]
97. ⸗***Andrena vaga*** Panzer, 1799 in Lebedev (1931); ZM coll. [LC]
98. ⸗***Andrena variabilis*** Smith, 1853 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Vorgin (1955); Lebedev (1931); AZ coll. [DD]
99. ***Andrena varians*** (Kirby, 1802) in Lebedev (1931); Vorgin (1955). [LC]
100. ***Andrena ventralis*** Imhoff, 1832 in Kuhlmann et al. (2020); Lebedev (1931). [DD]
101. ⸗***Andrena ventricosa*** Dours, 1873 in Markov (2017); Markov et al. (2016); Vorgin (1918). [DD]
102. ⸗***Andrena viridescens*** Viereck, 1916 in Lebedev (1931); ZM coll. [DD]
103. ***Andrena wilkella*** (Kirby, 1802) in Vorgin (1955); as *Andrena convexiuscula* Kirby, 1802 in Petrik (1958); Mocsáry (1897); Apfelbeck (1896). [DD]

Camptopoeum Spinola, 1843 (2 species)

104. ⸗***Camptopoeum frontale*** Fabricius 1804 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [DD]
105. ***Camptopoeum friesei*** Mocsáry 1894 in Grozdanić (1971b); Rafajlović and Seleši (1958); Živojinović (1950); Mocsáry (1897). [LC]

Clavipanurgus Warncke, 1972 (1 species)

106. ▪***Clavipanurgus sculpturatus*** Morawitz 1872 in Kuhlmann et al. (2020). [DD]

Melitturga Latreille, 1809 (1 species)

107. ⸗***Melitturga clavicornis*** Latreille 1808 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Petrik (1958); Mocsáry (1897). [NT]

Panurginus Nylander, 1848 (2 species)

108. ***Panurginus labiatus*** Eversmann 1852 in Kuhlmann et al. (2020); Lebedev (1931). [DD]
109. =***Panurginus herzi*** Morawitz, 1892 **New material examined:** 1 ♀; Vlasina, Vrtop; 42.7904°N, 22.372°E; 20 Jul. 2019; A. Đukić leg.; Andrej Gogala det.; AĐ coll. 1 ♀; Vlasina Rid; 42.7253°N, 22.3284°E; 22–23 Jul. 2019; A. Đukić leg.; Andrej Gogala det.; AĐ coll. [DD]

Panurgus Panzer, 1806 (2 species)

110. =***Panurgus banksianus*** Kirby 1802 in Kuhlmann et al. (2020); AĐ coll.; ZM coll. [LC]
111. =***Panurgus calcaratus*** Scopoli, 1763 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); AĐ coll.; as *Panurgus lobatus* (Panzer, 1799) in Petrik (1958). [LC]

Apidae (18 genera; 226 species)

Amegilla Friese, 1897 (5 species)

112. =***Amegilla albigena*** Lepeletier, 1841 in Kuhlmann et al. (2020); ZM coll.; as *Anthophora albigena* Lepeletier, 1841 in Rafajlović and Seleši (1958); Vorgin (1955, 1918); Mocsáry (1897). [LC]
113. =***Amegilla garrula*** Rossi, 1790 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); as *Anthophora garrula* Rossi, 1790 in Rafajlović and Seleši (1958); Živojinović (1950); as *Anthophora garrulus* in Mocsáry (1897). [LC]
114. ***Amegilla magnilabris*** (Fedtschenko 1875) as *Anthophora magnilabris* Fedtschenko, 1875 in Rafajlović and Seleši (1958); Mocsáry (1897). [DD]
115. =***Amegilla quadrifasciata*** de Villers, 1789 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Stanisavljević (2000); ZM coll.; as *Anthophora quadrifasciata* (de Villers, 1789) in Petrik (1958); Rafajlović and Seleši (1958); Lebedev (1931); as *Anthophora quadrifasciatus* in Mocsáry (1897). [DD]
116. =***Amegilla salviae*** Morawitz, 1876 in Kuhlmann et al. (2020); ZM coll. [DD]

Ammobatoides Radoszkowski, 1867 (1 species)

117. =***Ammobatoides abdominalis*** (Eversmann, 1852) in ZM coll. [EN]

Ammobates Latreille, 1809 (2 species)

118. ****Ammobates punctatus*** (Fabricius, 1804) in Mocsáry (1897). [LC]

119. ****Ammobates vinctus*** Gerstäcker, 1869 in Mocsáry (1897). [LC]

Anthophora Latreille, 1803 (18 species)

120. ***Anthophora aestivalis*** Panzer 1801 in Kuhlmann et al. (2020); Lebedev (1931). [LC]
121. ▪***Anthophora atroalba*** Lepeletier 1841 in Kuhlmann et al. (2020). [DD]
122. ⸗***Anthophora bimaculata*** Panzer, 1798 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); ZM coll.; as *Saropoda bimaculata* in Petrik (1958); as *Anthophora bimaculatus* in Mocsáry (1897). [LC]
123. ▪***Anthophora canescens*** Brullé 1832 in Kuhlmann et al. (2020). [DD]
124. ***Anthophora crassipes*** Lepeletier, 1841 in Lebedev (1931). [DD]
125. ▪***Anthophora dalmatica*** Pérez 1902 in Kuhlmann et al. (2020). [DD]
126. ▪***Anthophora dufourii*** Lepeletier 1841 in Kuhlmann et al. (2020). [DD]
127. ⸗***Anthophora fulvitarsis*** Brullé 1832 in ZM coll. [DD]
128. ⸗***Anthophora furcata*** Panzer, 1798 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Lebedev (1931); AĐ coll.; ZM coll.; as *Anthophora furcatus* in Mocsáry (1897). [LC]
129. ▪***Anthophora orientalis*** Morawitz 1877 in Kuhlmann et al. (2020). [DD]
130. ⸗***Anthophora plagiata*** Illiger, 1806 in Kuhlmann et al. (2020); as *Anthophora parietina* (Fabricius, 1793) in Mučalica (1987a, 1987b); Grozdanić (1971b); Grozdanić and Stevanović (1965); Grozdanić and Vasić (1965b); Rafajlović and Seleši (1958); Vorgin (1918); ZM coll.; *Anthophora parietinus* in Mocsáry (1897). [LC]
131. ⸗***Anthophora plumipes*** Pallas, 1772 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); AĐ coll.; ZM coll.; as *Anthophora acervorum* (Linnaeus, 1758) in Grozdanić (1971b); Grozdanić and Vasić (1965b, 1965c); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931). [LC]
132. ***Anthophora podagra*** Lepeletier, 1841 in Kuhlmann et al. (2020); as *Anthophora podagrus* in Mocsáry (1897). [DD]
133. ⸗***Anthophora pubescens*** Fabricius 1781 in Kuhlmann et al. (2020); Grozdanić and Radivojević (1972); Grozdanić (1971b); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); SG coll. [DD]
134. ***Anthophora quadrimaculata*** Panzer, 1798 in Kuhlmann et al. (2020); as *Anthophora vulpina* (Panzer, 1798) in Rafajlović and Seleši (1958); as *Anthophora vulpinus* Mocsáry (1897). [DD]
135. ⸗***Anthophora retusa*** Linnaeus, 1758 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Lebedev (1931); ZM coll.; as *Anthophora retusus* in Mocsáry (1897). [LC]
136. ▪***Anthophora robusta*** Klug 1845 in Kuhlmann et al. (2020). [DD]
137. ⸗***Anthophora salviae*** (Panzer, 1804) in Kuhlmann et al. (2020); Vorgin (1955, 1918); Lebedev (1931); Mocsáry (1897); Korlević (1890); also as *Anthophora crinipes* Smith, 1854 in Rafajlović and Seleši (1958); as *Anthophora crin-*

ipes in Markov (2017); Markov et al. (2016); Mučalica (1997, 1990, 1987b); Grozdanić (1971b); Grozdanić and Mučalica (1969); Grozdanić and Vasić (1966a, 1965b); AĐ coll.; ZM coll. [DD]

Apis Linnaeus, 1768 (1 species)

138. ⫽***Apis mellifera*** Linnaeus 1758 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Kulinčević et al. (1997); Krunić (1994, 1986); Grozdanić (1970, 1958b); Grozdanić and Vasić (1966a); Petrik (1958); Vlatković (1957); Živojinović (1950); Mocsáry (1897); Apfelbeck (1896); AĐ coll.; ZM coll. [DD]

Biastes Panzer, 1806 (3 species)

139. ⫽***Biastes brevicornis*** (Panzer, 1798) in Petrik (1958); Rafajlović and Seleši (1958); Mocsáry (1897); Apfelbeck (1896); SG coll. [LC]
140. ***Biastes emarginatus*** (Schenck, 1853) in Vorgin (1918). [LC]
141. ▪***Biastes truncatus*** (Nylander, 1848) in Kuhlmann et al. (2020). [VU]

Bombus Latreille, 1802 (47 species)

142. ⫽***Bombus argillaceus*** (Scopoli, 1763) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Rasmont et al. (2015); Grozdanić (1971b, 1970); Grozdanić and Vasić (1965c); Grozdanić and Čolović (1955b); Lebedev (1931); ZM coll. [LC]
143. ▪***Bombus armeniacus*** Radoszkowski, 1877 in Kuhlmann et al. (2020). [EN]
144. ⫽***Bombus barbutellus*** Kirby, 1802 in Kuhlmann et al. (2020); Rasmont et al. (2015); SG coll.; as *Psithyrus barbutellus* (Kirby, 1802) in Grozdanić and Vasić (1966a); Vorgin (1955); Mocsáry (1897). [LC]
145. ***Bombus bohemicus*** Seidl, 1838 in Kuhlmann et al. (2020); Rasmont et al. (2015). [LC]
146. ⫽***Bombus campestris*** Panzer, 1801 in Kuhlmann et al. (2020); Rasmont et al. (2015); AĐ coll; as *Psithyrus campestris* f. *francisanus* K. and also as *Psithyrus campestris* f. *rosiellus* K. in Vorgin (1955). [LC]
147. ***Bombus confusus*** Schenck, 1861 in Kuhlmann et al. (2020); Rasmont et al. (2015); Mocsáry (1897). [VU]
148. ▪***Bombus cryptarum*** Fabricius, 1775 in Kuhlmann et al. (2020). [LC]
149. ***Bombus cullumanus*** Kirby, 1802 in Kuhlmann et al. (2020); as *Bombus serrisquama* Morawitz, 1888 in Lebedev (1931). [CR]
150. ***Bombus deuteronymus*** Schulz, 1879 in Kuhlmann et al. (2020); Rasmont et al. (2015); as *Bombus bureschi* Pittioni, 1939 in Živojinović (1950). [DD]
151. ▪***Bombus distinguendus*** Morawitz, 1869 in Kuhlmann et al. (2020). [VU]
152. ▪***Bombus flavidus*** Eversmann, 1852 in Kuhlmann et al. (2020). [LC]

153. ***Bombus fragrans*** (Pallas, 1771) in Kuhlmann et al. (2020); Mocsáry (1897). [EN]
154. ▪***Bombus gerstaeckeri*** Morawitz, 1881 in Kuhlmann et al. (2020). [VU]
155. ⸗***Bombus haematurus*** Kriechbaumer, 1870 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rasmont et al. (2015); Grozdanić (1971b); Grozdanić and Vasić (1965c); Živojinović (1950); Lebedev (1931); ZM coll. [LC]
156. ⸗***Bombus hortorum*** Linnaeus, 1761 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rasmont et al. (2015); Grozdanić (1971b, 1970); Grozdanić and Vasić (1966a); Grozdanić and Vasić (1965c); Grozdanić and Baranov (1963); Vorgin (1955); Živojinović (1950); Lebedev (1931); Apfelbeck (1896); AĐ coll.; ZM coll. [LC]
157. ⸗***Bombus humilis*** Illiger, 1806 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Rasmont et al. (2015); Mudri-Stojnić et al. (2012); Grozdanić and Vasić (1966a, 1965c); Živojinović (1950); AĐ coll.; ZM coll.; as *Bombus helferanus* Seidl, 1838 in Vorgin (1955); Lebedev (1931); as *Bombus variabilis* Schmiedeknecht, 1878 in Mocsáry (1897); Apfelbeck (1896). [LC]
158. ⸗***Bombus hypnorum*** Linnaeus, 1758 in Kuhlmann et al. (2020); Markov (2017); Rasmont et al. (2015); Mudri-Stojnić et al. (2012); Živojinović (1950); Lebedev (1931); AĐ coll. [LC]
159. ▪***Bombus jonellus*** Kirby, 1802 in Kuhlmann et al. (2020). [LC]
160. ***Bombus laesus*** Morawitz, 1875 in Kuhlmann et al. (2020); Vorgin (1918); Mocsáry (1897). [NT]
161. ⸗***Bombus lapidarius*** Linnaeus, 1758 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Rasmont et al. (2015); Mudri-Stojnić et al. (2012); Grozdanić (1971b, 1970); Grozdanić and Vasić (1966a, 1965c); Vorgin (1955); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); AĐ coll.; ZM coll. [LC]
162. ⸗***Bombus lucorum*** Linnaeus, 1761 in Kuhlmann et al. (2020); Vorgin (1955); Živojinović (1950); Lebedev (1931); AĐ coll.; ZM coll. [LC]
163. ▪***Bombus mendax*** Gerstäcker, 1869 in Kuhlmann et al. (2020). [NT]
164. ▪***Bombus mesomelas*** Gerstäcker, 1869 in Kuhlmann et al. (2020). [LC]
165. ▪***Bombus mlokosievitzii*** Radoszkowski, 1877 in Kuhlmann et al. (2020). [DD]
166. ▪***Bombus mocsaryi*** Kriechbaumer, 1877 in Kuhlmann et al. (2020). [EN]
167. ▪***Bombus monticola*** Smith, 1849 in Kuhlmann et al. (2020). [LC]
168. ▪***Bombus mucidus*** Gerstäcker, 1869 in Kuhlmann et al. (2020). [NT]
169. ***Bombus muscorum*** Linnaeus, 1758 in Kuhlmann et al. (2020); Stevanović and Lazarov (1977); Vorgin (1955). [VU]
170. ***Bombus niveatus*** Kriechbaumer, 1870 in Kuhlmann et al. (2020); Rasmont et al. (2015); as *Bombus vorticosus* Gerstäcker, 1872 in Vorgin (1955). [LC]
171. ▪***Bombus norvegicus*** Sparre-Schneider, 1918 in Kuhlmann et al. (2020). [LC]
172. ⸗***Bombus pascuorum*** Scopoli, 1763 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Rasmont et al. (2015); Mudri-Stojnić et al. (2012); AĐ coll.; ZM coll.; as *Bombus cognatus* Stephens, 1846

in Grozdanić (1971b); Grozdanić and Vasić (1965c); Lebedev (1931); Vorgin (1918); as *Bombus agrorum* (Fabricius, 1787) in Grozdanić and Vasić (1966a, 1965c); Grozdanić (1960); Grozdanić and Stevanović (1959); Petrik (1958); Grozdanić and Čolović (1955a, 1955b); Vorgin (1955); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); Korlević (1890). [LC]

173. ⸗***Bombus pomorum*** Panzer, 1805 in Kuhlmann et al. (2020); Rasmont et al. (2015); Vorgin (1918); Mocsáry (1897); AĐ coll. [VU]
174. ⸗***Bombus pratorum*** Linnaeus, 1761 in Kuhlmann et al. (2020); Markov (2017); Rasmont et al. (2015); Grozdanić and Čolović (1955a, 1955b); Živojinović (1950); Lebedev (1931); Mocsáry (1897); AĐ coll. [LC]
175. ***Bombus pyrenaeus*** Pérez, 1879 in Kuhlmann et al. (2020); Rasmont et al. (2015). [LC]
176. ⸗***Bombus quadricolor*** Lepeletier, 1832 in Kuhlmann et al. (2020); Rasmont et al. (2015); AĐ coll. [LC]
177. ⸗***Bombus ruderarius*** Müller, 1776 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Rasmont et al. (2015); Mudri-Stojnić et al. (2012); AĐ coll.; as *Bombus derhamellus* (Kirby, 1802) in Lebedev (1931); Apfelbeck (1896). [LC]
178. ***Bombus ruderatus*** Fabricius, 1775 in Petrik (1958); Vorgin (1955). [LC]
179. ⸗***Bombus rupestris*** Fabricius, 1793 in Kuhlmann et al. (2020); Rasmont et al. (2015); AĐ coll.; ZM coll. [LC]
180. ▪***Bombus sichelii*** Radoszkowski, 1859 in Kuhlmann et al. (2020). [LC]
181. ⸗***Bombus soroeensis*** Fabricius, 1776 in Kuhlmann et al. (2020); Rasmont et al. (2015); Vorgin (1955); ZM coll.; as *Bombus proteus* Gerstäcker, 1869 in Lebedev (1931). [LC]
182. ***Bombus subterraneus*** (Linnaeus, 1758) in Kuhlmann et al. (2020); Rasmont et al. (2015). [LC]
183. ⸗***Bombus sylvarum*** Linnaeus, 1761 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Rasmont et al. (2015); Mudri-Stojnić et al. (2012); Grozdanić (1971b); Grozdanić and Vasić (1966a, 1965c); Vorgin (1955); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); Korlević (1890); SG coll. [LC]
184. ⸗***Bombus sylvestris*** Lepeletier, 1832 in Kuhlmann et al. (2020); Rasmont et al. (2015); AĐ coll. [LC]
185. ⸗***Bombus terrestris*** Linnaeus, 1758 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Rasmont et al. (2015); Mudri-Stojnić et al. (2012); Grozdanić (1971b, 1970); Grozdanić and Vasić (1966a, 1965c); Grozdanić and Baranov (1963); Petrik (1958); Grozdanić and Čolović (1955b); Vorgin (1955); Živojinović (1950); Lebedev (1931); Apfelbeck (1896); AĐ coll.; ZM coll. [LC]
186. ⸗***Bombus vestalis*** Geoffroy, 1785 in Kuhlmann et al. (2020); Rasmont et al. (2015); AĐ coll.; SG coll.; as *Psithyrus vestalis* Geoffroy, 1785 in Grozdanić and Vasić (1966a); Vorgin (1955); Lebedev (1931); Apfelbeck (1896). [LC]

187. ≡***Bombus wurflenii*** Radoszkowski, 1859 in Kuhlmann et al. (2020); Rasmont et al. (2015); AĐ coll.; as *Bombus mastrucatus* Gerstäcker, 1869 in Apfelbeck (1896). [LC]
188. ***Bombus zonatus*** Smith, 1854 in Kuhlmann et al. (2020); Živojinović (1950); Lebedev (1931); Mocsáry (1897). [EN]

Ceratina Latreille, 1802 (11 species)

189. ≡***Ceratina acuta*** Friese, 1896 in Grozdanić (1971b); Rafajlović and Seleši (1958); ZM coll. [LC]
190. ≡***Ceratina callosa*** Fabricius, 1794 in Grozdanić (1971b); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); ZM coll. [LC]
191. ≡***Ceratina chalcites*** Germar, 1839 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); Mocsáry (1897). [LC]
192. ≡***Ceratina chalybea*** Chevrier, 1872 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016). [LC]
193. ≡***Ceratina cucurbitina*** Rossi, 1792 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Grozdanić (1971b); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); ZM coll. [LC]
194. ≡***Ceratina cyanea*** Kirby, 1802 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); AĐ coll.; ZM coll. [LC]
195. ▪***Ceratina dallatorreana*** Friese, 1896 in Kuhlmann et al. (2020). [LC]
196. ▪***Ceratina dentiventris*** Gerstäcker, 1869 in Kuhlmann et al. (2020). [LC]
197. ≡***Ceratina loewi*** Gerstäcker, 1869 in ZM coll. [DD]
198. ***Ceratina nigroaenea*** Gerstäcker, 1869 in Rafajlović and Seleši (1958). [LC]
199. ≡***Ceratina nigrolabiata*** Friese, 1896 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Grozdanić (1971b); Rafajlović and Seleši (1958); AĐ coll.; ZM coll. [LC]

Epeoloides Giraud, 1863 (1 species)

200. ≡***Epeoloides coecutiens*** (Fabricius, 1775) **New material examined:** 1 ♂, 1 ♀; Vlasina, Blato, Božički kanal; 42.6786°N, 22.3543°E; 23 Jul. 2019; T. Tot, N. Veljković leg.; Andrej Gogala det.; AĐ coll. [LC]

Epeolus Latreille, 1802 (5 species)

201. ***Epeolus cruciger*** Panzer, 1799 in Kuhlmann et al. (2020); Bogusch and Hadrava (2018); Rafajlović and Seleši (1958). [NT]
202. ***Epeolus fasciatus*** Friese, 1895 in Bogusch and Hadrava (2018); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897). [DD]

203. ⸗***Epeolus schummeli*** Schilling, 1849 in SG coll. [NT]
204. ***Epeolus transitorius*** Eversmann, 1852 in Bogusch and Hadrava (2018); Petrik (1958); as *Epeolus julliani* Pérez, 1884 in Kuhlmann et al. (2020). Note: According to Bogusch and Hadrava (2018) *E. julliani* is syn. nov. under *E. transitorius*. [DD]
205. ⸗***Epeolus variegatus*** Linnaeus, 1758 in Kuhlmann et al. (2020); Bogusch and Hadrava (2018); Markov (2017); Markov et al. (2016); Petrik (1958); Apfelbeck (1896); also as *Epeolus productus* Thomson, 1870 in Mocsáry (1897). [LC]

Eucera Scopoli, 1770 (33 species)

206. ***Eucera alternans*** Brullé, 1832 in Kuhlmann et al. (2020); as *Tetralonia ruficollis* (Brullé, 1832) in Petrik (1958); as *Eucera ruficollis* (Brullé, 1832) in Vorgin (1918). [DD]
207. ***Eucera caspica*** Morawitz, 1873 in Vorgin (1918). [LC]
208. ⸗***Eucera chrysopyga*** Pérez, 1854 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896). [LC]
209. ⸗***Eucera cineraria*** Eversmann, 1852 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016). [LC]
210. ⸗***Eucera clypeata*** Erichson, 1835 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Lebedev (1931); Vorgin (1918); Mocsáry (1897); also as *Eucera similis* Lepeletier, 1841 in Rafajlović and Seleši (1958); Apfelbeck (1896). [LC]
211. ***Eucera dalmatica*** Lepeletier, 1841 in Kuhlmann et al. (2020); Lebedev (1931); Mocsáry (1897). [LC]
212. ⸗***Eucera excisa*** Mocsáry, 1879 in Grozdanić (1971b, 1969a); Grozdanić and Vasić (1967b); Vorgin (1918); Lebedev (1931); Mocsáry (1897); ZM coll. [DD]
213. ⸗***Eucera hungarica*** Friese, 1896 in Mocsáry (1897); SG coll.; also as *Tetralonia hungarica* (Friese, 1896) in Rafajlović and Seleši (1958). [LC]
214. ⸗***Eucera interrupta*** Bär, 1850 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897). [LC]
215. ⸗***Eucera longicornis*** Linnaeus, 1758 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Petrik (1958); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931); AĐ coll.; SG coll.; ZM coll.; also as *Eucera difficilis* Pérez, 1879 in Mocsáry (1897); Apfelbeck (1896). [LC]
216. ⸗***Eucera nigrescens*** Pérez, 1879 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); ZM coll.; as *Eucera tuberculata* (Fabricius, 1793) in Grozdanić and Vasić (1966a, 1965c); Rafajlović and Seleši (1958); Lebedev (1931). [LC]
217. ⸗***Eucera nigrifacies*** Lepeletier, 1841 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Mocsáry (1897). [LC]

218. ⫽***Eucera pollinaris*** Kirby, 1802 in Markov (2017); Markov et al. (2016); as *Eucera armeniaca* (Morawitz, 1877) in Rafajlović and Seleši (1958). [DD]
219. ***Eucera proxima*** Morawitz, 1875 as *Eucera nitidiventris* Mocsáry, 1879 in Rafajlović and Seleši (1958); Vorgin (1918); Apfelbeck (1896). [DD]
220. ▪***Eucera punctulata*** Alfken, 1942 in Kuhlmann et al. (2020). [DD]
221. ⫽***Eucera seminuda*** Brullé, 1832 in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Lebedev (1931); Vorgin (1918); ZM coll. [LC]
222. ⫽***Eucera taurica*** Morawitz, 1871 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016). [DD]
223. ***Eucera tricincta*** Erichson, 1835 in Vorgin (1918); also as *Tetralonia tricincta* (Erichson, 1835) in Rafajlović and Seleši (1958). [LC]
224. ▪***Eucera vittulata*** Noskiewicz, 1934 in Kuhlmann et al. (2020). [DD]
225. ***Eucera vulpes*** Brullé, 1832 in Kuhlmann et al. (2020); as *Eucera parvula* Friese, 1896 in Rafajlović and Seleši (1958). [DD]

Note: According to Dorchin et al. (2018), genera *Cubitalia* Friese, 1911, *Tetralonia* Spinola, 1838 and *Tetraloniella* Ashmead, 1899 are placed as subgenera within *Eucera* Scopoli, 1770 (and *Tetraloniella* is synonymised with *Tetralonia*):

226. ⫽***Eucera* (*Cubitalia*) *parvicornis*** Mocsáry, 1878 as *Cubitalia parvicornis* in ZM coll.; as *Eucera parvicornis* Mocsáry, 1878 in Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [DD]
227. ⫽***Eucera* (*Tetralonia*) *malvae*** Rossi, 1790 as *Tetralonia malvae* in Kuhlmann et al. (2020); Grozdanić (1971b); Vorgin (1955); Živojinović (1950); Lebedev (1931); ZM coll.; also as *Eucera malvae* (Rossi, 1790) in Rafajlović and Seleši (1958); as *Eucera malvae* in Mocsáry (1897); Apfelbeck (1896). [LC]
228. ⫽***Eucera* (*Tetralonia*) *alticincta*** Lepeletier, 1841 as *Tetraloniella alticincta* in Kuhlmann et al. (2020); Markov (2017); as *Tetralonia alticincta* (Lepeletier, 1841) in Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012). [LC]
229. ⫽***Eucera* (*Tetralonia*) *dentata*** Germar, 1839 as *Tetraloniella dentata* in Kuhlmann et al. (2020); as *Tetralonia dentata* (Klug, 1835) in Mudri-Stojnić (2018); Lebedev (1931); as *Eucera dentata* Germar, 1839 in Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [LC]
230. ***Eucera* (*Tetralonia*) *fulvescens*** Giraud, 1863 as *Tetraloniella fulvescens* in Kuhlmann et al. (2020); as *Tetralonia dufouri* (Pérez, 1879) in Vorgin (1955). [DD]
231. ▪***Eucera* (*Tetralonia*) *glauca*** Fabricius 1775 as *Tetraloniella glauca* in Kuhlmann et al. (2020). [DD]
232. ⫽***Eucera* (*Tetralonia*) *graja*** (Eversmann, 1852) as *Tetraloniella graja* in Grozdanić (1971b); ZM coll. [DD]
233. ⫽***Eucera* (*Tetralonia*) *lyncea*** Mocsáry, 1879 as *Tetraloniella lyncea* in Markov (2017); as *Tetralonia lyncea* Mocsáry, 1879 in Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Grozdanić (1971b); Grozdanić and Vasić (1966b); Lebedev (1931); SG coll.; ZM coll; as *Eucera lyncea* (Mocsáry, 1879) in Rafajlović and Seleši (1958); Mocsáry (1897). [DD]
234. ⫽***Eucera* (*Tetralonia*) *nana*** Morawitz, 1874 as *Tetraloniella nana* in Markov (2017); ZM coll.; as *Tetralonia nana* Morawitz, 1874 in Mudri-Stojnić (2018);

Mudri-Stojnić et al. (2012); Grozdanić (1971b); Grozdanić and Vasić (1967a); Lebedev (1931); SG coll.; as *Eucera nana* (Morawitz, 1874) in Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [DD]

235. ⸗***Eucera* (*Tetralonia*) *ruficornis*** Fabricius, 1804 as *Eucera ruficornis* Fabricius, 1804 in Rafajlović and Seleši (1958); Mocsáry (1897); as *Tetralonia ruficornis* (Fabricius, 1804) in Vorgin (1955); Lebedev (1931); SG coll. [DD]
236. ⸗***Eucera* (*Tetralonia*) *pollinosa*** Lepeletier, 1841 as *Tetralonia pollinosa* (Lepeletier, 1841) and also as *Eucera pollinosa* Lepeletier, 1841 in Mudri-Stojnić (2018); as *Eucera pollinosa* in Rafajlović and Seleši (1958); Mocsáry (1897); as *Macrocera fossulata* in Korlević (1890). [DD]
237. ⸗***Eucera* (*Tetralonia*) *salicariae*** Lepeletier, 1841 as *Eucera salicariae* (Lepeletier, 1841) in Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896); as *Tetralonia salicariae* (Lepeletier, 1841) in Vorgin (1955); Živojinović (1950); SG coll.; ZM coll. [DD]
238. ⸗***Eucera* (*Tetralonia*) *scabiosae*** Mocsáry, 1881 as *Tetraloniella scabiosae* in Kuhlmann et al. (2020); Markov (2017); as *Tetralonia scabiosae* (Mocsáry, 1881) in Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Grozdanić (1971b); Rafajlović and Seleši (1958); SG coll. ZM coll.; as *Eucera scabiosae* Mocsáry, 1881 in Rafajlović and Seleši (1958); Vorgin (1955, 1918); Mocsáry (1897). [DD]

Habropoda Smith, 1854 (2 species)

239. ▪***Habropoda tarsata*** Spinola, 1838 in Kuhlmann et al. (2020). [LC]
240. ▪***Habropoda zonatula*** Smith, 1854 in Kuhlmann et al. (2020). [DD]

Melecta Latreille, 1802 (7 species)

241. ⸗***Melecta albifrons*** Förster, 1771 in Kuhlmann et al. (2020); as *Melecta armata* (Panzer, 1799) in Rafajlović and Seleši (1958); Vorgin (1918); ZM coll. [LC]
242. ▪***Melecta duodecimmaculata*** Rossi 1790 in Kuhlmann et al. (2020). [DD]
243. ▪***Melecta fulgida*** Lieftinck, 1980 in Kuhlmann et al. (2020). [DD]
244. ▪***Melecta funeraria*** Smith, 1854 in Kuhlmann et al. (2020). [DD]
245. ▪***Melecta italica*** Radoszkowski, 1876 in Kuhlmann et al. (2020). [DD]
246. ⸗***Melecta luctuosa*** Scopoli, 1770 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); ZM coll. [LC]
247. ▪***Melecta obscura*** Friese, 1895 in Kuhlmann et al. (2020). [DD]

Nomada Scopoli, 1770 (77 species)

248. ***Nomada alboguttata*** Herrich-Schäffer, 1839 in Kuhlmann et al. (2020); Smit (2018); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897). [LC]
249. ***Nomada alpigena*** Schwarz, Gusenleitner, & Mazzucco, 1999 in Kuhlmann et al. (2020). Note: There are no type specimens listed from Serbia in Schwarz, Gusenleitner and Mazzucco (1999). [DD]

250. ***Nomada argentata*** Herrich-Schäffer, 1839 in Kuhlmann et al. (2020); Smit (2018). [NT]
251. =***Nomada armata*** Herrich-Schäffer, 1839 in Kuhlmann et al. (2020); Smit (2018); Rafajlović and Seleši (1958); Mocsáry (1897); Apfelbeck (1896); AĐ coll. [NT]
252. ***Nomada atroscutellaris*** Strand, 1921 in Kuhlmann et al. (2020); Smit (2018). [LC]
253. ***Nomada basalis*** Herrich-Schäffer, 1839 in Kuhlmann et al. (2020); Smit (2018); Petrik (1958); Rafajlović and Seleši (1958); as *Nomada tripunctata* Morawitz, 1872 in Vorgin (1955, 1918); as *Nomada flavomaculata* Lucas, 1849 in Mocsáry (1897); Apfelbeck (1896). [LC]
254. =***Nomada bifasciata*** Olivier, 1811 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); as *Nomada pusilla* in Rafajlović and Seleši (1958). [LC]
255. ***Nomada bispinosa*** Mocsáry, 1883 in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
256. =***Nomada bluethgeni*** Stoeckhert, 1943 in Kuhlmann et al. (2020); Smit (2018); Markov (2017); Markov et al. (2016). [LC]
257. ***Nomada braunsiana*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020); Lebedev (1931). [NT]
258. ****Nomada calimorpha*** Schmiedeknecht, 1882 in Mocsáry (1897). [DD]
259. ▪***Nomada castellana*** Dusmety Alonso, 1913 in Kuhlmann et al. (2020). [LC]
260. ▪***Nomada confinis*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020). [DD]
261. ***Nomada conjungens*** Herrich-Schäffer, 1839 in Kuhlmann et al. (2020); Lebedev (1931). [LC]
262. ***Nomada cruenta*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020); Smit (2018); Vorgin (1918). [LC]
263. =***Nomada distinguenda*** Morawitz, 1874 in Smit (2018); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Vorgin (1918); Apfelbeck (1896). [LC]
264. ▪***Nomada emarginata*** Morawitz, 1877 in Kuhlmann et al. (2020). [LC]
265. ***Nomada errans*** Lepeletier, 1841 in Kuhlmann et al. (2020); Smit (2018); Lebedev (1931). [NT]
266. ***Nomada erythrocephala*** Morawitz, 1870 in Rafajlović and Seleši (1958). [DD]
267. =***Nomada fabriciana*** Linnaeus, 1767 in Kuhlmann et al. (2020); Lebedev (1931); AĐ coll. [LC]
268. ▪***Nomada facilis*** Schwarz, 1967 in Kuhlmann et al. (2020). [LC]
269. ***Nomada femoralis*** Morawitz, 1869 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [LC]
270. ***Nomada ferruginata*** Linné 1767 in Kuhlmann et al. (2020); Smit (2018); Rafajlović and Seleši (1958); Vorgin (1955, 1918); Lebedev (1931). [LC]
271. =***Nomada flava*** Panzer, 1798 in Kuhlmann et al. (2020); Smit (2018); Lebedev (1931); AĐ coll. [LC]

272. ⸗***Nomada flavoguttata*** Kirby, 1802 in Kuhlmann et al. (2020); Smit (2018); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Lebedev (1931); Apfelbeck (1896); AĐ coll. [LC]
273. ▪***Nomada flavopicta*** Kirby, 1802 in Kuhlmann et al. (2020). [LC]
274. ⸗***Nomada fucata*** Panzer, 1798 in Kuhlmann et al. (2020); Smit (2018); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896); AĐ coll.; as *Nomada varia* Panzer, 1798 in Petrik (1958). [LC]
275. ***Nomada fulvicornis*** Fabricius, 1793 in Kuhlmann et al. (2020); Smit (2018); also as *Nomada lineola* Panzer, 1798 in Rafajlović and Seleši (1958); Lebedev (1931); as *Nomada lineola* in Vorgin (1955); Mocsáry (1897); as *Nomada robusta* Morawitz, 1870 in Apfelbeck (1896). [LC]
276. ***Nomada furva*** Panzer, 1798 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958). [DD]
277. ▪***Nomada furvoides*** Stoeckhert, 1944 in Kuhlmann et al. (2020). [DD]
278. ***Nomada fuscicornis*** Nylander, 1848 in Kuhlmann et al. (2020); Smit (2018); Vorgin (1918). [LC]
279. ▪***Nomada goodeniana*** Kirby, 1802 in Kuhlmann et al. (2020). [LC]
280. ****Nomada gribodoi*** Schmiedeknecht, 1882 as *Nomada elegans* Mocsáry, 1897 in Mocsáry (1897). [DD]
281. ***Nomada guttulata*** Schenck, 1861 in Kuhlmann et al. (2020); Smit (2018); Vorgin (1918). [LC]
282. ▪***Nomada hirtipes*** Pérez, 1884 in Kuhlmann et al. (2020). [LC]
283. ***Nomada hungarica*** Dalla Torre & Friese, 1894 in Rafajlović and Seleši (1958). [DD]
284. ***Nomada immaculata*** Morawitz, 1874 in Vorgin (1918). [DD]
285. ***Nomada incisa*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020); Smit (2018); Lebedev (1931). [DD]
286. ⸗***Nomada integra*** Brullé, 1832 in Kuhlmann et al. (2020); AĐ coll. [LC]
287. ***Nomada kohli*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020); Smit (2018); Apfelbeck (1896). [LC]
288. ⸗***Nomada lathburiana*** Kirby, 1802 in Kuhlmann et al. (2020); SG coll. [LC]
289. ⸗***Nomada leucophthalma*** (Kirby, 1802) **New material examined:** 1 ♀; Vlasina, Veliki čemernik; 42.7368°N, 22.2723°E; 25 May 2019; M. Vujić leg.; Andrej Gogala det.; AĐ coll. [LC]
290. ***Nomada marshamella*** Kirby, 1802 in Kuhlmann et al. (2020); Smit (2018). [LC]
291. ***Nomada mauritanica*** Lepeletier, 1841 in Smit (2018); as *Nomada chrysopyga* Morawitz, 1871 in Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896). [LC]
292. ***Nomada mocsaryi*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020); Smit (2018); Mocsáry (1897). [DD]
293. ▪***Nomada moeschleri*** Alfken, 1913 in Kuhlmann et al. (2020). [LC]

294. ***Nomada mutabilis*** Morawitz, 1870 in Kuhlmann et al. (2020); Smit (2018); Vorgin (1918); Apfelbeck (1896). [LC]
295. ***Nomada mutica*** Morawitz, 1872 in Kuhlmann et al. (2020); Lebedev (1931). [NT]
296. ***Nomada nobilis*** Herrich-Schäffer, 1839 in Kuhlmann et al. (2020); Smit (2018); Mocsáry (1897); Apfelbeck (1896). [LC]
297. ***Nomada numida*** Lepeletier, 1841 in Kuhlmann et al. (2020); Smit (2018). [LC]
298. ▪***Nomada obtusifrons*** Nylander, 1848 in Kuhlmann et al. (2020). [NT]
299. ▪***Nomada opaca*** Alfken, 1913 in Kuhlmann et al. (2020). [NT]
300. ▪***Nomada pallispinosa*** Schwarz, 1967 in Kuhlmann et al. (2020). [DD]
301. ***Nomada panzeri*** Lepeletier, 1841 in Kuhlmann et al. (2020); Smit (2018). [LC]
302. ***Nomada pectoralis*** Morawitz, 1877 in Vorgin (1918). [DD]
303. ***Nomada piccioliana*** Magretti, 1883 in Kuhlmann et al. (2020); Smit (2018). [LC]
304. ***Nomada pleurosticta*** Herrich-Schäffer, 1839 as *Nomada major* Morawitz, 1872 in Lebedev (1931). [NT]
305. ▪***Nomada propinqua*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020). [LC]
306. ***Nomada pulchra*** Arnold, 1888 in Smit (2018). [EN]
307. ***Nomada rhenana*** Morawitz, 1872 in Kuhlmann et al. (2020); Smit (2018); Rafajlović and Seleši (1958); Mocsáry (1897). [NT]
308. ⫽***Nomada ruficornis*** Linnaeus, 1758 in Kuhlmann et al. (2020); Smit (2018); Apfelbeck (1896); Mocsáry (1897); AĐ coll; also as *Nomada bifida* Thomson, 1872 in Rafajlović and Seleši (1958); as *Nomada bifida* in Lebedev (1931). [LC]
309. ***Nomada rufipes*** Fabricius, 1793 in Kuhlmann et al. (2020); Petrik (1958); Rafajlović and Seleši (1958). [LC]
310. ***Nomada sexfasciata*** Panzer, 1799 in Kuhlmann et al. (2020); Smit (2018); Rafajlović and Seleši (1958); Lebedev (1931). [LC]
311. ▪***Nomada sheppardana*** Kirby, 1802 in Kuhlmann et al. (2020). [LC]
312. ***Nomada signata*** Jurine, 1807 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958). [LC]
313. ***Nomada similis*** Morawitz, 1872 in Vorgin (1918). [LC]
314. ***Nomada stigma*** Fabricius, 1804 in Kuhlmann et al. (2020); as *Nomada austriaca* Schmiedeknecht, 1882 in Vorgin (1918). [LC]
315. ***Nomada striata*** Fabricius, 1793 in Kuhlmann et al. (2020); as *Nomada ochrostoma* (Kirby, 1802) in Apfelbeck (1896). [LC]
316. ▪***Nomada succincta*** Panzer, 1798 in Kuhlmann et al. (2020). [LC]
317. ▪***Nomada symphyti*** Stoeckhert, 1930 in Kuhlmann et al. (2020). [NT]
318. ***Nomada tenella*** Mocsáry, 1883 in Kuhlmann et al. (2020); Smit (2018). [NT]
319. ***Nomada transitoria*** Schmiedeknecht, 1882 in Smit (2018). [LC]
320. ▪***Nomada tridentirostris*** Dours, 1873 in Kuhlmann et al. (2020). [LC]
321. ***Nomada trispinosa*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Lebedev (1931). [LC]
322. ▪***Nomada verna*** Schmiedeknecht, 1882 in Kuhlmann et al. (2020). [DD]

323. ***Nomada villosa*** Thomson, 1870 in Kuhlmann et al. (2020); Lebedev (1931). [NT]
324. ***Nomada zonata*** Panzer, 1798 in Kuhlmann et al. (2020); Smit (2018); Lebedev (1931); Vorgin (1918). [LC]

Pasites Jurine, 1807 (1 species)

325. ***Pasites maculatus*** Jurine, 1807 in Petrik (1958); Rafajlović and Seleši (1958); Mocsáry (1897). [LC]

Thyreus Panzer, 1806 (7 species)

326. ***Thyreus affinis*** Morawitz, 1874 in Kuhlmann et al. (2020); as *Crocisa affinis* Morawitz, 1874 in Rafajlović and Seleši (1958). [DD]
327. ≡***Thyreus histrionicus*** Illiger, 1806 in Kuhlmann et al. (2020); ZM coll.; as *Crocisa major* Morawitz, 1875 in Rafajlović and Seleši (1958); Mocsáry (1897). [LC]
328. ≡***Thyreus orbatus*** Lepeletier, 1841 in Kuhlmann et al. (2020); ZM coll. [LC]
329. ▪***Thyreus picaron*** Lieftinck, 1968 in Kuhlmann et al. (2020). [DD]
330. ≡***Thyreus ramosus*** Lepeletier, 1841 in Kuhlmann et al. (2020); ZM coll.; as *Crocisa ramosa* Lepeletier, 1841 in Rafajlović and Seleši (1958); Mocsáry (1897). [LC]
331. ≡***Thyreus scutellaris*** Fabricius, 1781 in Kuhlmann et al. (2020); ZM coll.; as *Crocisa scutellaris* (Fabricius, 1781) in Petrik (1958); Vorgin (1918); Mocsáry (1897). [DD]
332. ***Thyreus truncatus*** Pérez, 1883 in Kuhlmann et al. (2020); as *Crocisa truncata* Pérez, 1883 in Mocsáry (1897). [DD]

Triepeolus Robertson, 1901 (1 species)

333. ****Triepeolus tristis*** (Smith, 1854) as *Epeolus tristis* Smith, 1854 in Mocsáry (1897). [NT]

Xylocopa Latreille, 1802 (4 species)

334. ≡***Xylocopa iris*** Christ, 1791 in Kuhlmann et al. (2020); ZM coll.; as *Xylocopa cyanescens* Brullé, 1832 in Grozdanić and Mučalica (1973); Grozdanić (1971b); Grozdanić and Vasić (1966a); Lebedev (1931). [LC]
335. ▪***Xylocopa olivieri*** Lepeletier, 1841 in Kuhlmann et al. (2020). [LC]
336. ≡***Xylocopa valga*** Gerstäcker, 1872 in Kuhlmann et al. (2020); Grozdanić and Mučalica (1973); Grozdanić (1971b, 1970, 1950b); Grozdanić and Vasić (1965c); Grozdanić and Baranov (1963); Rafajlović and Seleši (1958); Grozdanić and Čolović (1955b); Mocsáry (1897); Apfelbeck (1896); AĐ coll.; ZM coll. [LC]

337. ⸗***Xylocopa violacea*** Linnaeus, 1758 in Kuhlmann et al. (2020); Grozdanić and Mučalica (1973); Grozdanić (1971b, 1950b); Grozdanić and Vasić (1966a); Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Apfelbeck (1896); AĐ coll.; ZM coll. [LC]

Colletidae (2 genera; 69 species)

Colletes Latreille, 1802 (27 species)

338. ■***Colletes albomaculatus*** (Lucas, 1849) in Kuhlmann et al. (2020). [NT]
339. ⸗***Colletes anchusae*** Noskiewicz, 1924 Kuhlmann et al. (2020); Grozdanić and Vasić (1966a); ZM coll. [EN]
340. ***Colletes brevigena*** Noskiewicz, 1936 in Kuhlmann et al. (2020); Burger (2010). [LC]
341. ■***Colletes carinatus*** Radoszkowski, 1891 in Kuhlmann et al. (2020). [LC]
342. ■***Colletes caskanus*** (Strand, 1919) in Kuhlmann et al. (2020). [DD]
343. ■***Colletes chengtehensis*** Yasumatsu, 1935 in Kuhlmann et al. (2020). [VU]
344. ⸗***Colletes cunicularius*** (Linnaeus, 1761) in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Grozdanić (1971b, 1958a); Rafajlović and Seleši (1958); Mocsáry (1897); AĐ coll.; ZM coll.; as *Colletes cunicularia* in Apfelbeck (1896). [LC]
345. ⸗***Colletes daviesanus*** Smith, 1846 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); AĐ coll.; as *Colletes daviesana* in Apfelbeck (1896). [LC]
346. ***Colletes eous*** Morice, 1904 in Kuhlmann et al. (2020); Lebedev (1931). [LC]
347. ■***Colletes floralis*** Eversmann, 1852 in Kuhlmann et al. (2020). [VU]
348. ⸗***Colletes fodiens*** (Fourcroy, 1785) in Kuhlmann et al. (2020); Markov (2017); Petrik (1958); Rafajlović and Seleši (1958). [VU]
349. ■***Colletes foveolaris*** Pérez, 1903 in Kuhlmann et al. (2020). [LC]
350. ***Colletes gallicus*** Radoszkowski, 1891 in Rafajlović and Seleši (1958). [LC]
351. ■***Colletes graeffei*** Alfken, 1900 in Kuhlmann et al. (2020). [EN]
352. ***Colletes hederae*** Schmidt & Westrich, 1993 in Kuhlmann et al. (2020); Burger (2010). [LC]
353. ***Colletes hylaeiformis*** Eversmann, 1852 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [LC]
354. ■***Colletes inexpectatus*** Noskiewicz, 1936 in Kuhlmann et al. (2020). [LC]
355. ⸗***Colletes maidli*** Noskiewicz, 1936 in Kuhlmann et al. (2020); Markov (2017). [LC]
356. ***Colletes marginatus*** Smith, 1846 in Kuhlmann et al. (2020); Petrik (1958); Rafajlović and Seleši (1958); as *Colletes marginata* in Apfelbeck (1896). [LC]
357. ■***Colletes meyeri*** Noskiewicz, 1936 in Kuhlmann et al. (2020). [EN]
358. ■***Colletes mlokossewiczi*** Radoszkowski, 1891 in Kuhlmann et al. (2020). [LC]

359. ⸗***Colletes nasutus*** Smith, 1853 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897). [EN]
360. ▪***Colletes nigricans*** Gistel, 1857 in Kuhlmann et al. (2020). [LC]
361. ***Colletes punctatus*** Mocsáry, 1877 in Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [EN]
362. ▪***Colletes senilis*** (Eversmann, 1852) in Kuhlmann et al. (2020). [DD]
363. ***Colletes succinctus*** (Linnaeus, 1785) in Kuhlmann et al. (2020); Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Vorgin (1918). [NT]
364. ⸗***Colletes similis*** Schenck, 1853 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); as *Colletes picistigma* Thomson, 1872 in Vorgin (1918); Mocsáry (1897). [LC]

Hylaeus Fabricius, 1793 (42 species)

365. ▪***Hylaeus adriaticus*** (Warncke, 1972) in Kuhlmann et al. (2020). [DD]
366. ▪***Hylaeus alpinus*** (Morawitz, 1867) in Kuhlmann et al. (2020). [DD]
367. ***Hylaeus angustatus*** (Schenck, 1861) in Kuhlmann et al. (2020); as *Prosopis angustata* Schenck, 1861 in Rafajlović and Seleši (1958); Živojinović (1950). [LC]
368. ⸗***Hylaeus annularis*** (Kirby, 1802) in Markov (2017); Markov et al. (2016); AĐ coll.; as *Prosopis annularis* (Kirby, 1802) in Rafajlović and Seleši (1958); Živojinović (1950). Note: It is difficult to be certain about the correct status of specimens in the literature before Notton and Dathe (2008) who pointed out the confusion regarding previously understood interpretation of the name. [DD]
369. ***Hylaeus annulatus*** (Linnaeus, 1758) in Kuhlmann et al. (2020); as *Prosopis annulata* (Linnaeus, 1758) in Vorgin (1955); Lebedev (1931). [DD]
370. ⸗***Hylaeus brevicornis*** Nylander, 1852 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); as *Prosopis brevicornis* (Nylander, 1852) in Rafajlović and Seleši (1958); Lebedev (1931); Apfelbeck (1896). [LC]
371. ▪***Hylaeus clypearis*** (Schenck, 1853) in Kuhlmann et al. (2020). [LC]
372. ⸗***Hylaeus communis*** Nylander, 1852 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); AĐ coll.; as *Prosopis communis* (Nylander, 1852) in Rafajlović and Seleši (1958); Lebedev (1931); Apfelbeck (1896). [LC]
373. ⸗***Hylaeus confusus*** Nylander, 1852 in Kuhlmann et al. (2020); AĐ coll.; as *Prosopis confusa* (Nylander, 1852) in Rafajlović and Seleši (1958); Apfelbeck (1896). [LC]
374. ▪***Hylaeus coriaceus*** (Pérez, 1895) in Kuhlmann et al. (2020). [DD]
375. ⸗***Hylaeus cornutus*** Curtis, 1831 in Mudri-Stojnić (2018); as *Prosopis cornuta* (Curtis, 1831) in Rafajlović and Seleši (1958); Vorgin (1955, 1918); Mocsáry (1897). [LC]

376. ▪***Hylaeus crassanus*** (Warncke, 1972) in Kuhlmann et al. (2020). [NT]
377. ***Hylaeus difformis*** (Eversmann, 1852) in Kuhlmann et al. (2020); as *Prosopis difformis* Eversmann, 1852 in Rafajlović and Seleši (1958); Živojinović (1950); Vorgin (1918); Mocsáry (1897). [LC]
378. ***Hylaeus dilatatus*** (Kirby, 1802) in Kuhlmann et al. (2020); as *Prosopis dilatata* (Kirby, 1802) in Apfelbeck (1896). Note: It is difficult to be certain about the correct status of specimens in the literature before Notton and Dathe (2008) who pointed out the confusion regarding previously understood interpretation of the name. [LC]
379. ***Hylaeus duckei*** (Alfken, 1904) in Kuhlmann et al. (2020); as *Prosopis duckei* Alfken, 1904 in Rafajlović and Seleši (1958). [DD]
380. ***Hylaeus euryscapus*** Förster, 1871 in Kuhlmann et al. (2020); as *Prosopis euryscapus* (Föerster, 1871) in Rafajlović and Seleši (1958); *Prosopis euryscapa* in Vorgin (1955, 1918); Mocsáry (1897). Note: It is difficult to be certain about the correct status of specimens in the literature before Notton and Dathe (2008) who pointed out the confusion regarding previously understood interpretation of the name *H. annularis*. [DD]
381. ***Hylaeus gibbus*** Saunders, 1850 in Kuhlmann et al. (2020); as *Prosopis gibba* (Saunders, 1850) in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
382. ▪***Hylaeus gredleri*** Förster, 1871 in Kuhlmann et al. (2020). [LC]
383. ***Hylaeus hyalinatus*** Smith, 1842 in Kuhlmann et al. (2020); as *Prosopis hyalinata* Smith, 1842 in Rafajlović and Seleši (1958); Mocsáry (1897); Apfelbeck (1896). [LC]
384. ▪***Hylaeus hyperpunctatus*** (Strand, 1909) in Kuhlmann et al. (2020). [DD]
385. ▪***Hylaeus imparilis*** Förster, 1871 in Kuhlmann et al. (2020). [LC]
386. ***Hylaeus incongruus*** Förster, 1871 as *Prosopis genalis* Thoms. in Vorgin (1918). [DD]
387. ▪***Hylaeus kahri*** Förster, 1871 in Kuhlmann et al. (2020). [DD]
388. ***Hylaeus leptocephalus*** (Morawitz, 1870) in Kuhlmann et al. (2020); as *Prosopis bisinuata* Förster, 1871 in Rafajlović and Seleši (1958). [LC]
389. ⸗***Hylaeus lineolatus*** (Schenck, 1861) in Kuhlmann et al. (2020); AĐ coll.; ZM coll.; as *Prosopis lineolata* Schenck, 1861 in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
390. ***Hylaeus meridionalis*** Förster, 1871 in Kuhlmann et al. (2020); as *Prosopis meridionalis* Förster, 1871 in Rafajlović and Seleši (1958); Mocsáry (1897). [DD]
391. ⸗***Hylaeus nigritus*** (Fabricius, 1798) in Kuhlmann et al. (2020); AĐ coll.; as *Prosopis nigrita* (Fabricius, 1798) in Lebedev (1931). [LC]
392. ▪***Hylaeus nivaliformis*** Dathe, 1977 in Kuhlmann et al. (2020). [DD]
393. ▪***Hylaeus pfankuchi*** (Alfken, 1919) in Kuhlmann et al. (2020). [LC]
394. ***Hylaeus pictipes*** Nylander, 1852 in Kuhlmann et al. (2020); as *Prosopis pictipes* (Nylander, 1852) in Rafajlović and Seleši (1958); Vorgin (1918). [LC]
395. ***Hylaeus punctatus*** (Brullé, 1832) in Kuhlmann et al. (2020); as *Prosopis punctata* Brullé, 1832 in Rafajlović and Seleši (1958). [LC]

396. ▪***Hylaeus punctulatissimus*** Smith, 1842 in Kuhlmann et al. (2020). [DD]
397. ▪***Hylaeus punctus*** Förster, 1871 in Kuhlmann et al. (2020). [DD]
398. ▪***Hylaeus rugicollis*** Morawitz, 1873 in Kuhlmann et al. (2020). [DD]
399. ▪***Hylaeus scutellatus*** (Spinola, 1838) in Kuhlmann et al. (2020). [DD]
400. ***Hylaeus signatus*** (Panzer, 1798) in Kuhlmann et al. (2020); as *Prosopis pratensis* (Geoffroy in Fourcroy, 1785) in Rafajlović and Seleši (1958); Vorgin (1955); as *Prosopis bipunctata* (Fabricius, 1798) in Mocsáry (1897); Apfelbeck (1896). [LC]
401. ***Hylaeus sinuatus*** (Schenck, 1853) in Kuhlmann et al. (2020); Petrik (1958); as *Prosopis minuta* (Fabricius, 1793) in Rafajlović and Seleši (1958); as *Prosopis sinuata* (Schenck, 1853) in Mocsáry (1897). [LC]
402. ▪***Hylaeus soror*** (Pérez, 1903) in Kuhlmann et al. (2020). [DD]
403. ***Hylaeus styriacus*** Förster, 1871 in Kuhlmann et al. (2020); as *Prosopis styriaca* (Förster, 1871) in Rafajlović and Seleši (1958). [DD]
404. ▪***Hylaeus taeniolatus*** Förster, 1871 in Kuhlmann et al. (2020). [LC]
405. ▪***Hylaeus tyrolensis*** Förster, 1871 in Kuhlmann et al. (2020). [DD]
406. ***Hylaeus variegatus*** (Fabricius, 1798) in Kuhlmann et al. (2020); as *Prosopis variegata* (Fabricius, 1798) in Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [LC]

Halictidae (12 genera; 138 species)

Ceylalictus Strand, 1913 (1 species)

407. ***Ceylalictus variegatus*** (Olivier, 1789) in Kuhlmann et al. (2020); as *Nomioides jucunda* Morawitz, 1874 in Petrik (1958); as *Nomioides variegatus* (Olivier, 1789) in Rafajlović and Seleši (1958); Mocsáry (1897). [LC]

Dufourea Lepeletier, 1841 (4 species)

408. *****Dufourea alpina*** Morawitz, 1865 in Apfelbeck (1896). [LC]
409. ***Dufourea dentiventris*** (Nylander, 1848) in Kuhlmann et al. (2020); as *Halictoides dentiventris* Nylander, 1848 in Lebedev (1931). [NT]
410. ⸗***Dufourea inermis*** (Nylander, 1848) in Kuhlmann et al. (2020); AĐ coll. [NT]
411. ▪***Dufourea minuta*** Lepeletier, 1841 in Kuhlmann et al. (2020). [NT]

Halictus Latreille, 1804 (18 species)

412. ⸗***Halictus asperulus*** Pérez, 1895 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Grozdanić (1972a); Rafajlović and Seleši (1958); Lebedev (1931). [DD]
413. ⸗***Halictus brunnescens*** (Eversmann, 1852) in Markov (2017); Markov et al. (2016). [DD]
414. ▪***Halictus carinthiacus*** Blüthgen, 1936 in Kuhlmann et al. (2020). [EN]

415. ***Halictus cochlearitarsis*** Dours, 1872 in Grozdanić (1966); Rafajlović and Seleši (1958). [LC]
416. ≡***Halictus compressus*** (Walkenaer, 1802) as *Halictus eurygnathus* Blüthgen, 1930 in Markov (2017); Markov et al. (2016); Živojinović (1950). [LC]
417. ≡***Halictus fulvipes*** (Klug, 1817) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mučalica (1968); Lebedev (1931). [LC]
418. ≡***Halictus langobardicus*** Blüthgen, 1944 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Rafajlović and Seleši (1958). [LC]
419. ≡***Halictus maculatus*** Smith, 1848 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Grozdanić (1972a); Petrik (1958); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); Korlević (1890); AĐ coll.; ZM coll. [LC]
420. ***Halictus mucoreus*** Eversmann, 1852 in Vorgin (1955, 1918); Mocsáry (1897). [DD]
421. ≡***Halictus patellatus*** Morawitz, 1873 in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Rafajlović and Seleši (1958); Vorgin (1955); Mocsáry (1897); Apfelbeck (1896); AZ coll.; ZM coll. [LC]
422. ≡***Halictus quadricinctus*** (Fabricius, 1776) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Grozdanić (1971b, 1966); Vasić (1967); Grozdanić and Vasić (1966a, 1965c); Rafajlović and Seleši (1958); Vorgin (1955); Anđelković (1949); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); as *Halictus quadristrigatus* Latreille, 1805 in Petrik (1958); Vorgin (1955); Korlević (1890). [NT]
423. ***Halictus resurgens*** Nurse, 1903 as *Halictus holtzi* Schulz, 1906 in Lebedev (1931). [LC]
424. ≡***Halictus rubicundus*** (Christ, 1791) in Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931); AĐ coll.; as *Halictus quadrifasciatus* Smith, 1870 in Mudri-Stojnić (2018). [LC]
425. ≡***Halictus sajoi*** Blüthgen, 1923 in Grozdanić (1971a); ZM coll.; as *Halictus veneticus* Móczár, 1967 in Rafajlović and Seleši (1958). [DD]
426. ≡***Halictus scabiosae*** (Rossi, 1790) in Vasić (1979a); Grozdanić (1971b, 1970, 1966, 1960); Grozdanić and Vasić (1966a, 1965c); Krunić (1959); Vorgin (1955); Petrik (1958); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); ZM coll.; FSUNS. [LC]
427. ≡***Halictus sexcinctus*** (Fabricius, 1775) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Grozdanić (1960, 1950a); Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Apfelbeck (1896); Mocsáry (1897); Korlević (1890); AZ coll.; ZM coll. [LC]
428. ≡***Halictus simplex*** Blüthgen, 1923 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Rafajlović and Seleši (1958); Živojinović (1950); AĐ coll.; AZ coll.; ZM coll. [LC]

429. ⸗***Halictus tetrazonius*** (Klug, 1817) in Petrik (1958); Vorgin (1955); Mocsáry (1897); Apfelbeck (1896); SG coll.; ZM coll. [DD]

Lasioglossum Curtis, 1833 (72 species)

430. ***Lasioglossum aeratum*** (Kirby, 1802) as *Halictus viridiaeneus* Blüthgen, 1918 in Rafajlović and Seleši (1958); Vorgin (1955); as *Halictus aeratus* (Kirby, 1802) in Mocsáry (1897). [LC]
431. ⸗***Lasioglossum albipes*** (Fabricius, 1781) in Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); as *Halictus albipes* (Fabricius, 1781) in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); as *Halictus obovatus* Kirby in Petrik (1958). [LC]
432. ▪***Lasioglossum alpigenum*** (Dalla Torre, 1877) in Kuhlmann et al. (2020). [LC]
433. ▪***Lasioglossum angusticeps*** (Perkins, 1895) in Kuhlmann et al. (2020). [NT]
434. ▪***Lasioglossum apostoli*** Ebmer, 1970 in Kuhlmann et al. (2020). [DD]
435. ***Lasioglossum bischoffi*** (Blüthgen, 1931) in Kuhlmann et al. (2020); as *Halictus bischoffi* Blüthgen, 1931 in Rafajlović and Seleši (1958). [DD]
436. ⸗***Lasioglossum brevicorne*** (Schenck, 1868) in Markov (2017); Markov et al. (2016); AĐ coll.; ZM coll.; as *Halictus brevicornis* Schenck, 1870 ["1869"] in Rafajlović and Seleši (1958); Vorgin (1955). [NT]
437. ⸗***Lasioglossum calceatum*** (Scopoli, 1763) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); AĐ coll.; as *Halictus calceatus* (Scopoli, 1763) in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); as *Halictus cylindricus* (Fabricius, 1793) in Petrik (1958); Korlević (1890). [LC]
438. ⸗***Lasioglossum clypeare*** (Schenck, 1853) in Markov (2017); Markov et al. (2016); as *Halictus clypearis* (Schenck, 1853) in Vorgin (1955); Živojinović (1950); Lebedev (1931). [NT]
439. ***Lasioglossum convexiusculum*** (Schenck, 1853) as *Halictus convexiusculus* (Schenck, 1853) in Rafajlović and Seleši (1958). [NT]
440. ***Lasioglossum corvinum*** (Morawitz, 1877) in Kuhlmann et al. (2020); as *Halictus corvinus* Morawitz, 1877 in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
441. ***Lasioglossum costulatum*** (Kriechbaumer, 1873) as *Halictus costulatus* Kriechbaumer, 1873 in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897). [NT]
442. ⸗***Lasioglossum crassepunctatum*** (Blüthgen, 1923) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); as *Halictus crassepunctatus* Blüthgen, 1923 in Rafajlović and Seleši (1958); Vorgin (1955). [DD]
443. ⸗***Lasioglossum discum*** (Smith, 1853) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); ZM coll.; as *Halictus morbillosus* Kriechbaumer, 1873 in Grozdanić (1971b); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [LC]

444. ***Lasioglossum elegans*** (Lepeletier, 1841) in Kuhlmann et al. (2020); as *Halictus elegans* Lepeletier, 1841 in Rafajlović and Seleši (1958); Mocsáry (1897). [DD]
445. ⸗***Lasioglossum euboeense*** (Strand, 1909) as *Halictus euboeensis* Strand, 1909 in Rafajlović and Seleši (1958); Vorgin (1955); SG coll. [DD]
446. ⸗***Lasioglossum fratellum*** (Pérez, 1903) in Kuhlmann et al. (2020); AĐ coll.; ZM coll. [LC]
447. ⸗***Lasioglossum fulvicorne*** (Kirby, 1802) in AĐ coll.; as *Halictus fulvicornis* (Kirby, 1802) in Rafajlović and Seleši (1958); Živojinović (1950). [LC]
448. ⸗***Lasioglossum glabriusculum*** (Morawitz, 1872) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); as *Halictus glabriusculus* Morawitz, 1872 in Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931). [LC]
449. ***Lasioglossum griseolum*** (Morawitz, 1872) as *Halictus griseolus* Morawitz, 1872 in Rafajlović and Seleši (1958); Vorgin (1955). [LC]
450. ▪***Lasioglossum intermedium*** (Schenck, 1868) in Kuhlmann et al. (2020). [NT]
451. ⸗***Lasioglossum interruptum*** (Panzer, 1798) in Markov (2017); SG coll.; as *Halictus interruptus* (Panzer, 1798) in Grozdanić and Mučalica (1968b); Rafajlović and Seleši (1958); Vorgin (1955); Mocsáry (1897); Apfelbeck (1896). [LC]
452. ▪***Lasioglossum kussariense*** (Blüthgen, 1925) in Kuhlmann et al. (2020). [DD]
453. ***Lasioglossum laeve*** (Kirby, 1802) in Kuhlmann et al. (2020); as *Halictus laevis* (Kirby, 1802) in Vorgin (1918). [EN]
454. ***Lasioglossum laevigatum*** (Kirby, 1802) in Kuhlmann et al. (2020); as *Halictus laevigatus* (Kirby, 1802) in Rafajlović and Seleši (1958); Živojinović (1950). [NT]
455. ⸗***Lasioglossum laticeps*** (Schenck, 1868) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); as *Halictus laticeps* Schenck, 1868 in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931). [LC]
456. ⸗***Lasioglossum lativentre*** (Schenck, 1853) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); ZM coll.; as *Halictus lativentris* Schenck, 1853 in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931). [LC]
457. ***Lasioglossum leucopus*** (Kirby, 1802) in Kuhlmann et al. (2020); as *Halictus leucopus* (Kirby, 1802) in Rafajlović and Seleši (1958); Živojinović (1950). [LC]
458. ⸗***Lasioglossum leucozonium*** (Schrank, 1781) in Mudri-Stojnić (2018); Markov (2017); Mudri-Stojnić et al. (2012); AĐ coll.; ZM coll.; as *Halictus leucozonius* (Schrank, 1781) in Grozdanić (1971b); Rafajlović and Seleši (1958); Vorgin (1955, 1918); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [LC]
459. ***Lasioglossum limbellum*** (Morawitz, 1876) in Kuhlmann et al. (2020); as *Halictus limbellus* Morawitz, 1876 in Rafajlović and Seleši (1958). [DD]
460. ⸗***Lasioglossum lineare*** (Schenck, 1868) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); SG coll.; as *Halictus linearis* Schenck, 1868 in Grozdanić (1971b); Grozdanić and Vasić (1966a); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931). [DD]

461. ▪***Lasioglossum lissonotum*** (Noskiewicz, 1926) in Kuhlmann et al. (2020). [DD]
462. ***Lasioglossum lucidulum*** (Schenck, 1861) in Kuhlmann et al. (2020); as *Halictus lucidulus* (Schenck, 1861) in Rafajlović and Seleši (1958); Vorgin (1955). [LC]
463. ⸗***Lasioglossum majus*** (Nylander, 1852) in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); AĐ coll.; as *Halictus major* Nylander, 1852 in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Vorgin (1918). [NT]
464. ***Lasioglossum mandibulare*** (Morawitz, 1866) in Kuhlmann et al. (2020); as *Halictus mandibularis* Morawitz, 1866 in Rafajlović and Seleši (1958); Vorgin (1955). [NT]
465. ⸗***Lasioglossum malachurum*** (Kirby, 1802) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); SG coll.; as *Halictus malachurus* (Kirby, 1802) in Grozdanić (1971b, 1969c, 1966, 1960); Grozdanić and Vasić (1970, 1965c); Krunić (1959); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931). [LC]
466. ⸗***Lasioglossum marginatum*** (Brullé, 1832) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); ZM coll.; as *Halictus marginatus* Brullé, 1832 in Vasić (1979b, 1970, 1966); Grozdanić (1971b, 1970, 1969c, 1966, 1960, 1956); Grozdanić and Vasić (1965c); Krunić (1959); Rafajlović and Seleši (1958); Vorgin (1955); Lebedev (1931); as *Halictus fasciatellus* Schenck, 1868 in Vorgin (1955); Mocsáry (1897); Apfelbeck (1896). [LC]
467. ▪***Lasioglossum marginellum*** (Schenck, 1853) in Kuhlmann et al. (2020). [NT]
468. ***Lasioglossum mesosclerum*** (Pérez, 1903) in Kuhlmann et al. (2020); as *Halictus mesosclerus* Pérez, 1903 in Rafajlović and Seleši (1958); Vorgin (1955). [DD]
469. ***Lasioglossum minutissimum*** (Kirby, 1802) in Kuhlmann et al. (2020); as *Halictus minutissimus* (Kirby, 1802) in Rafajlović and Seleši (1958). [LC]
470. ***Lasioglossum minutulum*** (Schenck, 1853) as *Halictus minutulus* (Schenck, 1853) in Rafajlović and Seleši (1958); Živojinović (1950). [NT]
471. ⸗***Lasioglossum morio*** (Fabricius, 1793) in Kuhlmann et al. (2020); AĐ coll.; as *Halictus morio* (Fabricius, 1793) in Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [LC]
472. ⸗***Lasioglossum nigripes*** (Lepeletier, 1841) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); ZM coll.; as *Halictus nigripes* Lepeletier, 1841 in Vasić (1979b); Grozdanić and Vasić (1966a); Vorgin (1955); Živojinović (1950); Lebedev (1931); as *Halictus vulpinus* Nylander, 1853 (nec Fabricius, 1804) in Rafajlović and Seleši (1958); Mocsáry (1897). [LC]
473. ⸗***Lasioglossum nitidiusculum*** (Kirby, 1802) in Kuhlmann et al. (2020); AĐ coll.; as *Halictus nitidiusculus* (Kirby, 1802) in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
474. ***Lasioglossum nitidulum*** (Fabricius, 1804) as *Halictus aeneidorsum* Alfken, 1921 in Rafajlović and Seleši (1958); Vorgin (1955). [LC]
475. ⸗***Lasioglossum obscuratum*** (Morawitz, 1876) in Kuhlmann et al. (2020); ZM coll.; as *Halictus obscuratus* Morawitz, 1876 in Rafajlović and Seleši (1958); Živojinović (1950); Mocsáry (1897). [DD]

476. ***=Lasioglossum pallens*** (Brullé, 1832) in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); as *Halictus lineolatus* Lepeletier, 1841 in Mocsáry (1897). [LC]
477. ***Lasioglossum parvulum*** (Schenck, 1853) in Kuhlmann et al. (2020); as *Halictus minutus* (Kirby, 1802) in Rafajlović and Seleši (1958); Živojinović (1950). [LC]
478. ***=Lasioglossum pauxillum*** (Schenck, 1853) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); AĐ coll.; as *Halictus pauxillus* (Schenck, 1853) in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931). [LC]
479. ***=Lasioglossum politum*** (Schenck, 1853) in Markov (2017); Markov et al. (2016); as *Halictus politus* (Schenck, 1853) in Rafajlović and Seleši (1958); Vorgin (1955, 1918); Živojinović (1950); Lebedev (1931). [LC]
480. **▪*Lasioglossum pseudocaspicum*** (Blüthgen, 1923) in Kuhlmann et al. (2020). [DD]
481. ***Lasioglossum punctatissimum*** (Schenck, 1853) in Kuhlmann et al. (2020); as *Halictus punctatissimus* (Schenck, 1859) in Lebedev (1931). [LC]
482. ***=Lasioglossum puncticolle*** (Morawitz, 1872) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); as *Halictus puncticollis* Morawitz, 1872 in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
483. ***=Lasioglossum pygmaeum*** (Schenck, 1853) in Markov (2017); Markov et al. (2016); ZM coll.; as *Halictus pygmaeus* (Fabricius, 1804) in Rafajlović and Seleši (1958); Vorgin (1955). [NT]
484. ***Lasioglossum quadrinotatulum*** (Schenck, 1861) in Kuhlmann et al. (2020); as *Halictus quadrinotatulus* (Schenck, 1859) in Rafajlović and Seleši (1958); Vorgin (1955). [NT]
485. ***Lasioglossum quadrinotatum*** (Kirby, 1802) in Kuhlmann et al. (2020); as *Halictus quadrinotatus* (Kirby, 1802) in Vorgin (1955); Apfelbeck (1896). [NT]
486. **▪*Lasioglossum rufitarse*** (Zetterstedt, 1838) in Kuhlmann et al. (2020). [LC]
487. ***Lasioglossum semilucens*** (Alfken, 1914) in Kuhlmann et al. (2020); as *Halictus semilucens* Alfken, 1914 in Rafajlović and Seleši (1958). [LC]
488. ***Lasioglossum setulellum*** (Strand, 1909) as *Halictus setulellus* Strand, 1909 in Vorgin (1955). [NT]
489. **▪*Lasioglossum setulosum*** (Strand, 1909) in Kuhlmann et al. (2020). [NT]
490. ***=Lasioglossum sexnotatum*** (Kirby, 1802) in Kuhlmann et al. (2020); AĐ coll.; as *Halictus sexnotatus* (Kirby, 1802) in Vorgin (1918); Mocsáry (1897). [NT]
491. ***=Lasioglossum sexstrigatum*** (Schenck, 1868) in ZM coll.; as *Halictus sexstrigatus* Schenck, 1870["1869"] in Rafajlović and Seleši (1958); Vorgin (1955). [LC]
492. ***Lasioglossum smeathmanellum*** (Kirby, 1802) as *Halictus smeathmanellus* K. in Rafajlović and Seleši (1958); Vorgin (1955, 1918); Živojinović (1950); Apfelbeck (1896). [LC]
493. ***Lasioglossum subfasciatum*** (Imhoff, 1832) as *Halictus subfasciatus* (Imhoff, 1832) in Lebedev (1931). [EN]
494. **▪*Lasioglossum subfulvicorne*** (Blüthgen, 1934) in Kuhlmann et al. (2020). [LC]

495. ***Lasioglossum tarsatum*** (Schenck, 1868) as *Halictus tarsatus* Schenck, 1868 in Rafajlović and Seleši (1958); Vorgin (1955). [NT]

496. ⸗***Lasioglossum trichopygum*** (Blüthgen, 1923) in ZM coll.; as *Halictus trichopygus* Blüthgen, 1923 in Rafajlović and Seleši (1958); Grozdanić (1966); Grozdanić and Vasić (1966a). [DD]

497. ***Lasioglossum tricinctum*** (Schenck, 1874) in Kuhlmann et al. (2020); as *Halictus tricinctus* Schenck, 1874 in Živojinović (1950). [DD]

498. ⸗***Lasioglossum truncaticolle*** (Morawitz, 1877[“1878”]) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); as *Halictus truncaticollis* Morawitz, 1877[“1878”] in Vorgin (1955); Lebedev (1931). [DD]

499. ⸗***Lasioglossum villosulum*** (Kirby, 1802) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); SG coll.; as *Halictus villosulus* Kirby, 1802 in Rafajlović and Seleši (1958); Vorgin (1955); Lebedev (1931); Apfelbeck (1896). [LC]

500. ⸗***Lasioglossum xanthopus*** (Kirby, 1802) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); as *Halictus xanthopus* (Kirby, 1802) in Petrik (1958); Rafajlović and Seleši (1958); Vorgin (1955, 1918); Lebedev (1931); Mocsáry (1897); as *Lasioglossum xanthopum* (Kirby, 1802) in ZM coll. [NT]

501. ***Lasioglossum zonulum*** (Smith, 1848) as *Halictus zonulus* Smith, 1848 in Petrik (1958); Rafajlović and Seleši (1958); Vorgin (1955, 1918); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896). [LC]

Nomiapis Cockerell, 1919 (3 species)

502. ⸗***Nomiapis bispinosa*** (Brullé, 1832) as *Nomia ruficornis* Spinola, 1839 in Grozdanić (1971b); Petrik (1958); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); as *Nomia unidentata* Oliver, 1812 in Mudri-Stojnić (2018). [LC]

503. ⸗***Nomiapis diversipes*** (Latreille, 1806) in Mudri-Stojnić (2018); ZM coll.; as *Nomia diversipes* Latreille, 1806 in Markov (2017); Mudri-Stojnić et al. (2012); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897); Apfelbeck (1896); AZ coll.; as *Pseudapis diversipes* (Latreille, 1806) in Markov et al. (2016). [LC]

504. ⸗***Nomiapis femoralis*** (Pallas, 1773) in Kuhlmann et al. (2020); ZM coll.; as *Nomia femoralis* (Pallas, 1773) in Petrik (1958); Rafajlović and Seleši (1958); Mocsáry (1897). [DD]

Nomioides Schenck, 1867 (1 species)

505. ***Nomioides minutissimus*** (Rossi, 1790) in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); as *Nomioides pulchellus* Schenck, 1859 in Mocsáry (1897). [LC]

Rhophitoides Schenck, 1861 (1 species)

506. ⸗***Rhophitoides canus*** (Eversmann, 1852) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); as *Rophites canus* Eversmann, 1852 in Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896); ZM coll. [LC]

Rophites Spinola, 1808 (2 species)

507. ⸗***Rophites hartmanni*** Friese, 1902 in Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Vorgin (1918); AZ coll. [DD]
508. ⸗***Rophites quinquespinosus*** Spinola, 1808 in Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Grozdanić (1971b); Rafajlović and Seleši (1958); Lebedev (1931); Apfelbeck (1896); Mocsáry (1897); ZM coll. [NT]

Seladonia Robertson, 1918 (8 species)

509. ***Seladonia confusa*** (Smith, 1853) as *Halictus perkinsi* Blüthgen, 1926 in Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950). [LC]
510. ▪***Seladonia gavarnica*** (Pérez, 1903) as *Halictus gavarnicus* Pérez, 1903 in Kuhlmann et al. (2020). [LC]
511. ⸗***Seladonia kessleri*** (Bramson, 1879) as *Halictus kessleri* Bramson, 1879 in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Vasić (1979b); Grozdanić (1974, 1972b, 1971b, 1966); Grozdanić and Vasić (1966a); Rafajlović and Seleši (1958); Lebedev (1931); ZM coll. [LC]
512. ⸗***Seladonia seladonia*** (Fabricius, 1794) as *Halictus seladonius* (Fabricius, 1794) in Markov (2017); Markov et al. (2016); as *Halictus geminatus* Pérez, 1903 in Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950). [LC]
513. ⸗***Seladonia semitecta*** (Morawitz, 1873) as *Halictus semitectus* Morawitz, 1874 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Rafajlović and Seleši (1958); Vorgin (1955); Mocsáry (1897). [EN]
514. ⸗***Seladonia smaragdula*** (Vachal, 1895) as *Halictus smaragdulus* Vachal, 1895 in Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Vorgin (1955); AZ coll. [LC]
515. ⸗***Seladonia subaurata*** (Rossi, 1792) as *Halictus subauratus* (Rossi, 1792) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); AZ coll.; as *Halictus gramineus* Smith, 1849 in Petrik (1958); as *Halictus virescens* Lepeletier, 1841 in Vorgin (1955); Mocsáry (1897); Apfelbeck (1896). [LC]
516. ⸗***Seladonia tumulorum*** (Linnaeus, 1758) as *Halictus tumulorum* (Linnaeus, 1758) in Lebedev (1931); Apfelbeck (1896); AĐ coll.; as *Halictus fasciatus* Nylander, 1848 in Rafajlović and Seleši (1958); Vorgin (1955); Lebedev (1931). [LC]

Sphecodes Latreille, 1802 (25 species)

517. ⸗***Sphecodes albilabris*** Fabricius, 1793 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); ZM coll.; as *Sphecodes fuscipennis* (Germar, 1819) in Petrik (1958); Rafajlović and Seleši (1958); Mocsáry (1897); Apfelbeck (1896). [LC]
518. ⸗***Sphecodes alternatus*** Smith, 1853 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012). [LC]
519. ***Sphecodes crassus*** Thomson, 1870 in Kuhlmann et al. (2020); as *Sphecodes divisus* Hagens, 1882 in Živojinović (1950); Rafajlović and Seleši (1958). [LC]
520. ***Sphecodes cristatus*** Hagens, 1882 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958). Note: Bogusch and Straka (2012) reported this species as absent on Balkan Peninsula. [NT]
521. ▪***Sphecodes croaticus*** Meyer, 1922 in Kuhlmann et al. (2020). [NT]
522. ⸗***Sphecodes ephippius*** Linnaeus, 1767 in Kuhlmann et al. (2020); Vorgin (1918); AĐ coll.; ZM coll.; as *Sphecodes similis* Wesmael, 1836 in Apfelbeck (1896). [LC]
523. ***Sphecodes ferruginatus*** Hagens, 1882 in Kuhlmann et al. (2020); Lebedev (1931); as *Sphecodes rufescens* Hagens, 1874 in Apfelbeck (1896). [LC]
524. ***Sphecodes geoffrellus*** Kirby, 1802 in Kuhlmann et al. (2020); as *Sphecodes fasciatus* Hagens, 1882 in Živojinović (1950). [LC]
525. ⸗***Sphecodes gibbus*** Linnaeus, 1758 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896). [LC]
526. ▪***Sphecodes hyalinatus*** Hagens, 1882 in Kuhlmann et al. (2020). [NT]
527. ⸗***Sphecodes longulus*** Hagens, 1882 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958). [LC]
528. ▪***Sphecodes majalis*** Pérez, 1903 in Kuhlmann et al. (2020). [NT]
529. ⸗***Sphecodes miniatus*** Hagens, 1882 in Kuhlmann et al. (2020); AĐ coll. [LC]
530. ⸗***Sphecodes monilicornis*** Kirby, 1802 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Grozdanić (1971b); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); as *Sphecodes subquadratus* Smith, 1845 in Vorgin (1918); Mocsáry (1897); Apfelbeck (1896). [LC]
531. ***Sphecodes niger*** Hagens, 1874 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958). [LC]
532. ⸗***Sphecodes pellucidus*** Smith, 1845 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Rafajlović and Seleši (1958); Živojinović (1950); AĐ coll. [LC]
533. ▪***Sphecodes pseudofasciatus*** Blüthgen, 1925 in Kuhlmann et al. (2020). [DD]
534. ***Sphecodes puncticeps*** Thomson, 1870 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Živojinović (1950). [LC]
535. ***Sphecodes reticulatus*** Thomson, 1870 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897). [LC]

536. ***Sphecodes rubicundus*** Hagens, 1875 in Lebedev (1931). [NT]
537. ***Sphecodes rufiventris*** Panzer, 1798 in Kuhlmann et al. (2020); Mocsáry (1897); as *Sphecodes subovalis* Schenck, 1853 in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
538. ***Sphecodes scabricollis*** Wesmael, 1835 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958). [DD]
539. ⸗***Sphecodes schenckii*** Hagens, 1882 in Grozdanić (1971b); Rafajlović and Seleši (1958); ZM coll. [NT]
540. ▪***Sphecodes spinulosus*** Hagens, 1875 in Kuhlmann et al. (2020). [NT]
541. ▪***Sphecodes zangherii*** Noskiewicz, 1931 in Kuhlmann et al. (2020). Note: Bogusch and Straka (2012) stated that the distribution of this species is poorly known due the taxonomical problems in the past, as many specimens of this species (with previously suggested wide distribution in south and central Europe) were missidentified *S. croaticus.* [DD]

Systropha Illiger, 1805 (2 species)

542. ⸗***Systropha curvicornis*** (Scopoli, 1770) in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Grozdanić (1971b); Grozdanić and Mučalica (1966); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Vorgin (1918), Mocsáry (1897); ZM coll. [NT]
543. ⸗***Systropha planidens*** Giraud, 1861 in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Grozdanić (1971b); Grozdanić and Vasić (1968); Grozdanić and Mučalica (1966); Vorgin (1918); Mocsáry (1897); Apfelbeck (1896); SG coll. [VU]

Vestitohalictus Blüthgen, 1961 (2 species)

544. ⸗***Vestitohalictus pollinosus*** (Sichel, 1860) as *Halictus pollinosus* Sichel, 1860 in Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Petrik (1958); Rafajlović and Seleši (1958); as *Halictus carinaeventris* Fahringer & Friese, 1921 in Mocsáry (1897). [LC]
545. ⸗***Vestitohalictus vestitus*** (Lepeletier, 1841) as *Halictus vestitus* Lepeletier, 1841 in Rafajlović and Seleši (1958); Vorgin (1955); ZM coll. [LC]

Megachilidae (17 genera; 148 species)

Aglaoapis Cameron, 1901 (1 species)

546. ***Aglaoapis tridentata*** (Nylander, 1848) as *Dioxoides tridentata* (Nylander, 1848) in Stanisavljević (2000). [LC]

Anthidiellum Cockerell, 1904 (1 species)

547. ***Anthidiellum strigatum*** Panzer, 1805 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Anthidium strigatum* (Panzer, 1805) in Rafajlović and Seleši (1958); Vorgin (1955); Mocsáry (1897). [LC]

Anthidium Fabricius, 1804 (12 species)

548. ***Anthidium cingulatum*** Latreille, 1809 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Vorgin (1955); Lebedev (1931); Mocsáry (1897). [LC]
549. ▪***Anthidium diadema*** Latreille, 1809 in Kuhlmann et al. (2020). [DD]
550. ⸗***Anthidium florentinum*** Fabricius, 1775 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Stanisavljević (2000); Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897). [LC]
551. ***Anthidium loti*** Perris, 1852 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Anthidium variegatum* (Fabricius, 1781) in Rafajlović and Seleši (1958). [DD]
552. ⸗***Anthidium manicatum*** Linnaeus, 1758 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Stanisavljević (2000); Grozdanić and Vasić (1966a); Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Apfelbeck (1896). [LC]
553. ▪***Anthidium montanum*** Morawitz, 1864 in Kuhlmann et al. (2020). [NT]
554. ⸗***Anthidium oblongatum*** Illiger, 1806 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Krunić et al. (1988); Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897); AĐ coll.; as *Proanthidium oblongatum* (Illiger, 1806) in Stanisavljević (2000) [LC]
555. ⸗***Anthidium punctatum*** Latreille, 1809 in Kuhlmann et al. (2020); Markov (2017); Stanisavljević (2000); Rafajlović and Seleši (1958); Živojinović (1950); Mocsáry (1897). [LC]
556. ***Anthidium septemspinosum*** Lepeletier, 1841 in Kuhlmann et al. (2020); Stanisavljević (2000); Vorgin (1918). [DD]
557. ▪***Anthidium taeniatum*** Latreille, 1809 in Kuhlmann et al. (2020). [DD]
558. ▪***Anthidium undulatiforme*** Friese, 1917 in Kuhlmann et al. (2020). [NT]
559. ▪***Anthidium undulatum*** Dours, 1873 in Kuhlmann et al. (2020). [LC]

Chelostoma Latreille, 1809 (12 species)

560. ⸗***Chelostoma campanularum*** Kirby, 1802 in Stanisavljević (2000); AĐ coll. [LC]
561. ***Chelostoma distinctum*** Stoeckhert, 1929 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Eriades distinctus* Stoeckhert, 1929 in Živojinović (1950). [LC]

562. ⫽***Chelostoma emarginatum*** Nylander, 1856 in Kuhlmann et al. (2020); AĐ coll.; also as *Chelostoma appendiculatum* (Morawitz, 1871) in Stanisavljević (2000); as *Eriades emarginatus* Nylander, 1856 and also as *Eriades appendiculatus* in Vorgin (1918). [LC]
563. ⫽***Chelostoma florisomne*** Linnaeus, 1758 in Kuhlmann et al. (2020); Stanisavljević (2000); AĐ coll.; SG coll.; as *Chelostoma florisomnis* in Mocsáry (1897); as *Eriades maxillosus* (Linnaeus, 1758) in Rafajlović and Seleši (1958); Živojinović (1950); as *Eriades florisomnis* Spinola in Vorgin (1918); Apfelbeck (1896). [LC]
564. ▪***Chelostoma foveolatum*** Morawitz, 1868 in Kuhlmann et al. (2020). [LC]
565. ▪***Chelostoma grande*** Nylander, 1852 in Kuhlmann et al. (2020). [DD]
566. ***Chelostoma handlirschi*** Schletterer, 1889 as *Eriades handlirschi* (Schletterer, 1889) in Rafajlović and Seleši (1958); Lebedev (1931). Note: According to Müller (2015) there are possible errors in older literature records regarding identification and distribution ("Reliable records exist only for Romania and Bulgaria") of this species. [DD]
567. ▪***Chelostoma mocsaryi*** Schletterer, 1889 in Kuhlmann et al. (2020). [LC]
568. ⫽***Chelostoma nasutum*** Pérez, 1895 **New material examined:** 1 ♀; Vlasina Rid; 42.7253°N, 22.3284°E; 22–23 Jul. 2019; A. Đukić leg.; Jelle Devalez det.; AĐ coll. [LC]
569. ⫽***Chelostoma rapunculi*** Lepeletier, 1841 in Kuhlmann et al. (2020); Stanisavljević (2000); AĐ coll.; as *Eriades nigricornis* Nylander, 1848 in Rafajlović and Seleši (1958); Lebedev (1931). [LC]
570. ▪***Chelostoma styriacum*** Schwarz & Gusenleitner, 1999 in Kuhlmann et al. (2020). [LC]
571. ▪***Chelostoma ventrale*** Schletterer, 1889 in Kuhlmann et al. (2020). [LC]

Coelioxys Latreille, 1809 (17 species)

572. ▪***Coelioxys acanthura*** Illiger, 1806 in Kuhlmann et al. (2020). [DD]
573. ⫽***Coelioxys afer*** Lepeletier, 1841 as *Coelioxys afra* Lepeletier, 1841 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); Mocsáry (1897); AĐ coll.; SG coll.; as *Coelioxys coronata* Förster, 1853 in Petrik (1958). [LC]
574. ***Coelioxys alatus*** Förster, 1853 as *Coelioxys alata* Förster, 1853 in Kuhlmann et al. (2020); Stanisavljević (2000); Živojinović (1950). [LC]
575. ⫽***Coelioxys argenteus*** Lepeletier, 1841 as *Coelioxys argentea* Lepeletier, 1841 in Kuhlmann et al. (2020); Stanisavljević (2000); ZM coll. [LC]
576. ⫽***Coelioxys aurolimbatus*** Förster, 1853 as *Coelioxys aurolimbata* Förster, 1853 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); FSUNS. [LC]
577. ***Coelioxys brevis*** Eversmann, 1852 in Stanisavljević (2000); Rafajlović and Seleši (1958); as *Coelioxys erythropyga* Förster, 1853 in Petrik (1958); Mocsáry (1897). [LC]

578. ***Coelioxys conoideus*** (Illiger, 1806) as *Coelioxys conoidea* Illiger, 1806 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Živojinović (1950). [LC]
579. ***Coelioxys echinatus*** Förster, 1853 as *Coelioxys echinata* Förster, 1853 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Coelioxys rufocaudata* Smith, 1854 in Rafajlović and Seleši (1958); Mocsáry (1897). [LC]
580. ⸗***Coelioxys elongatus*** Lepeletier, 1841 as *Coelioxys elongata* Lepeletier, 1841 in Kuhlmann et al. (2020); ZM coll. [LC]
581. ***Coelioxys emarginatus*** Förster, 1853 as *Coelioxys emarginata* Förster, 1853 in Stanisavljević (2000); Petrik (1958); Rafajlović and Seleši (1958); Mocsáry (1897). [LC]
582. ***Coelioxys haemorrhoa*** Förster, 1853 in Stanisavljević (2000); Živojinović (1950). [LC]
583. ***Coelioxys inermis*** Kirby, 1802 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Coelioxys acuminata* Nylander, 1852 in Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931). [LC]
584. ***Coelioxys mandibularis*** Nylander, 1848 in Kuhlmann et al. (2020); Stanisavljević (2000). [LC]
585. ⸗***Coelioxys obtusus*** Pérez, 1884 as *Coelioxys obtusa* Pérez, 1884 in Kuhlmann et al. (2020); Stanisavljević (2000); SG coll. [LC]
586. ⸗***Coelioxys polycentris*** Förster, 1853 in Kuhlmann et al. (2020); Stanisavljević (2000); Petrik (1958); Rafajlović and Seleši (1958); Vorgin (1918); Mocsáry (1897); SG coll. [LC]
587. ⸗***Coelioxys quadridentatus*** (Linnaeus, 1758) in Krunić et al. (1988); ZM coll.; as *Coelioxys quadridentata* (Linnaeus, 1758) in Kuhlmann et al. (2020); Stanisavljević (2000). [LC]
588. ⸗***Coelioxys rufescens*** Lepeletier and Audinet-Serville, 1825 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Vorgin (1918); Mocsáry (1897); ZM coll. [LC]

Heriades Spinola, 1808 (2 species)

589. ⸗***Heriades crenulata*** Nylander, 1856 in Kuhlmann et al. (2020); as *Heriades crenulatus* Nylander, 1856 in Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Stanisavljević (2000); Krunić et al. (1988); as *Eriades crenulatus* in Rafajlović and Seleši (1958); Vorgin (1955); Mocsáry (1897). [LC]
590. ⸗***Heriades truncorum*** Linnaeus, 1758 in Stanisavljević (2000); Živojinović (1950); Lebedev (1931); AĐ coll.; FSUNS; as *Eriades truncorum* (Linnaeus) in Rafajlović and Seleši (1958); Mocsáry (1897). [LC]

Hofferia Tkalců, 1984 (1 species)

591. ***Hofferia schmiedeknechti*** Schletterer, 1889 in Stanisavljević (2000). [LC]

Hoplitis Klug, 1807 (17 species)

592. ***Hoplitis acuticornis*** Dufour & Perris, 1840 in Stanisavljević (2000); as *Osmia acuticornis* Dufour & Perris, 1840 in Rafajlović and Seleši (1958). [LC]
593. ⸗***Hoplitis adunca*** Panzer, 1798 in Kuhlmann et al. (2020); Markov (2017); Stanisavljević (2000); AĐ coll.; as *Hoplites* in Krunić et al. (1988); as *Osmia adunca* (Panzer, 1798) in Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); as *Osmia spinolae* Lepeletier, 1841 in Mocsáry (1897). [LC]
594. ***Hoplitis anthocopoides*** Schenck, 1853 in Stanisavljević (2000); as *Osmia caementaria* Gerstäcker, 1869 in Rafajlović and Seleši (1958). [LC]
595. ****Hoplitis bisulca*** Gerstäcker, 1869 as *Osmia bisulca* Gerstäcker, 1869 in Mocsáry (1897). [LC]
596. ▪***Hoplitis campanularis*** Morawitz, 1877 in Kuhlmann et al. (2020). [LC]
597. ⸗***Hoplitis claviventris*** (Thomson, 1872) **New material examined:** 1 ♀; Vlasina Rid; 42.7253°N, 22.3284°E; 21 Jul. 2019; A. Đukić leg.; Andrej Gogala det.; AĐ coll. [LC]
598. ⸗***Hoplitis dalmatica*** Morawitz, 1871 in SG coll.; as *Anthocopa dalmatica* (Morawitz, 1871) in Stanisavljević (2000); as *Osmia dalmatica* Morawitz, 1871 in Živojinović (1950). [LC]
599. ▪***Hoplitis illyrica*** Noskiewicz, 1926 in Kuhlmann et al. (2020). [LC]
600. ⸗***Hoplitis laevifrons*** Morawitz, 1872 in Kuhlmann et al. (2020); ZM coll. [LC]
601. ⸗***Hoplitis lepeletieri*** Pérez, 1879 in Stanisavljević (2000); SG coll. [LC]
602. ⸗***Hoplitis leucomelana*** Kirby, 1802 in Stanisavljević (2000); AĐ coll.; SG coll.; as *Osmia parvula* Dufour & Perris, 1840 in Rafajlović and Seleši (1958). [LC]
603. ⸗***Hoplitis loti*** Morawitz, 1867 in Stanisavljević (2000); SG coll. [LC]
604. ***Hoplitis manicata*** Morice, 1901 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Hoplites* in Krunić et al. (1988). [LC]
605. ▪***Hoplitis perezi*** Ferton, 1895 in Kuhlmann et al. (2020). [LC]
606. ▪***Hoplitis praestans*** Morawitz, 1893 in Kuhlmann et al. (2020). [LC]
607. ⸗***Hoplitis tridentata*** Dufour & Perris, 1840 in Stanisavljević (2000); SG coll. [LC]
608. ⸗***Hoplitis tuberculata*** Nylander, 1848 in Stanisavljević (2000); SG coll. [LC]

Icteranthidium Michener, 1948 (2 species)

609. ▪***Icteranthidium grohmanni*** Spinola, 1838 in Kuhlmann et al. (2020). [LC]
610. ***Icteranthidium laterale*** Latreille, 1809 in Stanisavljević (2000); as *Anthidium laterale* Latreille, 1809 in Petrik (1958); Rafajlović and Seleši (1958); Mocsáry (1897). [LC]

Lithurgus Latreille, 1825 (2 species)

611. ***Lithurgus chrysurus*** Fonscolombe, 1834 in Kuhlmann et al. (2020); Stanisavljević (2000); Krunić et al. (1988); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); Korlević (1890). [LC]

612. =***Lithurgus cornutus*** Fabricius, 1787 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); ZM coll.; also as *Lithurgus cornutus fuscipennis* Lepeletier, 1841 in Stanisavljević (2000); as *Lithurgus cornuta* ssp. *fuscipennis* Lep. in Krunić et al. (1988); as *Lithurgus fuscipennis* Lepeletier, 1841 Rafajlović and Seleši (1958); Živojinović (1950); Mocsáry (1897). [LC]

Megachile Latreille, 1802 (34 species)

613. =***Megachile albisecta*** Klug, 1817 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Mudri-Stojnić et al. (2012); as *Megachile sericans* Fonscolombe, 1832 in Grozdanić (1971b); Vasić (1968); Mocsáry (1897); as *Creightonella albisecta* (Klug, 1817) in Stanisavljević (2000); SG coll. [LC]
614. ▪***Megachile albocristata*** Smith, 1853 in Kuhlmann et al. (2020). [LC]
615. ▪***Megachile alpicola*** Alfken, 1924 in Kuhlmann et al. (2020). [DD]
616. =***Megachile apicalis*** Spinola, 1808 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Stanisavljević (2000); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918); Mocsáry (1897). [LC]
617. ***Megachile bombycina*** Radoszkowski, 1874 in Stanisavljević (2000); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Mocsáry (1897). [DD]
618. ▪***Megachile burdigalensis*** Benoist, 1940 in Kuhlmann et al. (2020). [DD]
619. =***Megachile centuncularis*** Linnaeus, 1758 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); Krunić et al. (1988); Grozdanić and Vasić (1966a); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); AĐ coll.; ZM coll. [LC]
620. ***Megachile circumcincta*** Kirby, 1802 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958). [LC]
621. =***Megachile concinna*** Smith, 1879 in Kuhlmann et al. (2020); as *Megachile argentata* (Fabricius, 1793) in Stanisavljević (2000); Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); ZM Coll. [DD]
622. =***Megachile deceptoria*** Pérez 1890 in Kuhlmann et al. (2020); FSUNS. [DD]
623. =***Megachile ericetorum*** Lepeletier, 1841 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Grozdanić (1971b); Grozdanić and Mučalica (1968a); Grozdanić and Vasić (1966a); Rafajlović and Seleši (1958); Vorgin (1918); as *Chalicodoma ericetorum* (Lepeletier, 1841) in Stanisavljević (2000); Krunić et al. (1988); ZM coll. [LC]
624. ***Megachile flabellipes*** Pérez, 1895 in Kuhlmann et al. (2020); Stanisavljević (2000). [DD]
625. ***Megachile fulvimana*** Eversman, 1852 in Stanisavljević (2000). [DD]
626. =***Megachile genalis*** Morawitz, 1880 in Kuhlmann et al. (2020); Stanisavljević (2000); ZM coll. [DD]
627. ▪***Megachile giraudi*** Gerstäcker, 1869 in Kuhlmann et al. (2020). [DD]

628. ***Megachile hungarica*** Mocsáry, 1877 as *Chalicodoma hungarica* Mocsáry, 1877 in Stanisavljević (2000). [DD]
629. ***Megachile lagopoda*** Linnaeus, 1761 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897). [LC]
630. **⸗*Megachile leachella*** Curtis, 1828 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); ZM coll. [LC]
631. ***Megachile leucomalla*** Gerstäcker, 1869 in Stanisavljević (2000); Petrik (1958); Mocsáry (1897). [DD]
632. ***Megachile ligniseca*** Kirby, 1802 in Kuhlmann et al. (2020); Stanisavljević (2000); Krunić et al. (1988); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Vorgin (1918). [DD]
633. **▪*Megachile manicata*** Giraud, 1861 in Kuhlmann et al. (2020). [DD]
634. **⸗*Megachile maritima*** Kirby, 1802 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); Krunić et al. (1988); Petrik (1958); Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897). [DD]
635. **⸗*Megachile melanopyga*** Costa, 1863 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Stanisavljević (2000); Rafajlović and Seleši (1958). [LC]
636. **▪*Megachile nigriventris*** Schenck, 1870 in Kuhlmann et al. (2020). [DD]
637. ***Megachile octosignata*** Nylander, 1852 in Kuhlmann et al. (2020); Lebedev (1931). [DD]
638. ***Megachile parietina*** Geoffroy, 1785 in Kuhlmann et al. (2020); also as *Chalicodoma muraria* auct. in Apfelbeck (1896); as *Chalicodoma parietina* (Geoffroy, 1785) in Stanisavljević (2000); Krunić et al. (1988). [LC]
639. **⸗*Megachile pilicrus*** Morawitz, 1877 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); Rafajlović and Seleši (1958); Živojinović (1950); AZ coll. [DD]
640. **⸗*Megachile pilidens*** Alfken, 1924 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Stanisavljević (2000); Grozdanić (1971b); Lebedev (1931); ZM coll. [LC]
641. **▪*Megachile pyrenaea*** Pérez, 1890 in Kuhlmann et al. (2020). [DD]
642. **⸗*Megachile pyrenaica*** Lepeletier, 1841 in Kuhlmann et al. (2020); as *Chalicodoma pyrenaica* (Lepeletier, 1841) in Stanisavljević (2000); ZM coll. [DD]
643. **⸗*Megachile rotundata*** Fabricius, 1793 in Kuhlmann et al. (2020); Stanisavljević and Tomanović (2006); Stanisavljević (2000); Krunić et al. (1997, 1995b, 1992b, 1992c, 1985, 1988); Mihajlović et al. (1989); Rafajlović and Seleši (1958); ZM coll.; as *Megachile pacifica* (Panzer, 1798) in Vorgin (1918); Mocsáry (1897). [DD]
644. **⸗*Megachile sculpturalis*** Smith, 1853 in Ćetković and Plećaš (2017). **New material examined:** 1 ♂, 1 ♀; Bački Maglić; 45.3686°N, 19.5381°E; 20 Jul. 2019; B. Šikoparija leg.; Sonja Mudri-Stojnić det.; FSUNS.
645. **⸗*Megachile versicolor*** Smith, 1844 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); AĐ coll. [DD]

646. ⫽***Megachile willughbiella*** Kirby, 1802 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Mučalica and Stanisavljević (2005); Stanisavljević (2000); Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); Mocsáry (1897); AĐ coll.; ZM coll. [LC]

Osmia Panzer, 1806 (26 species)

647. ⫽***Osmia andrenoides*** Spinola, 1808 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Mocsáry (1897); Apfelbeck (1896); as *Anthocopa andrenoides* Spinola, 1808 in Stanisavljević (2000); Krunić et al. (1988); SG coll. [LC]
648. ■***Osmia apicata*** Smith, 1853 in Kuhlmann et al. (2020). [LC]
649. ⫽***Osmia aurulenta*** Panzer, 1799 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); Mudri-Stojnić et al. (2012); Stanisavljević (2000); Krunić et al. (1988); Grozdanić (1971b); Grozdanić and Vasić (1965c); Rafajlović and Seleši (1958); Vorgin (1955); Lebedev (1931); SG coll. [LC]
650. ⫽***Osmia bicolor*** Schrank, 1781 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); Grozdanić (1971b, 1965); Grozdanić and Vasić (1965a, 1965c); Rafajlović and Seleši (1958); Lebedev (1931); SG coll. [LC]
651. ⫽***Osmia bicornis*** Linnaeus, 1758 in Markov (2017); Markov et al. (2016); Grozdanić and Vasić (1966a); Vorgin (1955); Grozdanić (1928); AĐ coll.; as *Osmia rufa* (Linnaeus, 1758) in Krunić and Stanisavljević (2006a, 2006b, 2006c, 2006d; 2000; 1996); Krunić et al. (2005, 1999, 1998, 1996, 1995a); Stanisavljević et al. (1999, 1997a, 1997b); Kulinčević et al. (1997); Grozdanić (1971b, 1960); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); ZM coll.; SG coll. [LC]
652. ⫽***Osmia bidentata*** Morawitz, 1876 in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Müller (2018); Markov (2017); Markov et al. (2016); Grozdanić and Radivojević (1972); Grozdanić (1971b); Lebedev (1931); Mocsáry (1897); as *Anthocopa bidentata* (Morawitz, 1876) in Stanisavljević (2000); Krunić et al. (1988); as *Osmia affinis* Frivaldszky, 1877 in Petrik (1958); as *Hoplosmia bidentata* (Morawitz, 1876) in SG coll. [LC]
653. ⫽***Osmia brevicornis*** Fabricius, 1798 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); as *Osmia atrocaerulea* Schilling, 1849 in Rafajlović and Seleši (1958); as *Osmia panzeri* Morawitz, 1869 in Mocsáry (1897). [LC]
654. ⫽***Osmia caerulescens*** Linnaeus, 1758 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); Krunić et al. (1988); Grozdanić and Vasić (1966a); Rafajlović and Seleši (1958); AĐ coll.; SG coll.; as *Osmia aenea* Linnaeus, 1761 in Živojinović (1950); Lebedev (1931). [LC]
655. ***Osmia cephalotes*** Morawitz, 1870 as *Osmia cephalotes longiceps* Morawitz, 1876 in Stanisavljević (2000). [LC]

656. ≠***Osmia cornuta*** Latreille, 1805 in Markov (2017); Markov et al. (2016); Stanisavljević et al. (2013, 2000a, b, 1999, 1997a, b); Stanisavljević (2009, 2000, 1996); Krunić and Stanisavljević (2006a, b, , d); Maccagnani et al. (2007); Krunić et al. (2005, 2001, 1999, 1998, 1996, 1995a, 1992a, 1991, 1989, 1988); Kulinčević et al. (1997); Rafajlović and Seleši (1958); Lebedev (1931); AĐ coll.; AZ coll.; ZM coll. [LC]
657. ▪***Osmia croatica*** Friese, 1893 in Kuhlmann et al. (2020). [LC]
658. ≠***Osmia emarginata*** Lepeletier, 1841 in Stanisavljević (2000); ZM coll. [LC]
659. ▪***Osmia erythrogastra*** Ferton, 1905 in Kuhlmann et al. (2020). [LC]
660. ***Osmia gallarum*** Spinola, 1808 in Stanisavljević (2000); Lebedev (1931). [LC]
661. ▪***Osmia jason*** Benoist, 1929 in Kuhlmann et al. (2020). [LC]
662. ≠***Osmia leaiana*** Kirby, 1802 in Stanisavljević (2000); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931); AĐ coll.; as *Osmia solskyi* Morawitz, 1870 in Mocsáry (1897). [LC]
663. ≠***Osmia melanogaster*** Spinola, 1808 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); as *Osmia melanogastra* in Rafajlović and Seleši (1958); Mocsáry (1897); as *Osmia aterrima* Morawitz, 1872 in Lebedev (1931). [LC]
664. ≠***Osmia niveata*** Fabricius, 1804 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); as *Osmia fulviventris* (Panzer, 1798) in Stanisavljević (2000); Krunić et al. (1988); Rafajlović and Seleši (1958); Vorgin (1955); Živojinović (1950); Lebedev (1931); Apfelbeck (1896). [LC]
665. ▪***Osmia padri*** Tkalcu, 1974 in Kuhlmann et al. (2020). [DD]
666. ▪***Osmia pilicornis*** Smith, 1846 in Kuhlmann et al. (2020). [LC]
667. ≠***Osmia rufohirta*** Latreille, 1811 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Grozdanić (1971b, 1969b); Grozdanić and Vasić (1965c); Rafajlović and Seleši (1958); Živojinović (1950); Mocsáry (1897); SG coll; as *Hoplitis rufohirta* (Latreille, 1811) in Stanisavljević (2000); as *Hoplites rufohirta* (Latr.) in Krunić et al. (1988). [LC]
668. ▪***Osmia saxicola*** Ducke, 1899 in Kuhlmann et al. (2020). [LC]
669. ▪***Osmia signata*** Erichson, 1835 in Kuhlmann et al. (2020). [LC]
670. ≠***Osmia spinulosa*** Kirby, 1802 in Mudri-Stojnić (2018); Mudri-Stojnić et al. (2012); Rafajlović and Seleši (1958); Vorgin (1955); as *Anhocopa spinulosa* (Kirby, 1802) in Stanisavljević (2000). [LC]
671. ***Osmia submicans*** Morawitz, 1870 in Stanisavljević (2000); Rafajlović and Seleši (1958). [LC]
672. ***Osmia versicolor*** Latreille, 1811 in Stanisavljević (2000); Apfelbeck (1896). [LC]

Protosmia Ducke, 1900 (1 species)

673. ***Protosmia longiceps*** Friese, 1899 as *Eriades longiceps* Friese, 1899 in Vorgin (1918). [DD]

Pseudoanthidium Friese, 1898 (3 species)

674. ***Pseudoanthidium scapulare*** (Latreille, 1809) as *Paranthidiellum lituratum* (Panzer, 1801) in Stanisavljević (2000); Krunić et al. (1988); as *Anthidium lituratum* (Panzer, 1801) in Rafajlović and Seleši (1958); Vorgin (1918). [DD]
675. ****Pseudoanthidium reticulatum*** Mocsáry, 1884 as *Anthidium mocsaryi* Friese, 1897 in Mocsáry (1897). [DD]
676. ****Pseudoanthidium tenellum*** Mocsáry, 1881 as *Anthidium tenellum* Mocsáry, 1881 in Mocsáry (1897). [DD]

Rhodanthidium Isensee, 1927 (2 species)

677. ***Rhodanthidium septemdentatum*** Latreile, 1809 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Anthidium septemdentatum* Latreille, 1809 in Grozdanić and Vasić (1965c); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931). [DD]
678. ▪***Rhodanthidium sticticum*** Fabricius, 1787 in Kuhlmann et al. (2020). [DD]

Stelis Panzer, 1806 (10 species)

679. ***Stelis annulata*** Lepeletier, 1841 in Stanisavljević (2000); as *Stelis frey-gessneri* Friese, 1885 in Rafajlović and Seleši (1958). [DD]
680. ***Stelis breviuscula*** Nylander, 1848 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Lebedev (1931); Vorgin (1918). [LC]
681. ***Stelis minuta*** Lepeletier and Audinet-Serville, 1825 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958). [LC]
682. ▪***Stelis nasuta*** Latreille, 1809 in Kuhlmann et al. (2020). [LC]
683. ▪***Stelis odontopyga*** Noskiewicz, 1926 in Kuhlmann et al. (2020). [LC]
684. ***Stelis ornatula*** Klug, 1807 in Kuhlmann et al. (2020); Apfelbeck (1896). [LC]
685. ***Stelis phaeoptera*** Kirby, 1802 in Kuhlmann et al. (2020); Stanisavljević (2000); Rafajlović and Seleši (1958); Živojinović (1950); Lebedev (1931). [DD]
686. ***Stelis punctulatissima*** Kirby, 1802 in Kuhlmann et al. (2020); Stanisavljević (2000); as *Stelis aterrima* (Panzer, 1798) in Rafajlović and Seleši (1958); Lebedev (1931); Mocsáry (1897). [LC]
687. ⸗***Stelis signata*** Latreille, 1809 in Kuhlmann et al. (2020); Markov (2017); Markov et al. (2016); Stanisavljević (2000); Rafajlović and Seleši (1958). [LC]
688. ***Stelis simillima*** Morawitz, 1876 in Kuhlmann et al. (2020); Kasparek (2015). [LC]

Trachusa Panzer, 1804 (5 species)

689. ⸗***Trachusa byssina*** Panzer, 1798 in Kuhlmann et al. (2020); Stanisavljević (2000); Lebedev (1931); ZM coll. [LC]

690. ▪***Trachusa dumerlei*** Warncke, 1980 in Kuhlmann et al. (2020). [LC]

691. ***Trachusa interrupta*** Fabricius, 1781 in Kuhlmann et al. (2020); Kasparek (2017); as *Paraanthidium interruptum* (Fabricius, 1781) in Stanisavljević (2000); as *Anthidium interruptum* (Fabricius, 1781) in Rafajlović and Seleši (1958); Mocsáry (1897). [EN]

692. ▪***Trachusa laticeps*** Morawitz, 1873 in Kuhlmann et al. (2020). [NT]

693. ***Trachusa pubescens*** Morawitz, 1872 in Kasparek (2017); as *Archianthidium pubescens* Morawitz, 1872 in Stanisavljević (2000); as *Anthidium pubescens* Morawitz, 1872 in Petrik (1958); Rafajlović and Seleši (1958); Živojinović (1950); Mocsáry (1897). [DD] Note: According to Kasparek (2018), *Trachusa pubescens* sensu lato is a complex of five species, and specimens from Serbia belong to the newly described *Trachusa balcanica* Kasparek, 2018.

Mellitidae (3 genera; 13 species)

Dasypoda Latreille, 1802 (4 species)

694. ***Dasypoda argentata*** Panzer, 1809 in Rafajlović and Seleši (1958); Mocsáry (1897). [NT]

695. ▪***Dasypoda braccata*** Eversmann, 1852 in Kuhlmann et al. (2020). [EN]

696. ⫽***Dasypoda hirtipes*** (Fabricius, 1793) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Markov (2017); Markov et al. (2016); AĐ coll.; also as *Dasypoda plumipes* Panzer, 1797 in Petrik (1958); as *Dasypoda plumipes* in Grozdanić (1971b); Rafajlović and Seleši (1958); Vorgin (1955, 1918); Živojinović (1950); Lebedev (1931); Mocsáry (1897); ZM coll. [LC]

697. ⫽***Dasypoda pyrotrichia*** Förster, 1855 **New material examined:** 2 ♀♀; Vlasina, Dejanova reka; 42.6888°N, 22.3954°E; 24 Jul. 2019; A. Đukić leg.; Denis Michez det.; AĐ coll. [LC]

Macropis Panzer, 1809 (3 species)

698. ⫽***Macropis europaea*** Warncke, 1973 in Kuhlmann et al. (2020); AĐ coll.; as *Macropis labiata* (Fabricius, 1804) in Apfelbeck (1896). [LC]

699. ***Macropis frivaldszkyi*** Mocsáry, 1878 in Kuhlmann et al. (2020); Vorgin (1918); Mocsáry (1897). [NT]

700. ***Macropis fulvipes*** (Fabricius, 1804) in Kuhlmann et al. (2020); Lebedev (1931). [LC]

Melitta Kirby, 1802 (6 species)

701. ***Melitta budensis*** (Mocsary, 1878) in Grozdanić (1971b); Rafajlović and Seleši (1958). [LC]

702. ****Melitta dimidiata*** Morawitz, 1876 in Apfelbeck (1896). [NT]

703. ⸗***Melitta haemorrhoidalis*** (Fabricius, 1775) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Rafajlović and Seleši (1958); Živojinović (1950). [LC]
704. ⸗***Melitta leporina*** (Panzer, 1799) in Kuhlmann et al. (2020); Mudri-Stojnić (2018); Rafajlović and Seleši (1958); Živojinović (1950); Morawitz (1876); Apfelbeck (1896). [LC]
705. ⸗***Melitta nigricans*** Alfken, 1905 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958); Živojinović (1950); AĐ coll.; AZ coll. [LC]
706. ***Melitta tricincta*** Kirby, 1802 in Kuhlmann et al. (2020); Rafajlović and Seleši (1958). [NT]

Discussion

Of the 706 species from six families of bees presented here for Serbia, more than half (53%) belong to only two families of the group of long-tongued bees, i.e. Apidae (32%) and Megachilidae (21%). Apidae is also the family represented with most genera, 31% of the total number of 58. The genus most rich in species is *Andrena* (fam. Andrenidae) with 104 reported species, followed by *Nomada* (fam. Apidae) – 77 and *Lasioglossum* (fam. Halictidae) – 72 species. Among all genera, 26 (44.8%) are represented with only one or two species. Regarding families, the lowest number of species is recorded within Mellitidae, only 13 (1.8%).

According to the first Red List of European bees (Nieto et al. 2014) and its addition (Rasmont et al. 2017), the pattern found here is similar to that at the European level (Table 1). The first checklist included 1,965 native European bee species, whereas the update presented 2,051 species for Europe and gave the first estimation of 3,408 species for the West Palaearctic biogeographical region. The most prominent and diverse bee family in Europe / West Palaearctic is the Apidae (28.1% / 27.2% of species), while the least diverse is Mellitidae (with only 1.9% / 1.7%). Considering there are approximately 20,000 bee species worldwide, Serbia hosts 3.5% of the total, 20.7% of Western-Palaearctic, and 34.4% of the European bee diversity, according to the list we present in this study. Regarding bee genera, more than half of Western-Palaearctic, and the majority of the European ones are represented in our list, 58 out of 105 and 77, respectively, the latter number updated form 75 (Nieto et al. 2014), since *Halictus* subgenera *Seladonia* and *Vestitohalictus* have recently been erected as distinct genera (Rasmont et al. 2017 and references therein).

For most of the species listed here, newer records (starting with year 2000) have been found in various bibliographic sources and collections. However, for 97 species there are no publicly available records from the 21st century. Furthermore, for 15 of these species the only found data of presence in Serbia are from the 19th century, most of them reported only once, therefore the current presence of these species in the given localities is not certain. Our knowledge of bee fauna is still somewhat fragmentary and uneven among different parts of Serbia, since many localities remain understudied or were investigated a long time ago. A comprehensive future research is needed in order to confirm and update the data in this provisional list that is meant to represent a review of so far published records and a basis for further studies. Moreover, among 706 species, the presence in Serbia for 314 species was confirmed by determination and review of materials, while data are from literature for 392 species. A third of all the species (227) are included in our list according to only one literature source each, and for almost a quarter (153) of all the species, the only source for their occurrence in Serbia is the "Checklist of the Western Palaearctic Bees" (Kuhlmann et al. 2020). Of the 706 species recorded in total, 510 are also listed in Kuhlmann et al. (2020) as being present in Serbia. Therefore, we present 196 bee species as potential additions to the distribution maps of that checklist. Furthermore, 14 of these species are presented here as the first published records for Serbia.

According to the European Red List (Nieto et al. 2014), most species (more than half) recorded for Serbia and listed here are in the Least Concern category (55.4%), followed by those classified as Data Deficient (31.4%) since there was not enough scientific information to evaluate their risk of extinction. A further 9.1% of species have been assessed as Near Threatened. Therefore, ca. 4% of bee species present in Serbia are considered threatened in Europe; i.e., ten Vulnerable and 18 Endangered species (Table 2). Only one species, *Bombus cullumanus* (fam. Apidae), is listed as Critically endangered at the European level. Three of the species categorised as Endangered according to the European Red List have not been recorded in Serbia in the 21st century. Therefore, Serbia hosts species of conservation concern in Europe; however, the current presence of some species requires re-confirmation and possible re-evaluation of their conservation status. Threatened species mostly belong to families Apidae (13: 6 VU, 6 EN, 1 CR), Colletidae (8: 3 VU, 5 EN) and Halictidae (5: 1 VU, 4 EN); there is one EN species in each of the remaining three families. The pattern is similar to that at the European level, with most threatened species in Apidae, followed by Colletidae and Halictidae. The overall proportion of threatened (VU, EN, and CR) bee species is the same (4%), but the proportional representation of Data Deficient species is higher at 56.7% (Nieto et al. 2014). Among species presented in our list, 77 not included in Kuhlmann et al. (2020) were assessed as Data Deficient (Nieto et al. 2014). Therefore, this study is an addition to the knowledge of the distribution of these species in Europe and thus a contribution to scientific information needed for their threat evaluation. Furthermore, since there is still no national Red List of bees in Serbia, the list presented here provides a baseline for future work in that direction. Only one species of the superfamily Apoidea in Serbia has been listed as protected by national law, *Bombus confusus* (Appendix 2 of the Code on Declaration and Protection of Strictly Protected and Protected Wild Species of Plants, Animals and Fungi, Official Gazette of RS No. 5/2010, 47/2011, 32/2016 and 98/2016); species assessed as Vulnerable in Europe. Comparing global and regional Red Lists has shown that species common within their overall geographical range can be threatened on a local scale, which also highlights the importance to implement conservation measures at various geographical scales (Drossart and Gérard 2020).

Two of the species presented in our list are without the category of threat, since they are not in the European Red List (Nieto et al. 2014) but they have been included in its addition (Rasmont et al. 2017). One is *Andrena confinis*, previously considered a synonym of *Andrena congruens* but now regarded as a distinct species (Rasmont et al. 2017; Kuhlmann et al. 2020). The second is *Megachile sculpturalis*, native to Eastern Asia. Until recently, European bee fauna has been without allochthonous species; however, this solitary bee has been imported, established, and is expanding rapidly, and the first record for south-east Europe was reported in Serbia in 2017 (Ćetković and Plećaš 2017).

An up-to-date species list is the foundation of biodiversity and conservation work, and knowing which species make up the diverse ecosystems will be critically important in order to protect and restore them. Bees represent one of the key components of global biodiversity, providing vital ecosystem services, being the primary pollinators of most agricultural crops and wild plants. Climate change, land-use change and other anthropogenic pressures have been affecting the diversity of bees throughout the world (Tscharntke et al. 2005; Winfree et al. 2009; Holzschuh et al. 2010, 2016; Potts et al. 2010; Gill et al. 2012; González-Varo et al. 2013; Senapathi et al. 2015). During the last decade, both scientific and public interest in the conservation of pollinators has increased considerably (Drossart and Gérard 2020). Identifying effective conservation practices for bees requires a continuous monitoring to assess their population trends and the most significant threats. The first step towards this aim is the comprehensive knowledge of bee diversity, thus the current study provides a baseline for further research in Serbia. However, our intention is to produce updates, and we hope other researchers will contribute and improve upon this list by providing new information.

Acknowledgements

We gratefully thank Aleksandar Stojanović for providing access to the collections of the Natural History Museum, Belgrade, Serbia and Aleksandra Zatezalo for providing material from collection of the Institute for Nature Conservation of Serbia, Belgrade, Serbia. Special thanks to Zsolt Józan (HU), Andrej Gogala (SI), Jelle Devalez (GR), and Denis Michez (BE) for the specimen identifications. We thank Laura Likov for translating literature from Hungarian. We thank Arijana Luburić – Cvijanović for English proofreading. We also thank the editor Thorleif Dörfel, the reviewer Petr Bogusch, and one anonymous reviewer who contributed with constructive suggestions that improved the final version of the paper. The authors acknowledge financial support of the Ministry of Education, Science and Technological Development of the Republic of Serbia (Grant No. 451-03-9/2021-14/200358; 451-03-9/2021-14/200125). The authors declare that no competing interests exist.

References

Anđelković V (1949) Ekološka ispitivanja na jednom naselju vrste *Halictus quadricinctus* F. Prirodnjak 1.

Apfelbeck V (1896) Balkanske Apide (pčele). Glasnik zemaljskog muzeja u Bosni i Hercegovini 8: 329–342.

Bogusch P, Straka J (2012) Review and identification of the cuckoo bees of central Europe (Hymenoptera: Halictidae: *Sphecodes*). Zootaxa 3311(1): 1–41. https://doi.org/10.11646/zootaxa.3311.1.1

Bogusch P, Hadrava J (2018) European bees of the genera *Epeolus* Latreille, 1802 and *Triepeolus* Robertson, 1901 (Hymenoptera: Apidae: Nomadinae: Epeolini): taxonomy, identification key, distribution, and ecology. Zootaxa 4437(1): 1–60. https://doi.org/10.11646/zootaxa.4437.1.1

Burger PR (2010) On the presence of *Colletes hederae* Schmidt & Westrich and *C. brevigena* Noskiewicz (Hymenoptera, Colletidae) in Serbia. Osmia 4: 11–14. https://doi.org/10.47446/OSMIA4.3

Ćetković A, Plećaš M (2017) Dalje širenje alohtone azijske pčele u Evropi: prvi nalaz *Megachile sculpturalis* na Balkanu. XI Symposium of entomologists of Serbia, Goč (Serbia), 17–21 September 2017, Book of Abstracts, 82–83.

Dorchin A, López-Uribe MM, Praz CJ, Griswold T, Danforth BN (2018) Phylogeny, new generic-level classification, and historical biogeography of the *Eucera* complex (Hymenoptera: Apidae). Molecular Phylogenetics and Evolution 119: 81–92. https://doi.org/10.1016/j.ympev.2017.10.007

Drossart M, Gérard M (2020) Beyond the decline of wild bees: Optimizing conservation measures and bringing together the actors. Insects 11(9): e649. [23 pp] https://doi.org/10.3390/insects11090649

Gill RJ, Ramos-Rodriguez O, Raine NE (2012) Combined pesticide exposure severely affects individual- and colony-level traits in bees. Nature 491: 105–108. https://doi.org/10.1038/nature11585

González-Varo JP, Biesmeijer JC, Bommarco R, Potts SG, Schweiger O, Smith HG, Steffan-Dewenter I, Szentgyörgyi H, Woyciechowski M, Vilà M (2013) Combined effects of global change pressures on animal-mediated pollination. Trends in Ecology & Evolution 28(9): 524–530. https://doi.org/10.1016/j.tree.2013.05.008

Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347(6229): e1255957. https://doi.org/10.1126/science.1255957

Grozdanić S (1926) Žuta banatska pčela. Glasnik entomološkog društva 1(1): 1–16.

Grozdanić S (1928) Zimski sympaedium *Osmia bicorns* L. Glasnik Hrvatskoga prirodoslovnoga društva, Zagreb.

Grozdanić S (1930) Iz života pčela: primenjena biologija pčelinje zajednice: (*Apis mellifica* L.). Srpska manastirska štamparija, Sremski Karlovci.

Grozdanić S (1950a) Posmatranje na jednom naselju vrste *Halictus sexcinctus* F. Zbornik radova Instituta za Ekologiju i Biogeografiju, Srpska Akademija Nauka, Beograd 1: 171–174.

Grozdanić S (1950b) Pčele drvenarice (*Xylocopa violacea* i *Xylocopa valga*) Zbornik radova Instituta za Ekologiju i Biogeografiju, Srpska Akademija Nauka, Beograd 1.

Grozdanić S (1956) *Halictus marginatus* Brullé kao prelazna forma između solitarnih i socijalnih pčela. Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 9: 73–81.

Grozdanić S (1958a) Instinkt parenja pčele svilarice (*Colletes cunicularis*). Zbornik Matice Srpske – serija prirodnih nauka, Novi Sad 14: 82–85.

Grozdanić S (1958b) Pčelinja flora Vojvodine. Matica Srpska, Novi Sad 24: 7–23.

Grozdanić S (1960) Instinktivna delatnost solitarnih i socijalnih pčela (Apidae). Zbornik Matice Srpske – serija prirodnih nauka, Novi Sad 19: 5–14.

Grozdanić S (1961) Funkcija mirisnog organa medonosne pčele u raznim situacijama. Zbornik Matice Srpske – serija prirodnih nauka, Novi Sad 20: 24–33.

Grozdanić S (1965) Zbrinjavanje potomstva kod dvobojne Osmije (*Osmia bicolor*, Hymenoptera). Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 29: 100–106.

Grozdanić S (1966) Nova posmatranja na nekim vrstama roda *Halictus* (Hymenoptera). Prilog poznavanju filogenetskog postanka pčelinje porodice. Institut za biološka istraživanja – Zbornik radova Beograd 10(15): 2–21.

Grozdanić S (1968) Biologische Beobachtungen an einige Arten der Gattung *Ceratina* Latr. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 23: 113–123.

Grozdanić S (1969a) Neue Untersuchungen an *Eucera excisa* Mocs. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 24: 57–61.

Grozdanić S (1969b) Biološka ispitivanja na pčelama (Apoidea) – *Osmia rufohirta* Latr. Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 24: 63–71.

Grozdanić S (1969c) Zoološka ispitivanja na nekim vrstama *Halictus* (Hymenoptera). Glas SANU, CCLXXVI, Odeljenje Prirodno-matematičkih nauka, Beograd 32: 9–34.

Grozdanić S (1970) Poseta insekata cvetovima nekih vrsta graorica (*Vicia*, Leguminosae). Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 38: 1–83.

Grozdanić S (1971a) Biologische Untersuchungen an den Bienen – *Halictus sajoi* (Blüthgen) – (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 26: 151–157.

Grozdanić S (1971b) Filogenetski postanak pčelinje porodice. Beogradski izdavačko-grafički zavod. Beograd.

Grozdanić S (1972a) Biološka ispitivanja na pčelama *Halictus maculatus* Sm. i *Halictus asperulus* Pz. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 27: 71–83.

Grozdanić S (1972b) Biološka ispitivanja na pčelama (Apoidea, Hymenoptera) – *Halictus kessleri* Bramson. Srpska Akademija Nauka, Beograd 34: 41–54.

Grozdanić S (1974) Biologische untersuchungen an den bienen (Apoidea, Hymenoptera) – *Halictus kessleri* Bramson. Académie Serbe des Sciences et des Arts, Beograd.

Grozdanić S, Čolović S (1955a) Nekoliko momenata iz života njivskog bumbara (*Bombus agrorum* F.) u oblasti Fruške gore. Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 9: 107–111.

Grozdanić S, Čolović SM (1955b) Mlađa (*Corydalis cava*) i njeni posetioci: prilog proučavanjima pčelinje paše u oblasti Fruške gore. Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 8: 69–74.

Grozdanić S, Stevanović A (1959) Dalja ispitivanja na njivskom bumbaru (*Bombus agrorum*) u oblasti Fruške gore. Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 16: 44–56.

Grozdanić S, Stevanović A (1965) Posmatranja na kolonijama kosmate pčele *Anthophora parietina* F. Glas SANU, CCLXII, Odeljenje Prirodno-matematičkih nauka, Beograd, 27 pp.

Grozdanić S, Krunić M (1961) Eksperimentalna biološka ispitivanja na izolovanim maticama u dvomatičnom sistemu pčelarenja. Zbornik Matice Srpske – serija prirodnih nauka, Novi Sad 20: 104–117.

Grozdanić S, Baranov O (1963) "Disteleologija" bumbara i pčela u svetlosti reflektorne teorije I. P. Pavlova. Prilog proučavanju plastičnosti insekata. Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 24: 21–36.

Grozdanić S, Vasić Ž (1965a) Prilog poznavanju biologije dvobojne osmije (*Osmia bicolor* Schr., Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 20: 185–195.

Grozdanić S, Vasić Ž (1965b) Proučavanje instinktivnog života kosmatih pčela *Anthophora acervorum* L., *A. parietina* F. i *A. crinipes* Sm. (Apoidea, Hym.). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 20: 197–216.

Grozdanić S, Vasić Ž (1965c) Prilog poznavanju entomofilije u okolini Beograda. Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 20: 217–243.

Grozdanić S, Vasić Ž (1966a) Nova ispitivanja entomofilije u okolini Beograda. Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 21: 51–70.

Grozdanić S, Vasić Ž (1966b) Prilog biologiji solitarne pčele *Tetralonia lyncea* Mocs. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 21: 119–132.

Grozdanić S, Vasić Ž (1967a) *Tetralonia nana* Morawitz (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 22: 135–143.

Grozdanić S, Vasić Ž (1967b) *Eucera excisa* Mocsary (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 22: 145–152.

Grozdanić S, Vasić Ž (1968) Biološka posmatranja na *Systropha planidens* Gir. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 23: 169–178.

Grozdanić S, Vasić Ž (1970) Biološka ispitivanja na pčelama – *Halictus malachurus* K. – (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 25: 271–303.

Grozdanić S, Mučalica Z (1966) Posmatranje na solitarnim pčelama *Systropha planidens* Gir. i *Systropha curvicornis* Scop. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 21: 133–136.

Grozdanić S, Mučalica Z (1968a) Über den nestbauinstinkt bei *Megachile ericetorum* Lep. (Apoidea, Hymenoptera). Arhiv bioloških nauka 20(1–2): 7–8.

Grozdanić S, Mučalica Z (1968b) Biologische untersuchungen an den bienen (Apoidea, Hymenoptera) – *Halictus interruptus* Panz. Arhiv bioloških nauka 20(1–2): 9–10.

Grozdanić S, Mučalica Z (1969) Biologische Untersuchungen an *Anthophora crinipes* Sm. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 24: 137–141.

Grozdanić S, Mučalica Z (1973) Prilog poznavanju biologije pčela drvenarica: *Xylocopa violacea* L., *X. valga* Gerst. i *X. cyanescens* Br. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 28: 103–110.

Grozdanić S, Radivojević V (1972) Biološka ispitivanja na pčelama – *Osmia bidentata* Mor. i *Anthophora pubescens* F. – (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 27: 63–69.

Holzschuh A, Steffan-Dewenter I, Tscharntke T (2010) How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? Journal of Animal Ecology 79(2): 491–500. https://doi.org/10.1111/j.1365-2656.2009.01642.x

Holzschuh A, Dainese M, González-Varo PJ, Mudri-Stojnić S, Riedinger V, Rundlöf M, Scheper J, Wickens JB, Wickens VB, Bommarco R, Kleijn D, Potts SG, Roberts SPM, Smith HG, Vilà M, Vujić A, Steffan-Dewenter I (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscape across Europe. Ecology Letters 19(10): 1228–1236. https://doi.org/10.1111/ele.12657

IUCN (2021) The IUCN Red List of threatened species. https://www.iucnredlist.org/ [Accessed on 31 Mar 2021]

Kasparek M (2015) The cuckoo bees of the genus *Stelis* Panzer, 1806 in Europe, North Africa and the Middle East: A review and identification guide. Entomofauna, Supplementum 18, Maximilian Schwarz, Ansfelden, 144 pp.

Kasparek M (2017) Resin bees of the anthidiine genus *Trachusa*: Identification, taxonomy, distribution and biology of the Old World species. Entomofauna, Supplementum 21, Maximilian Schwarz, Ansfelden (Austria), 151 pp.

Kasparek M (2018) Taxonomic revision proves *Trachusa pubescens* (Morawitz, 1872) sensu lato to be a complex of allopatric and sympatric species in South-Eastern Europe and Western Asia (Hymenoptera, Apoidea, Anthidiini). ZooKeys 764: 111–144. https://doi.org/10.3897/zookeys.764.24581

Korlević A (1890) Prilozi fauni hrvatskih opnokrilaca (Hymenoptera). Glasnik Hrvatskoga naravoslovnoga društva, Zagreb 5: 189–250.

Krunić M (1959) Prelazne forme između solitarnih i socijalnih pčela, *Halictus malachurus*, *H. marginatus*, *H. scabiosae*. Zbornik Matice srpske – serija prirodnih nauka, Novi Sad 17: 102–110.

Krunić M (1967) Varijabilitet *Apis mellifica* L. u Jugoslaviji sa posebnim osvrtom na diferencijaciju populacija u Panonskoj niziji. PhD Thesis, University of Belgrade, Belgrade, Serbia, 64 pp.

Krunić M (1986) Medonosne pčele Panonske nizije. Pčesa '86., Bagrem beli 2: 67–71.

Krunić M (1994) Karakteristike populacija medonosne pčele (*Apis mellifera* L.) u Panonskoj niziji. Deliblatska peščara. Zbornik radova 6(1): 223–228.

Krunić M, Brajković M, Radenović B (1985) Oprašivanje lucerke pomoću solitarne pčele *Megachile rotundata* Fabr. u Jugoslaviji. Glasilo Društva za semenarstvo Jugoslavije 2(3): 72–74.

Krunić MD, Radović IT, Brajković MM (1988) A contribution to the knowledge of the fauna of the Megachilidae family (Hymenoptera) in Yugoslavia (I). Glas CCCLIII de l'Academie Serbe des Sciences et des Arts, Classe des sciences mathématiques et naturelles, Belgrade 52: 25–30.

Krunić M, Janković D, Stanišić T (1989) *Osmia cornuta* Latr. (Megachilidae, Hymenoptera) – Potential orchard pollinator. Archives of Biological Sciences 41(1–2): 33–37.

Krunić MD, Brajković MM, Mihajlović LjS (1991) Management and Utilization of *Osmia cornuta* Latr. for Orchard Pollination in Yugoslavia. Acta Horticulturae 288: 190–193. https://doi.org/10.17660/ActaHortic.1991.288.27

Krunić M, Brajković M, Tomanović Ž (1992a) Utilization of *Osmia cornuta* Latr. as an orchard polinator. Archives of Biological Sciences 44(3–4): 19–20.

Krunić M, Brajković M, Tomanović Ž (1992b) Application of *Megachile rotundata* Fab. for the alfalfa pollination in Yugoslavia. Archives of Biological Sciences 44(3–4): 21–22.

Krunić M, Brajković M, Mihajlović Lj, Tomanović Ž (1992c) *Megachile rotundata* Fab. (Hymenoptera: Megachilidae) populations and their accompanying fauna in Yugoslavia. In: Proceedings of the Fourth European Congress of Entomology and the XIII Internationale Symposium für die Entomofaunistik Mitteleuropas, Gödöllő (Hungary), 1–6 September 1991, 2: 527–531.

Krunic M, Terzic L, Brajkovic M, Nikodinovic R (1994) Honeybee (*Apis mellifera* L.) as an Indicator of Environmental Contamination in Parts of Serbia. International symposium and exhibition on environmental contamination in central and eastern Europe, Budapest (Hungary), 20–23 September 1994. Technical University of Budapest / Florida State University, Budapest, 37–38.

Krunić M, Pinzauti A, Felicioli A, Stanisavljević Lj (1995a) Further observations on *Osmia cornuta* Latr. and *O. rufa* L. as alternative fruit pollinators, domestication and utilization. Archives of Biological Sciences 47(1–2): 59–66.

Krunić M, Tasei JN, Pinzauti M (1995b) Biology and management of *Megachile rotundata* Fabricius under European conditions. Apicoltura 10: 71–79.

Krunić M, Stanisavljević Lj, Brajković M, Tomanović Ž (1996) Further investigations of accompanying fauna of orchard bees *Osmia cornuta* Latr. and *O. rufa* L. 7th International congress on the zoogeography and ecology of Greece and adjacent regions, Athens (Greece), 1–5 April 1996, Book of Abstracts, 37.

Krunić M, Stanisavljević Lj, Brajković M, Tomanović Ž (1997) Uticaj pesticida na gajene populacije lucerkine solitarne pčele *Megachile rotundata* (Fab). u Banatu (Srbija). Zaštita životne sredine gradova i prigradskih naselja. Eko-konferencija 97, Novi Sad (Serbia), 24–26 September 1997, Monografija 1: 319–322.

Krunić M, Stanisavljević Lj, Brajković M, Tomanović Ž (1998) The effect of cold-hardiness and the way of ending diapause in *Osmia cornuta* and *O. rufa* (Megachilidae, Hymenoptera) on their distribution in Europe. Archives of Biological Science 50(4): 33–34.

Krunić M, Stanisavljević Lj, Brajković M, Tomanović Ž (1999) Further investigations on the accompanying fauna of orchard bees *Osmia cornuta* Latr. and *O. rufa* (L.). Contributions to the Zoogeography and Ecology of the Eastern Mediterranean Region 1: 287–291.

Krunić M, Stanisavljević Lj, Brajković M, Tomanović Ž, Radović I (2001) Ecological Studies of *Osmia cornuta* (Latr.) (Hymenoptera, Megachilidae) Populations in Yugoslavia with Special Attention to their Diapause. Proceedings of the eight International Pollination Symposium – Pollination: Integrator of Crops and Native Plant Systems, Mosonmagyaróvár (Hungary), 10–14 July 2000, Acta Horticulturae 561: 297–301. https://doi.org/10.17660/ActaHortic.2001.561.45

Krunić M, Stanisavljević Lj, Pinzauti M, Felicoli (2005) The accompanying fauna of *Osmia cornuta* and *Osmia rufa* and effective measures of protection. Bulletin of Insectology 58(2): 141–152. http://www.bulletinofinsectology.org/pdfarticles/vol58-2005-141-152krunic.pdf

Krunić M, Stanisavljević Lj (2006a) Population management in the mason bee species *Osmia cornuta* (Latr.) and *Osmia rufa* (L.) (Hymenoptera, Megachilidae) for orchard pollination in Serbia. Entomologia generalis 29(1): 27–38. https://doi.org/10.1127/entom.gen/29/2006/27

Krunić M, Stanisavljević Lj (2006b) Supercooling points and diapause termination in overwintering adults of orchard bees *Osmia cornuta* and *O. rufa* (Hymenoptera: Megachilidae). Bulletin of Entomological Research 96(3): 323–326. https://doi.org/10.1079/BER2006423

Krunić M, Stanisavljević Lj (2006c) Augmentation of managed populations of *Osmia cornuta* (Latr.) and *O. rufa* (L.) (Hymenoptera: Megachilidae) in South-eastern Europe. European Journal of Entomology 103: 695–697. https://doi.org/10.14411/eje.2006.091

Krunić M, Stanisavljević Lj (2006d) The biology of European orchard bee *Osmia cornuta* (Latr.) (Hymenoptera: Megachilidae). Monograph Paper. Faculty of Biology, University of Belgrade, Belgrade.

Kuhlmann M, Ascher JS, Dathe HH, Ebmer AW, Hartmann P, Michez D, Müller A, Patiny S, Pauly A, Praz C, Rasmont P, Risch S, Scheuchl E, Schwarz M, Terzo M, Williams PH, Amiet F, Baldock D, Berg Ø, Bogusch P, Calabuig I, Cederberg B, Gogala A, Gusenleitner F, Josan Z, Madsen HB, Nilsson A, Ødegaard F, Ortiz-Sanchez J, Paukkunen J, Pawlikowski T, Quaranta M, Roberts SPM, Sáropataki M, Schwenninger H-R, Smit J, Söderman G, Tomozei B (2020) Checklist of the Western Palaearctic Bees (Hymenoptera: Apoidea: Anthophila). http://westpalbees.myspecies.info [Accessed on 02 Dec 2020]

Kulinčević J, Krunić M, Stanisavljević Lj (1997) Medonosne i druge vrste domestifikovanih pčela kao genetički, ekološki i privredni resurs Jugoslavije. Savremena poljoprivreda, Novi Sad 46(1–2): 257–268.

Lebedev A (1931) Prilog poznavanju jugoslovenskih pčela. Glasnik Jugoslovenskog entomološkog društva, Beograd, Jugoslavija 5–6(1–2): 39–48.

Maccagnani B, Burgio G, Stanisavljević Lj, Maini S (2007) *Osmia cornuta* management in pear orchards. Bulletin of Insectology 60(1): 77–82. http://www.bulletinofinsectology.org/pdfarticles/vol60-2007-077-082maccagnani.pdf

Markov Z (2017) Fauna insekata polinatora u Vojvodini: diverzitet, brojnost i procena vrednosti ekosistemske usluge polinacije. PhD Thesis, University of Novi Sad, Novi Sad, Serbia, 229 pp.

Markov Z, Nedeljković Z, Ricarte A, Vujić A, Jovičić S, Józan Z, Mudri-Stojnić S, Radenković S, Ćetković A (2016) Bee (Hymenoptera: Apoidea) and hoverfly (Diptera: Syrphidae) pollinators in Pannonian habitats of Serbia, with a description of a new *Eumerus* Meigen species (Syrphidae). Zootaxa 4154(1): 27–50. https://doi.org/10.11646/zootaxa.4154.1.2

Michez D, Rasmont P, Terzo M, Vereecken NJ (2019) Bees of Europe. Hymenoptera of Europe 1. NAP Editions, Paris, 547 pp.

Mihajlović Lj, Krunić MD, Richards KW (1989) Hyperparasitism of *Physocephala vittata* (F.) (Diptera, Conopidae) by *Habrocytus conopidarium* (Bouček) (Hymenoptera, Pteromalidae) a pest of *Megachile rotundata* (F.) (Hymenoptera, Megachilidae) in Yugoslavia. Journal of the Kansas Entomological Society 62(3): 418–420. https://www.jstor.org/stable/25085112

Mocsáry S (1897) Hymenoptera. A Magyar Birodalom Állatvilága. Fauna Regni Hungariae 1–113.

Mudri-Stojnić S (2018) Distribucija i dinamika populacija najznačajnijih grupa polinatora u agroekosistemima Vojvodine. PhD Thesis, University of Novi Sad, Novi Sad, Serbia, 196 pp.

Mudri-Stojnić S, Andrić A, Józan Z, Vujić A (2012) Pollinator diversity (Hymenoptera and Diptera) in semi-natural habitats in Serbia during summer. Archives of Biological Sciences 64(2): 777–786. https://doi.org/10.2298/ABS1202777S

Mučalica Z (1968) Posmatranja na jednoj koloniji *Halictus fulvipes* Klug. (Apoidea, Hymenoptera). Glasnik Prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 23: 179–183.

Mučalica Z (1984) Nove vrste Apoidea nađene u Jugoslaviji. Entomološki kolokvij kratki sadržaj referata, Jugoslovensko entomološko društvo, Zemun-Beograd.

Mučalica Z (1987a) Rasprostranjenje i životni ciklus vrste *Anthophora parietina* F. (Anthophorinae, Apoidea). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 42: 85–102.

Mučalica Z (1987b) Temperature smrzavanja razvojnih stupnjeva i adulta *Anthophora parietina* F. i *Anthophora crinipes* Sm. (Hymenoptera) i njihovih parazita. Ekologija Beograd 22(2): 77–82.

Mučalica Z (1990) Prilog poznavanju biologije *Anthophora crinipes* Sm. (Hymenoptera, Apoidea). Zbornik Matice Srpske – serija prirodnih nauka, Novi Sad 79: 41–55.

Mučalica Z (1997) Natural enemies of solitary bee populations of *Anthophora* with a special reference to *Anthophora crinipes* Sm. and *A. parietina* F. (Hymenoptera: Anthophoridae). Acta entomologica serbica 2 (1/2): 47–59.

Mučalica Z, Stanisavljević Lj (2005) Prilog poznavanju biologije gnežđenja solitarne pčele *Megachile willughbiella* (Kirby, 1802) (Hymenoptera: Apoidea: Megachilidae). In: Simpozijum entomologa Srbije, Bajina Bašta (Serbia), 25–29 September 2005, Zbornik plenarnih referata i rezimea, 35.

Müller A (2015) Palaearctic *Chelostoma* bees of the subgenus *Gyrodromella* (Megachilidae, Osmiini): biology, taxonomy and key to species. Zootaxa 3936(3): 408–420. https://doi.org/10.11646/zootaxa.3936.3.6

Müller A (2018) Palaearctic *Osmia* bees of the subgenus *Hoplosmia* (Megachilidae, Osmiini): biology, taxonomy and key to species. Zootaxa 4415(2): 297–329. https://doi.org/10.11646/zootaxa.4415.2.4

NBN (2020) NBN (The National Biodiversity Network) Atlas. https://nbnatlas.org/ [Accessed on 13 Dec 2020]

Nieto A, Roberts SPM, Kemp J, Rasmont P, Kuhlmann M, García Criado M, Biesmeijer JC, Bogusch P, Dathe HH, De la Rúa P, De Meulemeester T, Dehon M, Dewulf A, Ortiz-Sánchez FJ, Lhomme P, Pauly A, Potts SG, Praz C, Quaranta M, Radchenko VG, Scheuchl E, Smit J, Straka J, Terzo M, Tomozii B, Window J, Michez D (2014) European Red List of bees. Publication Office of the European Union, Luxembourg.

Notton DG, Dathe HH (2008) William Kirby's types of *Hylaeus* Fabricius (Hymenoptera, Colletidae) in the collection of the Natural History Museum, London. Journal of Natural History 42(27): 1861–1865. https://doi.org/10.1080/00222930802128512

Official Gazette of RS No. 5/2010, 47/2011, 32/2016 and 98/2016 (2021) Code on Declaration and Protection of Strictly Protected and Protected Wild Species of Plants, Animals and Fungi. https://www.pravno-informacioni-sistem.rs/SlGlasnikPortal/eli/rep/sgrs/ministarstva/pravilnik/2010/5/3/reg [Accessed on 31 Mar 2021]

Official Gazette of RS No. 48/19 (2021) Spatial Plan Republic of Serbia 2021–2035. http://media1.opstinamalocrnice.rs/2020/03/PROSTORNI-PLAN-REPUBLIKE-SRBIJE-OD-2021.-DO-2035.GODINE.pdf [Accessed on 31 Mar 2021]

Petrik A (1958) Entomofauna Deliblatske peščare. Rad Vojvođanskih muzeja, Novi Sad 7: 87–113.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25(6): 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Rafajlović A, Seleši Đ (1958) Iz entomološke zbirke prof. A. Tauberta (Subotica). Zbornik Matice Srpske – serija prirodnih nauka, Novi Sad 14: 86–142.

Rasmont P, Haubruge E [Eds] (2020) Atlas Hymenoptera. http://www.atlashymenoptera.net [Accessed on 13 Dec 2020]

Rasmont P, Franzén M, Lecocq T, Harpke A, Roberts SPM, Biesmeijer JC, Castro L, Cederberg B, Dvorák L, Fitzpatrick Ú, Gonseth Y, Haubruge E, Mahé G, Manino A, Michez D, Neumayer J, Ødegaard F, Paukkunen J, Pawlikowski T, Potts SG, Reemer M, Settele J, Straka J, Schweiger O (2015) Climatic Risk and Distribution Atlas of European Bumblebees. Biorisk 10 (Special Issue), Pensoft Publishers, Sofia, 246 pp.

Rasmont P, Devalez J, Pauly A, Michez D, Radchenko VG (2017) Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea). Annales de la Société entomologique de France (N.S.) 53(1): 17–32. https://doi.org/10.1080/00379271.2017.1307696

Schwarz M, Gusenleitner F, Mazzucco K (1999) Weitere Angaben zur Bienenfauna Österreichs. Vorstudie zu einer Gesamtbearbeitung der Bienen Österreichs III (Hymenoptera, Apidae). Entomofauna 20(31): 461–524.

Schwenninger HR (2015) Revision of the Western Palaearctic species of the *Andrena taraxaci*-group with description of four new species (Hymenoptera: Andrenidae). Stuttgarter Beiträge zur Naturkunde A, Neue Serie 8: 251–270.

Senapathi D, Carvalheiro LG, Biesmeijer JC, Dodson C-A, Evans RL, McKerchar M, Morton RD, Moss ED, Roberts SPM, Kunin WE, Potts SG (2015) The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. Proceedings of the Royal Society B: Biological Sciences 282(1806): e20150294. https://doi.org/10.1098/rspb.2015.0294

Smit J (2018) Identification key to the European species of the bee genus *Nomada* Scopoli, 1770 (Hymenoptera: Apidae), including 23 new species. Entomofauna, Monographie 3, Maximilian Schwarz, Ansfelden, 253 pp.

Stanisavljević Lj (1996) Uticaj prateće faune na populacije novodomestifikovanih solitarnih pčela *Osmia cornuta* Latr. i *O. rufa* L. (Megachilidae, Hymenoptera). Magister's thesis, University of Belgrade, Belgrade.

Stanisavljević Lj (2000) Idioekološka studija vrsta *Osmia cornuta* (Latr.) i *O. rufa* (L.) (Megachilidae, Hymenoptera) sa posebnim osvrtom na njihov status i značaj kao oprašivača biljaka. PhD Thesis, University of Belgrade, Belgrade, 304 pp.

Stanisavljević Lj (2009) Doprinos poznavanju umnožavanja gajenih populacija evropske pčele voćnjaka *Osmia cornuta* u Srbiji. In: XVII Naučno savetovanje sa međunarodnim učešćem "Kvalitet meda i selekcija medonosne pčele", Poljoprivredni fakultet, Zemun (Serbia), 7 February 2009, 41–50.

Stanisavljević Lj (2013) Megachilidae (Apoidea: Hymenoptera) of Mt. Fruška Gora. In: Šimić S (Ed.) Invertebrates (Invertebrata) of the Fruška Gora Mountain. III. Matica Srpska, Novi Sad, 165–179.

Stanisavljević Lj, Tomanović Ž (2006) Proizvodnja semena lucerke pomoću solitarne pčele *Megachile rotundata* (Fab.) (Hymenoptera: Megachilidae

) U Srbiji. Zbornik abstrakata Trećeg simpozijuma sekcije za oplemenjivanje organizama društva genetičara Srbije i četvrtog naučno-stručnog sipozijuma iz selekcije i semenarstva društva selekcionara i semenara Srbije, Zlatibor (Serbia), 16–20 May 2006, 167.

Stanisavljević Lj, Nedić N (2008) Uloga pčela (Hymenoptera: Apoidea) u oprašivanju voćaka. In: XXIII Savetovanje – Unapređenje proizvodnje voća i grožđa, Grocka (Serbia), 25 July 2008. Institut PKB Agroekonomik, Beograd, Zbornik naučnih radova 14(5): 89–96.

Stanisavljević Lj, Krunić M, Brajković M, Tomanović Ž (1997a) Synchronization of emergence of *Osmia cornuta* Latr. and *O. rufa* L. (Hymenoptera, Megachilidae) with their cleptoparasites *Chaetodactylus osmiae* (Acarina, Chaetodactylidae) and *Cacoxenus indagator* Loew (Diptera, Drosophilidae). In: Biodiversity and ecological problems of Balkan fauna, Sofia, 26–29 May 1997, Abstracts, 84.

Stanisavljević Lj, Krunić M, Brajković M, Tomanović Ž (1997b) Utvrđivanje optimalnog trajanja hibernacije kod solitarnih pčela *Osmia cornuta* Latr. i *O. rufa* L. (Hymenoptera, Megachilidae) u eksperimentalnim uslovima. In: Simpozijum entomologa Srbije, Goč, 2–4 October 1997, Zbornik rezimea, 53.

Stanisavljević Lj, Krunić M, Brajković M, Tomanović Ž (1999) Prateća fauna kod gajenih populacija solitarnih pčela *Osmia cornuta* Latr. i *O. rufa* L. (Hymenoptera, Megachilidae) u Srbiji. In: Simpozijum entomologa Srbije, Goč, 21–23 October 1999, Zbornik rezimea, 40.

Stanisavljević Lj, Krunić M, Brajković M, Tomanović Ž, Radović I (2000a) Ecological studies of *Osmia cornuta* (Latr.) (Hymenoptera, Megachilidae) populations in Yugoslavia with special attention to their diapause. The 8th International Pollination Symposium, Mosonmagyaróvár, 10–14 July 2000, Book of Abstracts, 43.

Stanisavljević Lj, Krunić M, Brajković M, Tomanović Ž, Radović I (2000b) The study of accompanying fauna of *Osmia cornuta* (Latr.) (Hymenoptera, Megachilidae) populations in Yugoslavia. In: The 8th International Pollination Symposium, Mosonmagarovar, 10–14 July 2000, Book of Abstracts, 44.

Stanisavljević Lj, Popović A, Ćetković A (2013) Razlike u morfologiji krila kod obojenih formi vrste *Osmia cornuta* (Hymenoptera: Megachilidae) pomoću geometrijske morfometrije. In: Simpozijum entomologa Srbije, Tara, 18–22 September, Zbornik rezimea, 64.

Stevanović A, Lazarov A (1977) Prilog poznavanju gnežđenja *Bombus muscorum* L. (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 32: 105–112.

Stevanović V, Stevanović B (1995) Osnovni klimatski, geološki i pedološki činioci biodiverziteta kopnenih ekosistema Jugoslavije. In: Stevanović V, Vasić V (Eds) Biodiverzitet Jugoslavije sa pregledom vrsta od međunarodnog značaja. Ecolobri, Biološki fakultet, Beograd, 75–115.

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology letters 8(8): 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Vasić Ž (1966) Nekoliko momenata iz života vrste *Halictus marginatus* Brullé (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 21: 103–118.

Vasić Ž (1967) *Halictus quadricinctus* F. et le probleme de la polygynie. Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 21: 181–187.

Vasić Ž (1968) Aktivnost vrste *Megachile sericans* Fonsc. na izgradnji gnezda (Apoidea, Hymenoptera). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 23: 201–210.

Vasić Ž (1970) Ritam dnevnog saobraćaja sa okolinom pomoćnih ženki *Halictus marginatus* Brullé (Hymenoptera, Halictidae). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 25: 337–348.

Vasić Ž (1979a) Poliginija kod *Halictus scabiosae* Rossi (Hymenoptera, Apoidea). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 34: 211–217.

Vasić Ž (1979b) Die Überwinterung einiger Arten der Gatung *Halictus* (Hymenoptera, Apoidea). Glasnik prirodnjačkog muzeja u Beogradu, serija B, biološke nauke 34: 219–221.

Vlatković B (1957) Pčele sjeničke kotline i visoravni Peštera i uslovi pčelarenja. Acta Veterinaria 7(2): 3–18.

Vorgin V (1918) Pregled Apidae hrvatske Slavonije i hrvatskog Primorja s obzirom na faunu Apida Dalmacije. Glasnik Hrvatskoga prirodoslovnoga društva, Zagreb 30: 1–4.

Vorgin V (1955) Prilog fauni Hymenoptera-Aculeata iz Jugoslavije. Zaštita bilja, Beograd 31 (Supplement): 1–72.

Winfree R, Aguilar R, Vázquez DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90(8): 2068–2076. https://doi.org/10.1890/08-1245.1

Zicha O [Ed.] (2020) BioLib (Biological Library). https://www.biolib.cz [Accessed on 13.12.2020]

Živojinović S (1950) Fauna insekata šumske Domene Majdampek (Entomološka monografija). Srpska Akademija Nauka, Posebna izdanja knjiga CLX Institut za Ekologiju i Biogeografiju, Beograd, 252 pp.

ZooKeys 1053: 107–144 (2021)
doi: 10.3897/zookeys.1053.64268
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

An annotated checklist of ladybeetle species (Coleoptera, Coccinellidae) of Portugal, including the Azores and Madeira Archipelagos

António Onofre Soares[1], Hugo Renato Calado[2], José Carlos Franco[3],
António Franquinho Aguiar[4], Miguel M. Andrade[5], Vera Zina[3],
Olga M.C.C. Ameixa[6], Isabel Borges[1], Alexandra Magro[7,8]

1 *Centre for Ecology, Evolution and Environmental Changes and Azorean Biodiversity Group, Faculty of Sciences and Technology, University of the Azores, 9500-321, Ponta Delgada, Portugal* **2** *Azorean Biodiversity Group, Faculty of Sciences and Technology, University of the Azores, 9501-801, Ponta Delgada, Portugal* **3** *Centro de Estudos Florestais (CEF), Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017, Lisboa, Portugal* **4** *Laboratório de Qualidade Agrícola, Caminho Municipal dos Caboucos, 61, 9135-372, Camacha, Madeira, Portugal* **5** *Rua das Virtudes, Barreiros Golden I, Bloco I, R/C B, 9000-645, Funchal, Madeira, Portugal* **6** *Centre for Environmental and Marine Studies and Department of Biology, University of Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal* **7** *Laboratoire Evolution et Diversité biologique, UMR 5174 CNRS, UPS, IRD, 118 rt de Narbonne Bt 4R1, 31062, Toulouse cedex 9, France* **8** *University of Toulouse – ENSFEA, 2 rt de Narbonne, Castanet-Tolosan, France*

Corresponding author: António Onofre Soares (antonio.oc.soares@uac.pt)

Academic editor: J. Poorani | Received 10 February 2021 | Accepted 24 April 2021 | Published 2 August 2021

http://zoobank.org/79A20426-803E-47D6-A5F9-65C696A2E386

Citation: Soares AO, Calado HR, Franco JC, Aguiar AF, Andrade MM, Zina V, Ameixa OMCC, Borges I, Magro A (2021) An annotated checklist of ladybeetle species (Coleoptera, Coccinellidae) of Portugal, including the Azores and Madeira Archipelagos. ZooKeys 1053: 107–144. https://doi.org/10.3897/zookeys.1053.64268

Abstract

A comprehensive annotated checklist of the ladybeetle species of Portugal, including the Azores and Madeira archipelagos, is presented. The Coccinellidae fauna comprises a total of 101 species: 83 from the Mainland, 39 from Madeira, and 32 from the Azores. The listed species are distributed among 2 subfamilies and 13 tribes: within the subfamily Microweiseinae, Madeirodulini (1 species), Serangiini (2 species), and within the subfamily Coccinellinae, Azyini (1 species), Chilocorini (4 species), Coccidulini (7 species), Coccinellini (30 species), Epilachnini (4 species), Hyperaspidini (7 species), Noviini (2 species), Platynaspini (1 species), Scymnini (37 species), Stethorini (3 species), and Sticholotidini (2 species). The Portuguese fauna comprises 10 exotic species: 5 present in the Mainland, 7 in Madeira, and 6 in the

Azores. *Harmonia axyridis* (Pallas, 1773) from Madeira, *Propylea quatuordecimpunctata* (Linnaeus, 1758) from the Azores, *Delphastus catalinae* (Horn, 1895) from the Azores and Madeira, *Nephus* (*Geminosipho*) *reunioni* (Fürsch, 1974) and *Nephus* (*Nephus*) *voeltzkowi* Weise, 1910 from Madeira and *Microserangium* sp. from the Mainland, are reported for the first time. Some species are considered doubtful records, as explained in the text. These results were obtained by compiling information on the available literature regarding ladybeetle species on the Portuguese mainland and insular territories, and original data.

Keywords
Azores, Coccinellidae, Madeira, Palearctic Region, Portugal

Introduction

The book by Raimundo and Alves (1986) was the last review of the coccinellid (Coleoptera: Coccinellidae) fauna of Portugal. Since then, several studies on Portuguese ladybeetles have been published, including catalogues (e.g. Fürsch 1987; Kovář 2007; Eizaguirre 2015), new individual records (e.g., Serrano and Borges 1987; Raimundo 1992; Soares et al. 2003a, b; Raimundo et al. 2006; Soares et al. 2006), and studies on ladybeetle communities in agricultural ecosystems (e.g. Magro et al. 1994; Carlos et al. 2005; Silva et al. 2006; Silva et al. 2010; Benhadi-Marin et al. 2011; Santos et al. 2012), among others. However, the information is scattered and therefore difficult to analyse.

Ladybeetles comprise about 375 genera (Nedvěd 2020) and nearly 6000 species (Vandenberg 2002), distributed worldwide. They are characterised by a high diversity as regards to their life history, development, distribution, habitat, and food relationships (see Hodek et al. 2012 for review). This family of insects is very charismatic, in particular because most species are predators recognised as useful natural enemies of pests, including aphids (Aphidoidea), scale insects (Coccoidea), whiteflies (Aleyrodoidea) or mites (Acari). Largely used in biological control programmes, ladybeetles render important ecosystem services to agriculture and silviculture (Ameixa et al. 2018). In fact, the first successful case of classical biological control dates back to the late 1800s, when *Novius* (=*Rodolia*) *cardinalis* (Mulsant) was introduced in California from Australia to control the cottony cushion scale, *Icerya purchasi* Maskell, also of Australian origin (Caltagirone et al. 1989). The introduction of this ladybeetle in Portugal in 1897 was the first case of classical biological control in Europe (Amaro 1994). However, ladybeetles also have other food habits and a few species are herbivores causing heavy crop damages in Asia, America and Africa (Barrigossi et al. 2003; Beyene et al. 2007; Das et al. 2012).

Scientific evidence shows that human activities have huge negative impacts on biodiversity (e.g., Vitousek et al. 1997; Newbold et al. 2015; Jung et al. 2019). The structure and composition of insect communities have been particularly affected by these activities, with ecological domino effects along trophic chains (Dyer et al. 2003). Consequently, action in favour of insect conservation and recovery has been claimed (e.g., Harvey et al. 2020). Ladybeetle communities are no exception. For instance, several studies report long-term variations in the composition of ladybeetle communities following the introduction of *Harmonia axyridis* Pallas around the world (Roy et al. 2016). Honěk et al. (2014, 2017) included agricultural intensification, habitat (particularly urbanization) and climate changes as additional causes for ladybeetle community changes. In this context, and because it is important that each country should have an updated list of its fauna, from which we can detect changes in biodiversity and implement conservation and recovery programmes, we herein address the issue of the coccinellid fauna of Portugal, within the research project AZORESBIOPORTAL–PORBIOTA (ACORES-01-0145-FEDER-000072).

Based on the literature and unpublished data, we present an updated, comprehensive checklist of ladybeetles of Portugal, including the Azores and Madeira Archipelagos.

Materials and methods

In this work we follow the suprageneric classification of Coccinellidae proposed by Che et al. (2021). This recent revised classification recognises three subfamilies: Microweiseinae, Monocoryninae stat. nov., and Coccinellinae. It should be noted that the tribe Coccidulini *sensu* Seago et al. (2011), which comprises several species for Portugal, was redefined by Che et al. (2021) in which Scymnini and Stethorini were split independently.

Current taxonomic affiliation follows Kovář (2007). Species cited for Portugal after Kovář (2007) or those for which the taxonomic position has changed as a result of more recent studies, are indicated here following more recent publications.

The species are listed in alphabetic order according to their valid tribe and genera. Species of the genera *Nephus* and *Scymnus* are listed under the respective subgenera because they are particularly important for their identification. Synonymy is mentioned but is restricted to the original name.

For each species, we specify the regions where the species were recorded (Mainland, Azores and/or Madeira), under "Distribution" and we provide brief notes about the status of the species in each region, possible taxonomic incongruences, and the current biogeographical (limits as in Löbl and Smetana 2007) distribution under "Comments". New records are marked with a black spot (•), doubtful records with an asterisk (*) and exotic species with a dollar ($). The bibliographic references associated with each species recorded for Portugal are presented in Table 1.

Table 1. Checklist (by alphabetic order) and bibliographic references of Coccinellidae species recorded for Portugal, including the Azores and Madeira.

Species	References
Adalia bipunctata (Linnaeus, 1758)	12, 27, 29, 30, 32, 39, 42, 47, 50, 52, 53, 55, 59, 60, 64, 67, 68, 74, 75, 77
Adalia decempunctata (Linnaeus, 1758)	3, 4, 5, 9, 12, 14, 26, 30, 32, 39, 42, 47, 50, 52, 53, 55, 56, 57, 59, 60, 64, 65, 67, 68, 72, 73, 74, 75, 77, 82
Adalia testudinea (Wollaston, 1854)	1, 2, 8, 14, 29, 67, 68
Anatis ocellata (Linnaeus, 1758)	12, 67, 77
Anisosticta novemdecimpunctata (Linnaeus, 1758)	13, 12, 39, 67, 77
Calvia decemguttata (Linnaeus, 1767)	39, 67, 77

Species	References
Calvia quatuordecimguttata (Linnaeus, 1758)	12, 39, 77
Calvia quindecimguttata (Fabricius, 1777)	39
Ceratomegilla notata (Laicharting, 1781)	12, 39, 67
Ceratomegilla undecimnotata (Schneider, 1792)	12, 39, 55, 67, 77
Chilocorus bipustulatus (Linnaeus, 1758)	9, 12, 14, 26, 27, 29, 30, 39, 47, 50, 52, 53, 55, 59, 60, 64, 65, 66, 67, 68, 72, 75
Chnootriba elaterii (Rossi, 1794)	31, 39, 67, 77
Clitostethus arcuatus (Rossi, 1794)	1, 2, 8, 20, 29, 30, 39, 40, 47, 50, 52, 53, 55, 56, 57, 59, 64, 67, 68, 73, 75
Coccidula rufa (Herbst, 1783)	18, 39, 77
Coccidula scutellata (Herbst, 1783)	12, 39, 77
Coccinella genistae Wollaston, 1854	1, 2, 8, 14, 17, 29, 37, 42, 52, 67, 68
Coccinella septempunctata Linnaeus, 1758	9, 30, 32, 35, 39, 43, 47, 50, 55, 56, 57, 59, 60, 64, 66, 72, 73, 74, 75, 77
Coccinella undecimpunctata Linnaeus, 1758	3, 4, 5, 9, 30, 32, 35, 39, 45, 55, 59, 67, 77, 82
Coccinula quatuordecimpustulata (Linnaeus, 1758)	1, 2, 39
Coccinula sinuatomarginata (Faldermann, 1837)	29, 67
Coelopterus salinus Mulsant & Rey, 1852	67
Cryptolaemus montrouzieri Mulsant, 1853	39, 47, 50, 52, 53, 64
Delphastus catalinae (Horn, 1895)	Present study
Eriopis connexa (Germar, 1824)	44, 55, 59
Exochomus quadripustulatus (Linnaeus, 1758)	19, 39, 47, 50, 52, 53, 64, 66, 67, 72, 75
Halyzia sedecimguttata (Linnaeus, 1758)	12, 19, 39, 67, 77
Harmonia axyridis (Pallas, 1773)	Present study
Harmonia quadripunctata (Pontoppidan, 1763)	29, 30, 39, 40, 42, 47, 50, 64, 67, 68, 77
Henosepilachna angusticollis (Reiche, 1862)	77
Henosepilachna argus (Geoffrey, 1785)	12, 39, 67
Hippodamia variegata (Goeze, 1777)	1, 2, 8, 11, 14, 21, 23, 25, 29, 32, 36, 39, 42, 50, 52, 53, 55, 56, 57, 64, 67, 68, 72, 75, 77
Hyperaspis concolor (Suffrian, 1843)	67, 77
Hyperaspis duvergeri Fürsch, 1985	70
Hyperaspis hoffmannseggi (Gravenhorst, 1807)	39
Hyperaspis illecebrosa Mulsant, 1846	16, 67, 77
Hyperaspis pantherina Fürsch, 1975	58, 61, 68, 69
Hyperaspis reppensis (Herbst, 1783)	12, 47, 50, 52, 53, 60, 64, 66
Hyperaspis stigma (Olivier, 1808)	67
Iberorhyzobius rondensis (Eizaguirre, 2004)	62, 63, 74, 77, 78, 79
Madeirodula atlantica Szawaryn, Větrovec & Tomaszewska, 2020	85
Microserangium sp.	Present study
Myrrha octodecimguttata (Linnaeus, 1758)	6, 8, 14, 20, 29, 36, 38, 39, 42, 55, 59, 65, 67, 68,75, 77
Myzia oblongoguttata (Linnaeus, 1758)	39, 66
Nephus (Bipunctatus) bisignatus (Boheman, 1850)	38, 40, 49, 50, 52, 53, 55, 59, 64, 67, 72, 75, 77
Nephus (Bipunctatus) conjunctus (Wollaston, 1870)	48, 49, 50, 52, 53, 64, 67, 68, 77
Nephus (Bipunctatus) peyerimhoffi (Sicard, 1923)	49, 50, 64, 67, 77
Nephus (Geminosipho) reunioni (Fürsch, 1974)	47, 48, 49, 50, 52, 53, 64, 67, 71, 77
Nephus (Nephus) binotatus (Brisout de Barneville, 1863)	39, 47, 52, 53, 64
Nephus (Nephus) flavopictus (Wollaston, 1854)	1, 2, 8, 14, 15, 17, 21, 22, 25, 30, 26, 27, 29, 32, 35, 40, 41, 42, 46, 55, 57, 59, 67, 68, 83
Nephus (Nephus) quadrimaculatus (Herbst, 1783)	39, 64
Nephus (Nephus) schatzmayri Canepari & Tedeschi, 1977	67, 70
Nephus (Nephus) ulbrichi Fürsch, 1977	49, 52, 53, 64
Nephus (Nephus) voeltzkowi Weise, 1910	84
Nephus (Sidis) depressiusculus (Wollaston, 1867)	46, 68
Nephus (Sidis) hiekei (Fürsch, 1965)	49, 50, 52, 53, 55, 56, 57, 64, 72, 77
Nephus (Sidis) pooti Fürsch, 1999	77
Novius cardinalis (Mulsant, 1850)	30, 32, 35, 39, 42, 44, 45, 46, 47, 49, 50, 52, 53, 54, 55, 60, 64, 68 73, 67, 82
Novius cruentatus Mulsant, 1846	67
Oenopia conglobata (Linnaeus, 1758)	12, 39, 47, 50, 52, 53, 59, 63, 65, 73, 74, 76
Oenopia doublieri (Mulsant, 1846)	12, 39, 50, 52, 53, 64, 67, 72, 77, 81

Species	References
Oenopia lyncea (Olivier, 1808)	12, 39, 67
Parexochomus nigripennis (Erichson, 1843)	67
Parexochomus nigromaculatus (Goeze, 1777)	12, 39, 47, 50, 52, 53, 60, 64, 66, 72, 74, 75
Pharoscymnus decemplagiatus (Wollaston, 1857)	2, 7, 14, 29, 32, 42, 46, 55, 67, 68, 82
Platynaspis luteorubra (Goeze, 1777)	12, 39, 47, 50, 52, 53, 64, 72, 75
Propylea quatuordecimpunctata (Linnaeus, 1758)	11, 39, 47, 50, 52, 53, 60, 64, 67, 72, 73, 75
Psyllobora vigintiduopunctata (Linnaeus, 1758)	12, 39, 47, 50, 52, 53, 67, 77
Rhyzobius chrysomeloides (Herbst, 1792)	10, 12, 36, 39, 47, 50, 52, 53, 55, 56, 57, 64, 65, 66, 67, 68, 72, 73, 74, 75, 82
Rhyzobius forestieri (Mulsant, 1853)	80
Rhyzobius litura (Fabricius, 1787)	1, 2, 3, 4, 5, 7, 8, 9, 11, 14, 25, 26, 27, 29, 30, 32, 35, 36, 39, 42, 47, 50, 52, 53 55, 56, 57, 64, 65, 67, 68, 72, 73, 75
Rhyzobius lophanthae (Blaisdell, 1892)	36, 39, 42, 44, 46, 47, 50, 51, 52, 53, 55, 56, 59, 64, 65, 66, 67, 68, 72
Scymniscus fuerschi (Plaza, 1981)	50, 52, 64
Scymniscus helgae (Fürsch, 1965)	38, 39, 40, 55, 59, 72, 74, 75
Scymniscus semirufus (Weise, 1885)	39, 47, 48, 64, 72, 77
Scymnus (Mimopullus) epistemoides Wollaston, 1867	10, 14, 29, 30, 40, 66, 67
Scymnus (Mimopullus) limnichoides Wollaston, 1854	1, 2, 8, 14,.30, 40, 51, 67, 68
Scymnus (Mimopullus) marinus (Mulsant, 1850)	1, 2, 8, 12, 14, 30, 39, 40, 47, 50, 51, 52, 53, 64, 65, 68, 74, 75
Scymnus (Neopullus) ater Kugelann, 1794	13, 34, 39, 77
Scymnus (Neopullus) haemorrhoidalis Herbst, 1797	2, 8, 14, 40, 41, 55, 67, 68.
Scymnus (Neopullus) limbatus Stephens, 1832	27, 29, 67, 68
Scymnus (Parapullus) abietis (Paykull, 1798)	2, 11, 39, 56, 57, 68, 77
Scymnus (Pullus) auritus Thunberg, 1795	12, 39, 49, 50, 52, 53, 64, 67, 77
Scymnus (Pullus) subvillosus (Goeze, 1777)	1, 2, 8, 9, 11, 12, 14, 26, 29, 32, 34, 35, 39, 43, 47, 50, 52, 53, 55, 59, 64, 65, 66, 67, 68, 72, 74, 75, 82
Scymnus (Pullus) suturalis Thunberg, 1795	24, 12, 27, 29, 30, 38, 39, 40, 46, 47, 50, 51, 52, 53, 55, 59, 73, 66, 67, 68, 82
Scymnus (Scymnus) apetzi Mulsant, 1846	1, 2, 4, 8, 14, 25, 27, 29, 32, 39, 40, 42, 46, 47, 50, 52, 53, 55, 64, 67, 68, 72, 74, 75
Scymnus (Scymnus) bivulnerus Baudi di Selve, 1894	39, 77
Scymnus (Scymnus) frontalis (Fabricius, 1787)	12, 39, 60, 64, 67, 75, 77
Scymnus (Scymnus) interruptus (Goeze, 1777)	5, 11, 32, 35, 39, 40, 43, 47, 50, 52, 53, 55, 57, 60, 64, 66, 67, 72, 74, 75, 82
Scymnus (Scymnus) laetificus Weise, 1879	77
Scymnus (Scymnus) nubilus Mulsant, 1850	2, 20, 30, 38, 39, 40, 43, 50, 52, 53, 55, 56, 57, 64, 65, 67, 68, 82
Scymnus (Scymnus) rubromaculatus (Goeze, 1777)	27, 29, 30, 32, 40, 55, 67, 68
Scymnus (Scymnus) rufipes (Fabricius, 1798)	12, 39, 47, 54, 52, 53, 60, 64, 72, 67, 77
Scymnus (Scymnus) schmidti Fürsch, 1958	40, 55, 77
Scymnus (Scymnus) suffrianioides Sahlberg, 1913	33, 39, 64, 72
Sospita vigintiguttata (Linnaeus, 1758)	12, 39, 77
Stethorus pusillus (Herbst, 1797)	9, 19, 20, 26, 32, 35, 39, 40, 47, 50, 52, 53, 55, 59, 60, 64, 72, 73, 74, 75, 82
Stethorus tenerifensis Fürsch, 1987	42, 51, 67
Stethorus wollastoni Kapur, 1948	1, 2, 7, 8, 14, 15, 22, 28, 29, 32, 56, 57, 67, 68
Subcoccinella vigintiquatuorpunctata (Linnaeus, 1758)	12, 39, 50, 52, 53, 67, 72
Tytthaspis sedecimpunctata (Linnaeus, 1761)	12, 39, 52, 53, 67, 73, 75
Vibidia duodecimguttata (Poda von Neuhaus, 1761)	12, 39, 67, 75

1. Wollaston (1854), 2. Wollaston (1857), 3. Drouet (1859), 4. Drouet (1861), 5. Tarnier (1861), 6. Wollaston (1862), 7. Wollaston (1864), 8. Wollaston (1865), 9. Crotch (1867), 10. Wollaston (1867), 11. Hayden (1870), 12. Oliveira (1894), 13. Barros (1896), 14. Fauvel (1897), 15. Cameron (1901), 16. Barros (1913), 17. Winkler (1924-1932), 18. Barros (1926), 19. De la Fuente (1928), 20. De la Fuente (1929), 21. Uyttenboogaart (1930 in Fürsch 1966), 22. Korschefky (1931), 23. Alluaud (1935), 24. Liebmann, (1939), 25. Jansson (1940), 26. Méquignon (1942), 27. Uyttenboogaart (1947), 28. Kapur (1949), 29. Lundblad (1958), 30. Bielawski (1963), 31. Fürsch (1964), 32. Fürsch (1966), 33. Capra and Fürsch (1967), 34. Gourreau (1974), 35. Serrano (1982), 36. Israelson (1984), 37. Mitter (1984), 38. Gillerfors (1986), 39. Raimundo and Alves (1986), 40. Fürsch (1987), 41. Serrano and Borges (1987), 42. Erber and Hinterseher (1988), 43. Borges and Serrano (1989), 44. Borges (1990a), 45. Borges (1990b), 46. Erber (1990), 47. Franco et al. (1992), 48. Magro et al. (1992), 49. Raimundo (1992), 50. Magro et al. (1994), 51. Erber and Aguiar (1996), 52. Magro et al. (1999), 53. Magro and Hemptinne (1999), 54. Soares et al. (1999), 55. Soares et al. (2003a), 56. Soares et al. (2003b), 57. Soares et al. (2003c), 58. Félix et al. (2004), 59. Borges et al. (2005b), 60. Carlos et al. (2005), 61. Félix et al. (2005), 62. Branco et al. (2006), 63. Raimundo et al. (2006), 64. Silva et al. (2006), 65. Soares et al. (2006), 66. Gonçalves et al. (2007), 67. Kovář (2007), 68. Boieiro et al. (2008), 69. Félix et al. (2008), 70. Canepari (2009), 71. Borges et al. (2010), 72. Santos et al. (2010), 73. Silva et al. (2010), 74. Benhadi-Marin et al. (2011), 75. Santos et al. (2012), 76. Tavares et al. (2014), 77. Eizaguirre (2015), 78. Tavares et al. (2015a), 79. Tavares et al. (2015b), 80. Borges et al. (2017), 81. Borges et al. (2018), 82. Calado (2018), 83. Romanowski et al. (2019), 84. Magro et al. (2020b), 85. Szawaryn et al. (2020).

Results

Subfamily MICROWEISEINAE

Tribe MADEIRODULINI

***Madeirodula atlantica* Szawaryn, Větrovec and Tomaszewska 2020 (following Szawaryn et al. 2020)**

Distribution. Madeira.

Comments. This is a recently described new tribe, genus and species, endemic to Madeira.

Tribe SERANGIINI

$^{\$}$*Delphastus catalinae* (Horn, 1895)

= *Cryptognatha catalinae* Horn 1895

Distribution. Madeira• and Azores•.

Comments. A native species of Nearctic and Neotropical regions, currently established in the Palearctic region following introductions in biological control programs. Its presence in the Azores probably originated from deliberate releases for biological control of whiteflies. A large population was first recorded by Isabel Borges, from kales in a vegetable garden (S. Miguel Island 37°48'02"N, 25°36'42"W), August 2018, where both adults and larvae were abundant. In Madeira, Délia Cravo collected in October 2006 from *Musa acuminata* Colla (Funchal 32°39'26"N, 16°55'56"W) and José Jesus collected in September 2020 on *Citrus reticulata* Blanco, (Santana 32°48'27"N, 16°53'13"W). First records for Portugal.

$^{\$}$*Microserangium* sp.

= *Microserangium* Miyatake, 1961

Distribution. Mainland•.

Comments. Oriental origin. First observations by Vera Zina, in 2012, Algarve. A few individuals were collected in August 2012, and May, July and November 2013 from the canopy of citrus (Carocha, Boliqueime 37°08'55.9"N, 8°08'11.6"W; Estibeira, Boliqueime 37°07'27"N, 8°07'16"W; Benafim 37°14'17"N, 8°06'36"W). First record for Portugal.

Subfamily COCCINELLINAE

Tribe AZYINI

$^{\$}$ *Cryptolaemus montrouzieri* Mulsant, 1853

Distribution. Mainland.

Comments. Currently established in Palearctic, Afrotropical, Nearctic and Neotropical regions. This exotic species of Australian origin, used around the world for biological control since the 19th century, was introduced from France in the early 20th century for the biological control of the citrus mealybug, *Planococcus citri* (Risso) (Franco et al. 1994), but the first record in Europe was in Italy, 1908 (Roy and Migeon 2010).

Tribe CHILOCORINI

***Chilocorus bipustulatus* (Linnaeus, 1758)**

= *Coccinella bipustulata* Linnaeus, 1758

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic, Afrotropical, and Nearctic distribution.

***Exochomus quadripustulatus* (Linnaeus, 1758)**

= *Coccinella quadripustulata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic and Nearctic distribution.

***Parexochomus nigripennis* (Erichson, 1843)**

= *Chilocorus nigripennis* Erichson, 1843

Distribution. Mainland.

Comments. Palearctic and Afrotropical distribution.

***Parexochomus nigromaculatus* (Goeze, 1777)**

= *Coccinella nigromaculata* Goeze, 1777

Distribution. Mainland

Comments. Palearctic distribution.

Tribe COCCIDULINI

Coccidula rufa (Herbst, 1783)

= *Dermestes rufus* Herbst, 1783

Distribution. Mainland.

Comments. Palearctic distribution.

Coccidula scutellata (Herbst, 1783)

= *Chrysomela scutellata* Herbst, 1783

Distribution. Mainland.

Comments. Palearctic distribution.

Iberorhyzobius rondensis (Eizaguirre, 2004)

= *Coccidula rondensis* Eizaguirre, 2004

Distribution. Mainland.

Comments. This is an endemic species of the Iberian Peninsula, associated with maritime pine forests, and is a specialist predator of the maritime pine bast scale, *Matsucoccus feytaudi* Ducasse (Tavares et al. 2014; Tavares et al. 2015a; Tavares et al. 2015b). Adults and mostly larvae were shown to be attracted by the sex pheromone of their prey (Branco et al. 2006).

Rhyzobius chrysomeloides (Herbst, 1792)

= *Strongylus chrysomeloides* Herbst, 1792

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic distribution.

$ *Rhyzobius forestieri* (Mulsant, 1853)

= *Platyomus forestieri* Mulsant, 1853

Distribution. Azores.

Comments. Palaearctic, Nearctic and Australian distribution. This exotic species of Australian origin was introduced in Europe in the 1980´s for the biological control of scale insects (Coccoidea), and became established in different countries, including Italy, France, Greece and Albania (Roy and Migeon 2010; Soares et al. 2018). The first record in Europe was in Italy in 1982 (Roy and Migeon 2010). It was recently recorded in the Azores (Borges et al. 2017).

***Rhyzobius litura* (Fabricius, 1787)**

= *Nitidula litura* Fabricius, 1787

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic distribution.

$^{\$}$ ***Rhyzobius lophanthae* (Blaisdell, 1892)**

= *Scymnus lophanthae* Blaisdell, 1892

Distribution. Mainland, Madeira and Azores.

Comments. Palaearctic, Afrotropical, Nearctic, Neotropical, and Australian distribution. This species, native to Queensland, Australia (Tomaszewska 2010) was first introduced in Europe (Italy), in 1908, for the biological control of armoured scale insects (Coccoidea: Diaspididae) and imported to Portugal in the 1930's and 1980's (Roy and Migeon 2010).

Tribe COCCINELLINI

***Adalia bipunctata* (Linnaeus, 1758)**

= *Coccinella bipunctata* Linnaeus, 1758

Distribution. Mainland, Madeira and Azores.

Comments. Worldwide distributed (Palaearctic, Afrotropical, Australian, Nearctic and Neotropical regions).

***Adalia decempunctata* (Linnaeus, 1758)**

= *Coccinella decempunctata* Linnaeus, 1758

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic distribution.

Adalia testudinea (*Wollaston, 1854*)

= *Coccinella testudinea* Wollaston, 1854

Distribution. Madeira.

Comments. Macaronesian endemic species.

Anatis ocellata (Linnaeus, 1758)

=*Coccinella ocellata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic distribution.

Anisosticta novemdecimpunctata (Linnaeus, 1758)

= *Coccinella novemdecimpunctata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic distribution.

Calvia decemguttata (Linnaeus, 1767)

= *Coccinella decemguttata* Linnaeus, 1767

Distribution. Mainland.

Comments. Palearctic distribution.

Calvia quatuordecimguttata (Linnaeus, 1758)

= *Coccinella quatuordecimguttata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic, Nearctic and Oriental distribution.

Calvia quindecimguttata (Fabricius, 1777)

= *Coccinella quindecimguttata* Fabricius, 1777

Distribution. Mainland.

Comments. Palearctic distribution.

Ceratomegilla notata (Laicharting, 1781)

= *Coccinella notata* Laicharting, 1781

Distribution. Mainland.

Comments. Palearctic distribution.

Ceratomegilla undecimnotata (Schneider, 1792)

= *Coccinella undecimnotata* Schneider, 1792

Distribution. Mainland and Azores.

Comments. Palearctic distribution.

Coccinella genistae Wollaston, 1854

Distribution. Madeira.

Comments. Macaronesian endemic species.

Coccinella septempunctata Linnaeus, 1758

Distribution. Mainland, Madeira and Azores*.

Comments. Palearctic, Afrotropical, Nearctic and Oriental distribution. Relatively important species in cereal crops in the Azores, especially in the first half of the 20th century, having eventually disappeared when these crops became scarce (Soares et al. 2008; Soares et al. 2017). The taxonomic status of *C. algerica* has been under discussion because of its morphological similarities to the geographically widespread *Coccinella septempunctata* L. Although Lecompte et al. (2016) revealed a high genetic structuring pattern, with an Algerian rear-edge population highly differentiated, consistent with their morphological distinctiveness, a recent study by Romanowski et al. (2019) demonstrated that individuals from Canarian populations, usually classified as *C. algerica*, can hybridise with individuals from European populations of *C. septempunctata* giving rise to fertile F1 descendants. These authors therefore propose to synonymise *C. algerica* with *C. septempunctata* but, taking into account the morphological peculiarities of the North African and the Canarian populations, they consider that this species is a subspecies: *Coccinella septempunctata algerica* Kovář, 1977.

Coccinella undecimpunctata Linnaeus, 1758

Distribution. Mainland and Azores.

Comments. Palaeartic, Australian and Nearctic distribution. In the Azores, it is a threatened species due to anthropogenic pressures on the coastal areas (Soares et al. 2017).

Coccinula quatuordecimpustulata (Linnaeus, 1758)

= *Coccinella quatuordecimpustulata* Linnaeus, 1758

Distribution. Mainland and Madeira*.

Comments. Palearctic and Afrotropical distribution. Although previously recorded in the Madeira archipelago, there are doubts regarding its present occurrence. It might have been introduced but did not establish (Franquinho Aguiar, personal communication).

Coccinula sinuatomarginata (Faldermann, 1837)

= *Coccinella sinuatomarginata* Faldermann, 1837

Distribution. Mainland and Madeira*.

Comments. Palearctic distribution. Although previously recorded for the Madeira archipelago, there are doubts as to its present occurrence. It might have been introduced but did not establish (Franquinho Aguiar, personal communication).

$^{\$}$ *Eriopis connexa* (Germar, 1824)

= *Coccinella connexa* Germar, 1824

Distribution. Azores*.

Comments. Of Neotropical origin where it is very common. Although previously reported for the Azores, it did not become established (*fide* A. O. Soares, after intensive surveys).

Halyzia sedecimguttata (Linnaeus, 1758)

= *Coccinella sedecimguttata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic distribution.

$ *Harmonia axyridis* (Pallas, 1773)

= *Coccinella axyridis* Pallas, 1773

Distribution. Madeira•.

Comments. Worldwide distribution. Several specimens (adults, larvae and pupae) collected by Miguel M. Andrade, in September 2019, from *Enterolobium* sp. (Funchal 32°38'39"N, 16°55'31"W), Graça Freitas and Franquinho Aguiar, collected in September and October 2020, from *Annona cherimola* Mill. (Funchal 32°39'47"N, 16°53'41"W). *Harmonia axyridis* is the most invasive insect of the world (Roy et al. 2016). However, despite deliberate attempts to introduce the species in the Azores, she has not became established. The apparent failure can be explained by a combination of resource availability and inter-specific competition (Soares et al. 2017; Soares et al. 2018) and climate conditions (Alaniz et al. 2021). The fate of this introduction in Madeira, whose conditions are like those of the Azores, will be important to follow. First record for Portugal.

Harmonia quadripunctata (Pontoppidan, 1763)

= *Coccinella quadripunctata* Pontoppidan, 1763

Distribution. Mainland, Madeira.

Comments. Palearctic and Nearctic distribution.

Hippodamia variegata (Goeze, 1777)

= *Coccinella variegata* Goeze, 1777

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic, Afrotropical, Nearctic and Oriental distribution.

Myrrha octodecimguttata (Linnaeus, 1758)

= *Coccinella octodecimguttata* Linnaeus, 1758

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic distribution.

Myzia oblongoguttata (Linnaeus, 1758)

= *Coccinella oblongoguttata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic distribution.

Oenopia conglobata (Linnaeus, 1758)

= *Coccinella conglobata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic distribution.

Oenopia doublieri (Mulsant, 1846)

= *Harmonia doublieri* Mulsant, 1846

Distribution. Mainland and Azores.

Comments. Palearctic distribution.

Oenopia lyncea (Olivier, 1808)

= *Coccinella lyncea* Olivier, 1808

Distribution. Mainland.

Comments. Palearctic distribution.

Propylea quatuordecimpunctata (Linnaeus, 1758)

= *Coccinella quatuordecimpunctata* Linnaeus, 1758

Distribution. Mainland and Azores•.

Comments. Palearctic and Nearctic distribution. First record for the Azores. Several adults were collected in July 2019 by António O. Soares and Isabel Borges, in a vegetable garden, of the parish of Castelo Branco (GPS coordinates: 38°31'23.2"N, 28°41'21.0"W), Faial Island.

Psyllobora vigintiduopunctata (Linnaeus, 1758)

= *Coccinella vigintiduopunctata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic distribution.

Sospita vigintiguttata (Linnaeus, 1758)

= *Coccinella vigintiguttata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic distribution.

Tytthaspis sedecimpunctata (Linnaeus, 1761)

= *Coccinella sedecimpunctata* Linnaeus, 1761

Distribution. Mainland.

Comments. Palearctic distribution.

Vibidia duodecimguttata (Poda von Neuhaus, 1761)

= *Coccinella duodecimguttata* Poda von Neuhaus, 1761

Distribution. Mainland.

Comments. Palearctic and Oriental distribution.

Tribe EPILACHNINI

Chnootriba elaterii (Rossi, 1794)

= *Coccinella elaterii* Rossi, 1794

Distribution. Mainland.

Comments. Palearctic and Afrotropical distribution. Reported by Fürsch (1964) as the subspecies *portugalensis*. Based on molecular and morphological data, it was suggested to transfer this species to the genus *Chnootriba* (Szawaryn et al. 2015; Tomaszewska and Szawaryn 2016).

Henosepilachna angusticollis (Reiche, 1862)

= *Epilachna angusticollis* Reiche, 1862

Distribution. Mainland.

Comments. Distributed in the Mediterranean region.

Henosepilachna argus (Geoffrey, 1785)

= *Coccinella argus* Geoffrey, 1785

Distribution. Mainland.

Comments. Palearctic and Afrotropical distribution.

Subcoccinella vigintiquatuorpunctata (Linnaeus, 1758)

= *Coccinella vigintiquatuorpunctata* Linnaeus, 1758

Distribution. Mainland.

Comments. Palearctic and Nearctic distribution.

Tribe HYPERASPIDINI

Hyperaspis concolor (Suffrian, 1843)

= *Coccinella concolor* Suffrian, 1843

Distribution. Mainland.

Comments. Palearctic distribution.

Hyperaspis duvergeri Fürsch, 1985

Distribution. Mainland.

Comments. Palearctic distribution.

Hyperaspis hoffmannseggi (Gravenhorst, 1807)

= *Coccinella hoffmannseggi* Gravenhorst, 1807

Distribution. Mainland.

Comments. Palearctic distribution.

Hyperaspis illecebrosa Mulsant, 1846

Distribution. Mainland.

Comments. Palearctic distribution. Eizaguirre (2015) refers to the existence of two subspecies for the Iberian Peninsula; *illecebrosa* Mulsant, 1846 and *castiliana* Eizaguirre ssp. nov.; only the first one is mentioned for Portugal.

$ *Hyperaspis pantherina* Fürsch, 1975, following Félix et al. (2004), Félix et al. (2005), Félix et al. (2008)

Distribution. Madeira.

Comments. Established in Palearctic/Madeira, originally from Afrotropical region. The first record for Europe was in 2002, in Madeira archipelago (Roy and Migeon 2010). In Madeira, it was introduced as a biological control agent against *Insignorthezia insignis* (Browne 1887).

Hyperaspis reppensis (Herbst, 1783)

= *Coccinella reppensis* Herbst, 1783

Distribution. Mainland*.

Comments. Palearctic distribution. According to Eizaguirre (2015), this species does not exist in the Iberian Peninsula and has been mistaken for the endemic species, *H. illecebrosa*.

Hyperaspis stigma (Olivier, 1808)

= *Coccinella stigma* Olivier, 1808

Distribution. Mainland.

Comments. Palearctic distribution.

Tribe NOVIINI

$ *Novius cardinalis* (Mulsant, 1850), following Pang et al. (2020)

= *Vedalia cardinalis* Mulsant, 1850

Distribution. Mainland, Madeira and Azores.

Comments. Established in Palaeartic, Afrotropical, Nearctic and Neotropical, Oriental. Native to Australian region. This exotic species was introduced in California and South Africa in the 1890´s for the control of the cottony cushion scale, *Icerya purchasi* Maskell (Roy and Migeon 2010). The first introduction in Europe was made in Portugal, 1897 (Amaro 1994; Roy and Migeon 2010). *Rodolia cardinalis* is the widely known name and it was included in the genus *Novius* by Pang et al. (2020).

Novius cruentatus **Mulsant, 1846**

Distribution. Mainland.

Comments. Palearctic distribution.

Tribe PLATYNASPIDINI

Platynaspis luteorubra **(Goeze, 1777)**

= *Coccinella luteorubra* Goeze, 1777

Distribution. Mainland.

Comments. Palearctic distribution.

Tribe SCYMNINI

Clitostethus arcuatus **(Rossi, 1794)**

=*Coccinella arcuata* Rossi, 1794

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic, Afrotropical, Nearctic distribution.

Nephus **(*Bipunctatus*)** ***bisignatus*** **(Boheman, 1850)**

= *Scymnus bisignatus* Boheman, 1850

Distribution. Mainland and Azores.

Comments. Palearctic distribution.

Nephus **(*Bipunctatus*)** ***conjunctus*** **(Wollaston, 1870)**

= *Scymnus conjunctus* Wollaston, 1870

Distribution. Mainland and Madeira.

Comments. Palearctic and Afrotropical distribution. This species was first reported as *N.* (*bipunctatus*) *includens* (Kirsch 1871) based on adults emerged from larvae collected in 1988 from citrus fruits infested with mealybugs, in the South of Portugal (Algarve) (Raimundo 1992). However, Eizaguirre (2015) indicates that *N.* (*bipunctatus*) *includens* is a junior synonym of *N. conjuntus*. Taking this into account and knowing that specimens previously collected in 1984 in the Algarve and identified as *N. quadrimaculatus* Herbst were in fact shown to be *N. includens* (Raimundo and Alves 1986; Magro et al. 1992; Raimundo 1992), we have to consider that the first report of this species dates from 1984. The distribution is apparently restricted to the Algarve (Magro et al. 1992).

Nephus (*Bipunctatus*) *peyerimhoffi* (Sicard, 1923)

= *Scymnus peyerimhoffi* Sicard, 1923

Distribution. Mainland.

Comments. Palearctic and Afrotropical distribution.

$ *Nephus* (*Geminosipho*) *reunioni* (Fürsch, 1974a)

= *Scymnus reunioni* Fürsch, 1974a

Distribution. Mainland, Azores and Madeira•.

Comments. Palearctic and Afrotropical distribution. The first record in Europe was in France in 1983 (Roy and Migeon 2010). This species of Afrotropical origin was imported from France (laboratory rearing in Antibes) in the early 1980´s and released in Oeiras, in 1984 (Magro et al. 1992). Its presence in Portugal was detected for the first time in 1990, in citrus orchards in the Setúbal region (Franco et al. 1992). In his Catalogue of the African species of the genus *Nephus*, Fürsch (2007) mentions that the distribution of *N. reunioni* is apparently restricted to Reunion Island and Mauritius, and that the references to its presence in South Africa and other Mediterranean countries, such as Portugal and Israel, are due to misidentifications by the author himself, which most likely correspond to *N. derroni* Fürsch 1974b, a species described from São Tomé Island and that is common in South Africa. However, Magro et al. (2020a) analysed specimens from Portugal and showed that they corresponded to the original description of *N. reunioni* made by Fürsch in Chazeau et al. (1974). Raimundo (1992), who first described *N. reunioni* for Portugal, also illustrated the external morphology and genitalia corresponding to the original description by Fürsch in Chazeau et al. (1974). In both cases, the observations showed that the specimens from the Portuguese population are distinct from *N. derroni*. In Madeira, collected by Aguiar and Jesus, in October 2008, from *Dombeya wallichii* (Lindl.) Baill. (Funchal 32°38'49"N, 16°56'16"W), Celestina Brazão in February 2003, from *Dombeya wallichii* (Lindl.)

Baill. (Funchal 32°39'49"N, 16°55'44"W), Aguiar and Jesus, in April 2005, from *Olea europaea* L. (Machico 32°38'49"N, 16°56'16"W), Délia Cravo, in September 2006, from *Jacaranda mimosifolia* D. Don (Funchal 32°39'05"N, 16°54'18"W), J.D. Sardinha, in January 2010, from *Persea americana* Mill. (Funchal 32°39'30"N, 16°54'34"W), Graça Freitas, in August 2011, from *Persea americana* Mill. (Funchal 32°39'00"N, 16°53'27"W), Graça Freitas, in July 2013, from *Persea americana* Mill. (Calheta 32°42'23"N, 17°08'39"W), Paula Rocha, in January 2015, from *Annona cherimola* Mill. (Funchal 32°39'47"N, 16°50'40"W), Florasanto, in June 2015, from *Pinus pinaster* Aiton (São Vicente 32°47'46"N, 17°01'55"W), Natália Nunes, in January 2016, from *Laurus novocanariensis* Rivas Mart., Lousã, Fern. Prieto, E. Díaz, J.C. Costa & C. Aguiar (Ponta do Sol 32°40'57"N, 17°06'01"W), Celestina Brazão, in August 2017, from *Nerium oleander* L. (Funchal 32°38'11"N, 16°56'02"W), Fátima Rocha, in November 2019, from *Psidium guajava* L. (Funchal 32°39'34"N, 16°52'33"W), Graça Freitas, in September 2020, from *Annona cherimola* Mill. (Funchal 32°39'47"N, 16°53'40"W), and Alexandra Magro and Miguel Sequeira, in September 2018, from herbaceous plants (Anjos 32°69'11"N, 17°11'96"W and Ribeira de Natal, Caniçal 32°73'57"N, 16°74'62"W). New record for Madeira.

***Nephus* (*Nephus*) *binotatus* (Brisout de Barneville, 1863)**

= *Scymnus binotatus* Brisout de Barneville, 1863

Distribution. Mainland.

Comments. Palearctic distribution.

***Nephus* (*Nephus*) *flavopictus* (Wollaston, 1854)**

= *Scymnus flavopictus* Wollaston, 1854

Distribution. Madeira and Azores.

Comments. Macaronesian endemic species.

***Nephus* (*Nephus*) *quadrimaculatus* (Herbst, 1783)**

= *Sphaeridium quadrimaculatum* Herbst, 1783

Distribution. Mainland.

Comments. Palearctic distribution.

Nephus (*Nephus*) *schatzmayri* Canepari & Tedeschi, 1977

Distribution. Mainland.

Comments. Palearctic distribution.

Nephus (*Nephus*) *ulbrichi* Fürsch, 1977

Distribution. Mainland.

Comments. Palearctic distribution.

$ *Nephus* (*Nephus*) *voeltzkowi* Weise, 1910, following Magro et al. (2020b)

Distribution. Azores and Madeira•.

Comments. Afrotropical origin. Very recently, two parthenogenetic populations of this species were found in the Azores and Mascarene archipelagos, becoming the first reported case of asexuality in the Coccinellidae (Magro et al. 2020b). Observations by António Onofre Soares, in September of 1997, Madeira Island (Anjos; approximately at 32°41'15"N, 17°06'54"W; Faial approximately 32°47'24"N, 16°51'02"W; Caniçal approximately 32°44'49"N, 16°44'26"W), and Alexandra Magro and Miguel Sequeira in September 2018, from herbaceous plants (Anjos 32°69'11"N, 17°11'96"W; Ribeira de Natal, Caniçal 32°73'57"N, 16°74'62"W; Ribeira Brava 32°66'98"N, 17°06'09"W; Fajã dos Padres 32°65'45"N, 17°02'13"W). New record for Madeira.

Nephus (*Sidis*) *depressiusculus* (Wollaston, 1867)

= *Scymnus depressiusculus* Wollaston, 1867

Distribution. Madeira.

Comments. Palearctic and Afrotropical distribution.

Nephus (*Sidis*) *hiekei* (Fürsch, 1965)

= *Scymnus hiekei* Fürsch, 1965

Distribution. Mainland.

Comments. Palearctic distribution.

Nephus (*Sidis*) *pooti* Fürsch, 1999

Distribution. Mainland.

Comments. Palearctic distribution.

Scymniscus fuerschi (Plaza, 1981)

= *Nephus fuerschi* Plaza, 1981

Distribution. Mainland.

Comments. Palearctic distribution.

Scymniscus helgae (Fürsch, 1965)

= *Scymnus helgae* Fürsch, 1965

Distribution. Mainland and Azores.

Comments. Palearctic distribution.

Scymniscus semirufus (Weise, 1885)

=*Scymnus semirufus* Weise, 1885

Distribution. Mainland.

Comments. Palearctic distribution.

Scymnus (*Mimopullus*) *epistemoides* Wollaston, 1867

Distribution. Madeira.

Comments. Palearctic distribution.

Scymnus (*Mimopullus*) *limnichoides* Wollaston, 1854

Distribution. Madeira.

Comments. Palearctic distribution.

Scymnus (*Mimopullus*) *marinus* (Mulsant, 1850)

= *Rhyzobius marinus* Mulsant, 1850

Distribution. Mainland and Madeira.

Comments. Palearctic distribution.

Scymnus (*Neopullus*) *ater* Kugelann, 1794

Distribution. Mainland.

Comments. Palearctic distribution.

Scymnus (*Neopullus*) *haemorrhoidalis* Herbst, 1797

Distribution. Madeira and Azores.

Comments. Palearctic distribution.

Scymnus (*Neopullus*) *limbatus* Stephens, 1832

Distribution. Madeira.

Comments. Palearctic distribution.

Scymnus (*Parapullus*) *abietis* (Paykull, 1798)

= *Coccinella abietis* Paykull, 1798

Distribution. Mainland and Madeira.

Comments. Palearctic distribution.

Scymnus (*Pullus*) *auritus* Thunberg, 1795

Distribution. Mainland.

Comments. Palearctic distribution.

Scymnus (*Pullus*) *subvillosus* (Goeze, 1777)

= *Coccinella subvillosa* Goeze, 1777

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic and Afrotropical distribution.

Scymnus (*Pullus*) *suturalis* Thunberg, 1795

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic and Nearctic distribution.

Scymnus (*Scymnus*) *apetzi* Mulsant, 1846

Distribution. Mainland.

Comments. Palearctic distribution.

Scymnus (*Scymnus*) *bivulnerus* Baudi di Selve, 1894

Distribution. Mainland.

Comments. Palearctic distribution.

Scymnus (*Scymnus*) *frontalis* (Fabricius, 1787)

= *Coccinella frontalis* Fabricius, 1787

Distribution. Mainland.

Comments. Palearctic distribution.

Scymnus (*Scymnus*) *interruptus* (Goeze, 1777)

= *Coccinella interrupta* Goeze, 1777

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic distribution.

Scymnus (*Scymnus*) *laetificus* Weise, 1879

Distribution. Mainland.

Comments. Palearctic distribution. However, it only occurs in the Western Mediterranean.

***Scymnus* (*Scymnus*) *nubilus* Mulsant, 1850**

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic distribution. On Portugal's mainland, this species was wrongly identified as *Scymnus levaillanti* Mulsant.

***Scymnus* (*Scymnus*) *rubromaculatus* (Goeze, 1777)**

= *Coccinella rubromaculata* Goeze, 1777

Distribution. Mainland, Madeira and Azores.

Comments. Palearctic and Afrotropical distribution.

***Scymnus* (*Scymnus*) *rufipes* (Fabricius, 1798)**

= *Coccinella rufipes* Fabricius, 1798

Distribution. Mainland.

Comments. Palearctic distribution.

***Scymnus* (*Scymnus*) *schmidti* Fürsch, 1958**

Distribution. Mainland and Azores.

Comments. Palearctic distribution.

***Scymnus* (*Scymnus*) *suffrianioides* Sahlberg, 1913**

Distribution. Mainland.

Comments. Palearctic distribution.

Tribe STETHORINI

***Stethorus pusillus* (Herbst, 1797)**

= *Scymnus pusillus* Herbst, 1797

Distribution. Mainland and Azores.

Comments. Palearctic distribution.

Stethorus tenerifensis Fürsch, 1987

Distribution. Madeira.

Comments. Macaronesian endemic species.

Stethorus wollastoni Kapur, 1948

Distribution. Madeira.

Comments. Macaronesian endemic species.

Tribe STICHOLOTIDINI

Coelopterus salinus Mulsant & Rey, 1852

Distribution. Mainland.

Comments. Palearctic and Afrotropical distribution.

Pharoscymnus decemplagiatus (Wollaston, 1857)

= *Scymnus decemplagiatus* Wollaston, 1857

Distribution. Madeira and Azores.

Comments. Palearctic distribution.

Acknowledgments

In Memoriam of Armando Américo Cardoso Raimundo (2.V.1942–9.Xi.2019): A farewell to colleague and friend.

Thanks are due to Claudio Canepari for helping in the identification of *Microserangium sp.* and Jaroslav Větrovec of *Harmonia axyridis* Pallas from Madeira.

This study was financed by FEDER in 85% and by Azorean Public funds by 15% through Operational Program Azores 2020, under the following projects AZORESBIOPORTAL –PORBIOTA (ACORES-01-0145-FEDER-000072), and under the project ECO2 – TUTA (ACORES-01-0145-FEDER-000081). The Forest Research Centre is funded by Fundação para a Ciência e a Tecnologia I.P. (FCT), Portugal (UIDB/00239/2020). Thanks are also due to FCT/MCES for financial support to CESAM (UIDB/50017/2020+UIDP/50017/2020) through national funds, and the co-funding by the FEDER, within the PT2020 Partnership Agreement and Compete 2020. OMCCA is funded by national funds (OE), through FCT, in the scope of the framework contract foreseen in the numbers 4, 5 and 6 of the article

23, of the Decree-Law 57/2016, of August 29, changed by Law 57/2017, of July 19. AM was supported by the "Laboratoires d'Excellence" LabEx TULIP (ANR-10-LABX-41). The Open Access of this manuscript was supported by the project FCT-UIDB/00329/2020-2024.

References

Alaniz AJ, Soares AO, Azevedo EB, Grez AA (2021) The failed invasion of *Harmonia axyridis* in the Azores, Portugal: Climatic restriction or wrong population origin? Insect Science 28: 238–250. https://doi.org/10.1111/1744-7917.12756

Alluaud C (1935) Les coléoptères des Iles Salvages. Revue francaise d'Entomologie 2(1): 35–44.

Amaro P (1994) Portugal pioneiro da luta biológica na Europa através do combate à Icéria com a Vedália. In: Amaro P, Franco JC (Eds) 1° Congresso de Citricultura, Silves (Portugal), Janeiro de 1993. Câmara Municipal de Silves, Silves, 393–402.

Ameixa OMCC, Soares AO, Soares AMVM, Lillebø AI (2018) Ecosystem Services Provided by the Little Things That Run the World. In: Şen B, Grillo O (Eds) Selected Studies in Biodiversity, 267–302. https://doi.org/10.5772/intechopen.74847

Barrigossi JA, Hein GL, Higley, LG (2003) Economic injury levels and sequential sampling plans for Mexican bean beetle (Coleoptera: Coccinellidae) on dry beans. Journal of Economic Entomology 96(4): 1160–1167. https://doi.org/10.1093/jee/96.4.1160

Barros JMC (1896) Subsídios para o estudo da fauna entomológica transmontana. Coleópteros do Concelho de Saborosa. Anais de Sciencias Naturaes 3: 39–44. [109–114, 186–194.]

Barros JMC (1913) Adições ao catálogo dos Coleópteros de Portugal. Brotéria, Série Zoológica 6: 105–118.

Barros JMC (1926) Notas Entomológicas. Memórias e Estudos do Museu Zoológico da Universidade de Coimbra 6: 7–16.

Baudi di Selve F (1894) Viaggio del Dr. E. Festa in Palestina, nel Libano e regioni vicine. Bollettino dei Musei di Zoologia e Anatomia Comparata della Reale Universita di Torino 9(173): 1–13. https://doi.org/10.5962/bhl.part.8049

Benhadi-Marin J, Pereira JA, Barrientos JA, Bento A, Santos, SAP (2011) Diversity of predaceous arthropods in the almond tree canopy in Northeastern Portugal: A methodological approach. Entomological Science 14(3): 347–58. https://doi.org/10.1111/j.1479-8298.2011.00444.x

Beyene Y, Hofsvang T, Azerefegne F (2007) Population dynamics of tef epilachna (*Chnootriba similis* Thunberg) (Coleoptera, Coccinellidae) in Ethiopia. Crop Protection 26(11): 1634–1643. https://doi.org/10.1016/j.cropro.2007.01.005

Bielawski R (1963) X. Coccinellidae (Coleoptera) von Madeira. In: Lindberg H (Ed.) A Contribution to the Study of Beetles in the Madeira Islands. Social Science Fennica Communication Biology XXV(2): 72–102.

Blaisdell FE (1892) A new species of Coleoptera from California. Entomological News 3: e51.

Boheman CH (1850) Bildrag till Gottlands insekten-fauna. Ófversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 1(3): 70–76.

Boieiro M, Serrano ARM, Aguiar AMF (2008) Coccinellidae In: Borges PAV, Abreu C, Aguiar AMF, Carvalho P, Jardim R, Melo I, Oliveira P, Sérgio C, Serrano ARM, Vieira P (Eds) A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos. Direcção Regional do Ambiente da Madeira, Funchal and Universidade dos Açores, Angra do Heroísmo, 314–315.

Borges I, Canepari C, Rodriguez I, Soares AO (2017) First record of *Rhyzobius forestieri* (Mulsant) (Coleoptera: Coccinellidae) for the Azores archipelago of Portugal. The Coleopterists Bulletin 71(4): 796–797. https://doi.org/10.1649/0010-065X-71.4.796

Borges PAV (1990a) A checklist of Coleoptera from the Azores with some systematic and biogeographic comments. Boletim do Museu Municipal do Funchal 42(220): 87–136.

Borges PAV (1990b) Estudo preliminar dos coleópteros (Insecta, Coleoptera) da ilha das Flores. Relatórios e Comunicações do Departamento de Biologia 18: 47–61.

Borges PAV, Bried J, Costa A, Cunha R, Gabriel R, Gonçalves V, Martins AF, Melo I, Parente M, Raposeiro P, Rodrigues P, Santos RS, Silva L, Vieira P, Vieira V, Mendonça E, Boieiro M (2010) A list of the terrestrial and marine biota from the Azores. Princípia, Cascais, 432 pp.

Borges PAV, Oromí P, Dinis P, Jarroca S (2005) Coleoptera. In: Borges PAV, Cunha R, Gabriel R, Martins AF, Silva L, Vieira V (Eds) A list of the terrestrial fauna (Mollusc and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores. Direcção Regional do Ambiente and Universidade dos Açores, Horta, Angra do Heroísmo and Ponta Delgada, 197–207.

Borges PAV, Serrano ARM (1989) New records of the coleopterous fauna (Insecta, Coleoptera) from the Azores. Boletim do Museu Municipal do Funchal 41 (209): 5–24.

Borges PAV, Gabriel R, Pimentel C, Brito M, Serrano A, Crespo L, Assing V, Stüben P, Fattorini S, Soares AO, Mendonça E, Nogueira E (2018) Biota from the coastal wetlands of Praia da Vitória (Terceira, Azores, Portugal): Part 1 – Arthropods. Biodiversity Data Journal 6: e27194. https://doi.org/10.3897/BDJ.6.e27194

Branco M, Franco JC, Dunkelblum E, Assael F, Protasov A, Ofer D, Mendel Z (2006) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). Bulletin of Entomological Research 96: 179–185. https://doi.org/10.1079/BER2005415

Brisout de Barneville CNF (1863) New taxa. In: Grenier A (Ed.) Catalogue des coléoptěres de France et matériaux pour servir à Iα faune des coléoptères français. Paris: L. Toinon, iv + 3–79 + 135 pp.

Calado HRMG (2018) Ciência Cidadã nos Açores: O uso de Joaninhas (Coleoptera: Coccinellidae) como espécies-modelo. Dissertação de Mestrado em Biodiversidade e Biotecnologia, Universidade dos Açores, Ponta Delgada, 82 pp.

Caltagirone LE, Doutt RL (1989) The history of the vedalia beetle importation to California and its impact on the development of biological control. Annual Review of Entomology 34: 1–16. https://doi.org/10.1146/annurev.en.34.010189.000245

Cameron M (1901) Notes on a few day's collecting (Coleoptera) at Madeira. Entomologist's Monthly Magazine 12(S. 2): 220–222.

Canepari C (2009) New data on some Coccinellidae (Coleoptera) from the Mediterranean Region. Zootaxa 2318: 394–399. https://doi.org/10.11646/zootaxa.2318.1.14

Canepari C, Tedeschi M (1977) Le sottospecie del *Nephus quadrimaculatus* (Herbst) (Coleoptera Coccinellidae). Memorie della Società Entomologica Italiana 55[1976]: 101–105.

Capra F, Fürsch H, Kreissl E (1967) Revision einigier europaischer *Scymnus* (S. str.) – Arten. Abteilung für Zoologie und βotanük am Landes museum "Joanneum" in Graz 28: 207–259.

Carlos C, Tão CB, Domingos JA, Costa JR, Alves F, Torres LM (2005) Insectos predadores associados à vinha na Região Demarcada do Douro. VII Encontro Nacional de Protecção Integrada. Escola Superior Agrária de Coimbra, Coimbra, Dezembro 2005, 388–397

Che L, Zhang P, Deng S, Escalona HE, Wang X, Li Y, Pang H, Vandenberg N, Ślipiński A, Tomaszewska W, Liang D (2021) New insights into the phylogeny and evolution of lady beetles (Coleoptera: Coccinellidae) by extensive sampling of genes and species. Molecular Phylogenetics and Evolution 156: e107045. https://doi.org/10.1016/j.ympev.2020.107045

Crotch GR (1867) On the Coleoptera of the Azores. Proceedings of the Zoological Society of London, 359–391.

Das S, Uddin MM, Islam KS (2012) Effect of temperature on the behaviour of Epilachna Beetle (*Epilachna dodecastigma* Wied.) among different brinjal varieties. Journal of Environmental Science and Natural Resources 5(1): 167–172. https://doi.org/10.3329/jesnr.v5i1.11572

De la Fuente JM (1928) Catálogo sistemático-geográfico de los Coleópteros observados en la Península Ibérica, Pirineos, propriamente dichos y Baleares. Boletín de la Sociedad Entomológica de España 11: 115–157.

De la Fuente JM (1929) Catálogo sistemático-geográfico de los Coleópteros observados en la Península Ibérica, Pirineos, propriamente dichos y Baleares. Boletín de la Sociedad Entomológica de España 12: 21–32.

Dixon AFG (2000) Insect Predator-Prey Dynamics: Ladybird Beetles and Biological Control. Cambridge University Press, Cambridge, 257 pp.

Drouet H (1859) Coléoptères açoréennes. Revue et Magasin de Zoologie Pure et Appliquée 7: 5–22. https://doi.org/10.5962/bhl.title.120161

Drouet H (1861) Élements de la faune açoréenne. Baillière JB and Fils, Libraires de l'Académie de Médecine, Paris, 245 pp.

Dyer LA, Letourneau D (2003) Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecology Letters 6(1): 60–68. https://doi.org/10.1046/j.1461-0248.2003.00398.x

Eizaguirre S (2015) Coleoptera, Coccinellidae. In: Ramos MA, Alba J, Bellés X, Gosálbez J, Sierra A, Macpherson E, Serrano J, Templado J (Eds) Fauna Ibérica (Vol. 40). Museo Nacional de Ciencias Naturales. CSIC. Madrid, 514 pp.

Eizaguirre S (2004) Revisión de la tribu Coccidulini en la Peninsula Ibérica (Coleoptera: Coccinellidae). Estudios del Museo de Ciencias Naturales de Álava [2003–2004], 18–19: 153–169.

Erber D, Aguiar AMF (1996) New and remarkable species of the coleopterous fauna of Madeira. Boletim do Museu Municipal do Funchal 48(265): 41–62.

Erber D, Hinterseher W (1988) Contribution to the knowledge of the Madeira beetles. Boletim do Museu Municipal do Funchal 40(202): 139–214.

Erber D, Hinterseher W (1990) Additional notes to the knowledge of the Madeira beetles. Boletim do Museu Municipal do Funchal 42(222): 141–146.

Erichson WF (1843) Beitrag zur Insecten-Fauna von Angola, in besonderer Beziehung zur geographischen Verbreitung der Insecten. Archiv fiir Naturgeschichte 9: 199–267.

Fabricius JC (1777) Genera Insectorum Eorumoue Characteres Anturales Secundum Numerům, Figurám, Situm et Proportionem Omnium Partium Oris Adiecta Mantissa Specierum Nuper Detectarum. Chilonii: Mich. Friedr. Bartschii, 310 pp. https://doi.org/10.5962/bhl.title.119827

Fabricius JC (1787) Mantissa Insectorum Sistens Eorum Species Nuper Detectas Adiectis Characteribus Genericis, Differentiis Specificis, Emendationibus, Observationibus. Tom I. Hafhiae: Chist. Gottl. Profit, 348 pp. https://doi.org/10.5962/bhl.title.36471

Fabricius JC (1798) Supplementum entomologiae systematicae. Hafhiae: Profit et Storch, [2], 572 pp.

Faldermann F (1837) Fauna entomologica Trans-Caucasica. Coleoptera. Pars II. Nouveaux Mémoires de la Société Imperiále des Naturalistes de Moscou 5: 1–433.

Fauvel A (1897) Catalogue des coléoptères des iles Madère, Porto Santo et Desertas. Revue d'Entomologie de la Societé Française d'Entomologie 16: 45–75.

Félix AP, Vasconcelos J, Brazão CI, Aguiar AMF, Rocha P (2004) Aspectos bioecológicos de *Hyperaspis pantherina* Fürsch (Coleoptera: Coccinellidae) predador de *Orthezia insignis* Browne (Homoptera: Ortheziidae). Boletin de Sanidad Vegetal, Plagas 30(2): 347–354.

Félix AP, Rocha P, Brazão CI, Aguiar AMF (2005) Criação laboratorial e aspectos morfológicos de *Hyperaspis pantherina* Fürsch (Coleoptera: Coccinellidae) predador de *Orthezia insignis* Browne (Homoptera: Ortheziidae). Boletin de Sanidad Vegetal, Plagas 31(3): 473–481.

Félix AP, Aguiar AMF, Brazão C, Rocha P (2008) Luta biológica clássica com *Hyperaspis pantherina* Fürsh (Coleoptera: Coccinellidae) no combate *Orthezia insignis* Browne (Homoptera: Ortheziidae) em Jacarandá. Revista de Ciências Agrárias. Sociedade de Ciências Agrárias de Portugal 31(2): 22–28.

Franco JC, Magro A, Raimundo A (1992) Estudo comparativo da dinâmica de populações de coccinelídeos em pomares de citrinos no Sul de Portugal. Boletín de Sanidad Vegetal Plagas 18: 69–80.

Franco JC, Magro A, Carvalho CJ (1994) Situação da luta biológica contra as cochonilhas algodão (Homoptera; Pseudococcidae) em pomares de citrinos. Anais UTAD 5(1): 405–412.

Fürsch H (1958) Zwei für Deutschland neue Adalia-Arten? Nachrichtenblatt der Bayerischen Entomologen 7: 9–11.

Fürsch H (1964) Die Arten der Verwandtschaftsgruppe Henosepilachna elaterii (Rossi) (=*E. chrysomelina* auct.). (Coleoptera, Coccinellidae). Reichenbachia, Mus. Tierk. Dresden 3(16): 181–208.

Fürsch H (1965) Die palaearktischen Arten der *Scymnus-bipunctatus*-Gruppe und die europaischer Vertreter der Untergattung Sidis (Col. Cocc). Mitteilungen der Münchener Entomologischen Gesellschaft 55: 178–213.

Fürsch H (1966) Die coccinelliden der Azoren. Boletim do Museu do Funchal 20: 29–33.

Fürsch H (1974a) [new taxa]. In: Chazeau J, Étienne J and Fürsch H (Eds) Les Coccinellidae de l'île de La Reunion (Insecta Coleoptera). Bulletin du Museum National d'Histoire Naturelle (3) 210 (Zoologie 140): 275–276.

Fürsch H (1974b) Die Coccinelliden von São Tomé. Mitteilungen der Münchner Entomologischen Gesellschaft 64: 13–39.

Fiirsch H (1975) Zwei bemerkenswerte *Hyperaspis*-Arten aus Ostafrika (Coleoptera: Coccinellidae). Senckenbergiana Biologica 56: 43–45.

Fürsch H (1977) Coccinellidenausbeuten aus Libanon und dem Iran im Museum Genf mit Beschreibung neuer Scymnini-Arten (Col. Cocc.). Revue Suisse de Zoologie 84: 645–657. https://doi.org/10.5962/bhl.part.91413

Fürsch H (1985) [new taxa]. In: Canepari C, Fürsch H, Kreissl E (Eds) Die Hyperaspis-Arten Mittel-, West- und Südeuropa. Systematik und Verbreitung (Coleoptera Coccinellidae). Giornale Italiano di Entomología 2: 223–252.

Fürsch H (1987) Die Scymninae der Kanaren, Azoren und Madeiras. Acta Coleopterologica 3: 1–14.

Fürsch H (1999) Eine neue Nephus-Art aus Portugal (Coleoptera, Coccinellidae). Mitteilungen Münchener Entomologischen Gesellschaft 89: 75–76.

Germar EF (1824) Insectorum species: novae aut minus cognitae, descriptionibus illustratae. Coleoptera. Volumen primum (Vol. 1). JC Hendelii. https://doi.org/10.5962/bhl.title.130964

Gillerfors G (1986) Contribution to the coleopterous fauna of the Azores. Boletim do Museu Municipal do Funchal 38(172): 16–27.

Goeze JAE (1777) Entomologische Beytraege zu des Ritters Linné zwolften Ausgabe des Natursystems. Erster Theil. Leipzig: Weidmanns Erben und Reich [16] + 736 pp. https://doi.org/10.5962/bhl.title.45974

Gonçalves MF, Santos SAP, Raimundo A, Pereira JA, Torres LM (2007) Coccinellids associated with olive groves in north-eastern Portugal. Bulletin OILB/SROP 30: e211.

Gourreau JM (1974) Systematique de la Tribu des Scymnini (Coccinellidae). Annales de Zoologie Ecologie Animale (INRA) n. hors serie, 221 pp.

Gravenhorst JLC (1807) Vergleichende Uebersicht des Linnéischen und einiger neueren zoologischen Systéme, nebst dem eingeschalteten Verzeihniss der zoologischen Sammlung des Verfassers und den Beschreibungen neuer Thierarten, die in derselben vorhanden sind. Goettingen: H. Dietrich, 476 pp.

Harvey JA, Heinen R, Armbrecht I, Basset Y, Baxter-Gilbert JH, Bezemer TM, Böhm M, Bommarco R, Borges PAV, Cardoso P, Clausnitzer V, Cornelisse T, Crone EE, Dicke M, Dijkstra K-DB, Dyer L, Ellers J, Fartmann T, Forister ML, Furlong MJ, Garcia-Aguayo A, Gerlach J, Gols R, Goulson D, Habel J-C, Haddad NM, Hallmann CA, Henriques S, Herberstein ME, Hochkirch A, Hughes AC, Jepsen S, Jones TH, Kaydan BM, Kleijn D, Klein A-M, Latty T, Leather SR, Lewis SM, Lister BC, Losey JE, Lowe EC, Macadam CR, Montoya-Lerma J, Nagano CD, Ogan S, Orr MC, Painting CJ, Pham T-H, Potts SG, Rauf A, Roslin TL, Samways MJ, Sanchez-Bayo F, Sar SA, Schultz CB, Soares AO, Thancharoen A, Tscharntke T,. Tylianakis JM, Umbers KDL, Vet LEM, Visser ME, Vujic A, Wagner DL, WallisDeVries MF, Westphal C, White TE, Wilkins VL, Williams PH, Wyckhuys KAG, Zhu Z-R, de Kroon H (2020) International scientists formulate a roadmap for insect conservation and recovery. Nature Ecology & Evolution 4: 174–176. https://doi.org/10.1038/s41559-019-1079-8

Hayden L von (1870) Entomologische Reise nach dem Sudlichen Spanien der Sierra Guadarrama und Sierra Morena, Portugal und den Cantabrischen gebirgen. Bei dr. G. Kraatz. Berlin, 221 pp.

Hayden L von (1906) Catalogus Coleopterum Europae, Caucassi et Armeniae Russicae. R. Friedländer, 1891, Berlin, 420 pp.

Herbst JFW (1783) Kritisches Verzeichniss meiner Insektensammlung. Archiv der Insectengeschichte (Zürich: J. C. Fuessly) 4: 1–72.

Herbst JFW (1792) Natursystem aller bekannten in- und auslandischen insecten, als eine Fortsetzung der von Büffonschen Naturgeschichte. Der Kâfer vierter Theil. J. Pauli, Berlin, 197 pp.

Herbst JFW (1797) Natursystem aller bekannten in- und auslandischen lnsekten, als eine Fortsetzung der von Büffonschen Naturgeschichte. Der Kâfer siebenten Theil. Berlin: Paulischen Buchhandlung, 346 pp.

Hodek I, van Emden H, Honěk A (2012) Ecology and Behaviour of the Ladybird Beetles (Coccinellidae). Blackwell Publishing Ltd., Oxford, 500 pp. https://doi.org/10.1002/9781118223208

Honěk A, Martinkova Z, Kindlmann P, Ameixa OM, Dixon AF (2014) Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe. Insect Conservation and Diversity 7(1): 55–63. https://doi.org/10.1111/icad.12032

Honěk A, Dixon AFG, Soares AO, Skuhrovec J, Martinkova Z (2017) Spatial and temporal changes in the abundance and composition of ladybird (Coleoptera: Coccinellidae) communities. Current Opinion in Insect Science 20: 61–67. https://doi.org/10.1016/j.cois.2017.04.001

Horn GH (1895) Studies in Coccinellidae. Transactions of the American Entomological Society 12: 81–114.

Israelson G (1984) Coleoptera from the Azores. Boletim do Museu Municipal do Funchal 36(161): 142–161.

Israelson G (1985) Notes of the coleopterous fauna of the Azores, with description of new species of Atheta Thomson (Coleoptera). Boletim do Museu Municipal do Funchal 37(165): 5–9.

Jansson A (1940a) XXIX – Coleoptera: Sämtliche Familien unter Ausschluss der Familie der Carabidae, Dytiscidae, Hydrophilidae und der Gattung Cryptophagus Herbst aus der Familie Cryptophagidae. Die Arthropodenfauna von Madeira nach den Ergebnissen der Reise von Prof. Dr. O. Lundblad, Juli-August 1935. Arkiv for Zoologie, Bd. 32A (24): 1–64.

Jung M, Rowhani P, Scharlemann JPW (2019) Impacts of past abrupt land change on local biodiversity globally. Nature Communications 10: e5474. https://doi.org/10.1038/s41467-019-13452-3

Kapur AF (1948) On the Old World species of the genus *Stethorus* Weise (Coleoptera, Coccinellidae). Bulletin of Entomological Research 39(2): 297–320.

Korschefsky R (1931) Coccinellidae I. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus. Part 118. W. Junk, Berlin, 224 pp.

Kovář I (2007) "Coccinellidae". In: Löbl I, Smetana A (Eds) Catalogue of Palearctic Coleoptera (Vol. 4). Apollo Books, Denmark, 568–630. https://doi.org/10.1017/S0007485300022434

Kugelann JG (1794) Verzeihniss der in einigen Gegenden Preussens bis jetzt entdeckten Kâferarten, nebst kurzen Nachrichten von denselben. Neuestes Magazin fur die Liebhaber der Entomologie 1(5): 513–582.

Laicharting JN von (1781) Verzeichnis und Beschreibung der Tyroler — Insecten. I. Theil. Káferartige Insecten. I. Zürich: Johann Gaspar Füessli, [4] + xii + [1]+ 248 pp.

Lecompte É, Bouanani MA, Magro A, Crouau-Roy B (2016) Genetic diversity and structuring across the range of a widely distributed ladybird: focus on rear-edge populations phenotypically divergent. Ecology and Evolution 6(15): 5517–5529. https://doi.org/10.1002/ece3.2288

Liebmann W (1939) Kurze koleopterologische sammeltage auf Madeira. Entomologische Blatter 35: 149–157.

Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiae: Laurentii Salvii, 823 pp. https://doi.org/10.5962/bhl.title.542

Linnaeus C (1761) Fauna Suecica sistens Animalia Sueciae Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per classes et ordines, genera et species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus Insectorum. Editio altera, auctior. Stockholmiae: Laurentii Salvii, 578 pp. [2 pis.] https://doi.org/10.5962/bhl.title.46380

Linnaeus C (1767) Systema naturae, per regna tria naturae, secundum classes, ordines, genera. Species cum characteribus, differentiis, synonimis, locis. Tomus I. Editio duodecima. Tomus I, Pars II. Holmiae: Laurentii Salvii, 2 + 533–1327 + [37] pp. https://doi.org/10.5962/bhl.title.156772

Lundblad O (1958) XXXV – Die Käferfauna der Insel Madeira. In: Die Arthropodenfauna von Madeira nach den Ergebnissen der Reise von Prof. Dr. O. Lundblad, Juli-August 1935. Arkiv for Zoologie, Bd. 11(30): 461–524.

Mader L (1955) Evidenz der palaearktischen Coccinelliden und ihrer Abberrationen in wort und Bild. II. Ent. Arb. Museum G. Frey, München 6(3): 764–1035.

Magro A, Franco JC, Raimundo A (1992) Dados preliminares sobre a distribuição de duas espécies do género *Nephus* (Col.: Coccin.), novas para Portugal, referenciadas em ecossistemas citrícolas. Boletim da Socidedade Portuguesa de Entomologia, 2 (supl. 3): 281–289.

Magro A, Franco JC, Raimundo A (1994) Os coccinelídeos associados aos citrinos. In: Amaro P, Franco JC (Eds) 1° Congresso de Citricultura. Câmara Municipal, Silves, 443–450.

Magro A, Araújo J, Hemptinne JL (1999) Coccinellids (Coleoptera: Coccinellidae) in citrus groves in Portugal: listing and analysis of geographical distribution. Boletin de Sanidad Vegetal Plagas 25: 335–345.

Magro A, Hemptinne JL (1999) The pool of coccinellids (Coleoptera: Coccinellidae) to control coccids (Homoptera: Coccoidea) in portuguese citrus groves. Boletin de Sanidad Vegetal Plagas 25: 311–320.

Magro A, Churata-Salcedo J, Lecompte E, Hemptinne J-L, Almeida LM (2020a) A new species of *Nephus* (*Nephus*) (Coleoptera, Coccinellidae) described from Reunion Island. Zookeys 962: 123–137. https://doi.org/10.3897/zookeys.962.51520

Magro A, Lecompte E, Hemptinne J-L, Soares AO, Dutrillaux A-M, Murienne J, Fürsch H, Dutrillaux B (2020b) First case of parthenogenesis in ladybirds (Coleoptera: Coccinellidae) suggests new mechanisms for the evolution of asexual reproduction. Journal of Zoological Systematics and Evolutionary Research 58(1): 194–208. https://doi.org/10.1111/jzs.12339

Méquignon A (1942) Catalogue des Coléoptères Açoréens. Annales de la Société Entomologique de France. CXI Paris.

Miyatake M (1961) A new genus of the Coccinellidae from Japan and the Ryukyu Islands (Coleoptera). Memoirs of the College of Agriculture, Ehime University 6(2): 37–43.

Mitter H (1984) Beitrag zur kenntnis der käferfauna der Insel Madeira. Bocagiana, Museu Municipal do Funchal 80: 1–7.

Mulsant E (1846) Histoire Naturelle des coléoptěres de France. Sulcicolles – Sécuripalpes. Paris: Maison, 280 pp. [1 pl.]

Mulsant E (1850) Species des coléoptères trimères sécuripalpes. Annales des Sciences Physiques et Naturelles, dȂgriculture et d'Industrie de Lyon 2: 451–1104. https://doi.org/10.5962/bhl.title.8953

Mulsant E (1853) Supplément à la monographie des coléoptères trimères sécuripalpes. Annales de Iα Société Linnéenne de Lyon (N. S.), (2)1 [1852–1853]: 129–333. https://doi.org/10.5962/bhl.title.60609

Mulsant E, Rey C (1852) Description de trois coléoptěres nouveaux de la famille des scymniens. Mémoires de Academie Imperiále des Sciences, Belles-Lettres et Arts de Lyon (2)2: 221–225.

Newbold T, Hudson LN, Hill SL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, Day J (2015) Global effects of land use on local terrestrial biodiversity. Nature 520(7545): 45–50. https://doi.org/10.1038/nature14324

Nedvěd O (2020) Brouci čeledi slunéčkovití (Coccinellidae) střední Evropy. Ladybird beetles (Coccinellidae) of Central Europe. 2nd edition. Academia, Praha, 382 pp.

Olivier AG (1808) Entomologie, ou histoire naturelle des insectes, avec leur caractéres génériques et spécifiques, leur description, leur synonymie, et leur figure eluminée. Coléoptères. Tome sixième. Desray, Paris, 613–1104.

Oliveira MP (1894) Catalogue des Insectes du Portugal. Universidade de Coimbra, Coimbra, 393 pp.

Pallas PS (1773) Reise durch verschiedene Provinzen des russischen Reichs. Zweiter Theil. Zweytes Buch vom Jahr 1771. St.-Peterburg: Kayserliche Akademie der Wissenschaften, 371–744.

Pang H, Tang XF, Booth RG, Vandenberg N, Forrester J, Mchugh J, Ślipiński A (2020) Revision of the Australian Coccinellidae (Coleoptera). Genus *Novius* Mulsant of Tribe Noviini. Annales Zoologici 70(1): 1–24. https://doi.org/10.3161/00034541ANZ2020.70.1.001

Paykull G von (1798) Anmârkningar vid genus *Coccinella*, och beskisning öfver de Svânska arter deraf som âro med fina hâr beströdde. Kongliga Vetenskaps Akademiens nya Handlingar 19: 144–156.

Plaza E (1981) Los representantes espanioles de *Nephus* del subgenera *Sidis* Muls. 1851 (Col., Coccinellidae). Boletin de Ia Asociacion Espanola de Entomologia 4 [1980]: 235–242.

Poda von Neuhaus N (1761) Insecta Musei Graecensis, que in ordines, genera et species juxta Systema Naturae Linnaei digessit. Graecii, Widmanstad, 127 pp.

Pontoppidan EL (1763) Den Danske atlas, eller Konge-Riget Dannemark, med dets naturlige egenskaber, elementer, inbyggere, vaexter, dyr og andre qffbdninger, dets gamle tildragelser og naervaerende omstaendigheder i aile provintzer, staeder, kirkzer, slotte og herregaarde. Forestillet ved en udf0rlig Lands-Beskrivelse, saa og oplyst med dertil forfaerdigede landkort over enhver provintz, samt ziret med staedernes prospecter, grund-ridser, og andre merkvaerdige kaaber-stykker. Efter Hoy-Kongelig allernaadigst Befalning. Tomus I. Kİ0benhavn: A.H. Godieche, xl + [iv] + 723 + [1] pp.

Raimundo AAC (1992) Novas Espécies de Scymnini para a Fauna de Coccinelídeos de Portugal. Actas do V Congresso Ibérico de Entomologia. Boletim da Sociedade Portuguesa Entomologia, 1 (supl. 3): 373–384.

Raimundo AAC, Alves MMLG (1986) Revisão dos Coccinelídeos de Portugal. Universidade de Évora, Évora, 103 pp.

Raimundo A, Canepari C, Mendel Z, Branco M, Franco JC (2006) *Iberorhyzobius* Raimundo & Canepari gen. nov., for *Coccidula rondensis* Eizaguirre (Coleoptera: Coccinellidae). Zootaxa 1312: 49–58. https://doi.org/10.11646/zootaxa.1312.1.4

Romanowski J, Ceryngier P, Větrovec J, Szawaryn K (2019) The Coccinellidae (Coleoptera) from Fuerteventura, Canary Islands. Zootaxa 4646: 101–123. https://doi.org/10.11646/zootaxa.4646.1.6

Rossi P (1794) Mantissa insectorum exhibens species nuper in Etruria collectas, adiectis faunae Etruscae illustrationibus, ac emendationibus. Tomus II. Pisis: Typographia Prosperi, 154 pp.

Roy HE, Brown PMJ, Adriaens T, Berkven N, Borges I, Clusella-Trullas S, De Clercq P, Eschen R, Estoup A, Evans EW, Facon B, Gardiner MM, Gil A, Grez A, Guillemaud T, Haelewaters D, Honěk A, Howe AG, Hui C, Hutchison WD, Kenis M, Koch RL, Kulfan J, Handley LL, Lombaert E, Loomans A, Losey J, Lukashuk AO, Maes D, Magro A, Murray KM, Martin GS, Martinkova Z, Minnaar I, Nedvěd O, Orlova-Bienkowskaja MJ, Rabitsch W, Ravn HP, Rondoni G, Rorke SL, Ryndevich SK, Saethre MG, Sloggett J, Soares AO, Stals R, Tinsley MC, Vandereycken A, Wielink P, Vigláová S, Zach P, Zaviezo T, Zhao ZZ (2016) The harlequin ladybird, *Harmonia axyridis*: An inspiration for global collaborations on invasion Biology. Biological Invasions 18(4): 997–1044. https://doi.org/10.1007/s10530-016-1077-6

Roy HE, Migeon A (2010) Ladybeetles (Coccinellidae). In: Roques A, Kenis M, Lees D, Lopez-Vaamonde C, Rabitsch W, Rasplus J-Y, Roy D (Eds) Alien terrestrial arthropods of Europe. BioRisk 4(1): 293–313. https://doi.org/10.3897/biorisk.4.49

Sahlberg JR (1913) Coleoptera mediterranea orientalia quae in Aegypto, Palaestina, Syria, Caramania atque in Anatolia occidentali anno 1904 collegerunt John Sahlberg et Unio Saalas. Öfversigt af Finska Vetenskaps-Societetens Förhandlingar (A) 55(19) [1912–1913]: 1–282.

Santos SAP, Pereira JA, Raimundo A, Torres LM, Nogueira AJA (2010) Response of coccinellid community to the dimethoate application in olive groves in Northeastern Portugal. Spanish Journal of Agricultural Research 8(1): e126. https://doi.org/10.5424/sjar/2010081-1151

Santos SAP, Raimundo A, Bento A, Pereira JA (2012) Species abundance patterns of coccinellid communities associated with olive, chestnut and almond crops in north-eastern Portugal. Agricultural and Forest Entomology 14(4): 376–82. https://doi.org/10.1111/j.1461-9563.2012.00578.x

Schneider DH (1792) Verzeichniss und Beschreibung der in der Sammlung des Herausgebers befindlichen zur Gattung *Coccinella* gehörigen europâischen Kâfer (Sonnen-Kâfer oder Blattlaus-Kafer). Neuestes Magazin für die Liebhaber der Entomologie 2: 128–256.

Seago AE, Giorgi JA, Li J, Slipiński A (2011) Phylogeny, classification and evolution of ladybird beetles (Coleoptera: Coccinellidae) based on simultaneous analysis of molecular and morphological data. Molecular Phylogenetics and Evolution 60(1): 137–51. https://doi.org/10.1016/j.ympev.2011.03.015

Serrano ARM (1982) Contribuição para o conhecimento do povoamento, distribuição e origem dos Coleópteros do arquipélago dos Açores (Insecta, Coleóptera). Boletim do Museu Municipal do Funchal 36(147): 67–104.

Serrano ARM, Borges PAV (1987) A further contribution to the knowledge of the coleoptera (Insecta) from Azores. Boletim do Museu Municipal do Funchal 39(187): 51–69.

Sicard A (1923) Coccinellides nouveaux de l'Afrique du Nord. Bulletin de Iα Société d'Histoire Naturelle de l'Afrique du Nord 14: 78–80.

Silva EB, Franco JC, Vasconcelos T, Branco M (2010) Effect of ground cover vegetation on the abundance and diversity of beneficial arthropods in citrus orchards. Bulletin of Entomological Research 100: 489–99. https://doi.org/10.1017/S0007485309990526

Silva EB, Costa L, Mateus C, Franco JC (2006) Principais grupos de artrópodes auxiliares referenciados em citrinos em Portugal: insectos. In: Franco JC, Ramos AP, Moreira I (Eds) Infra-estruturas Ecológicas e Protecção Biológica: Caso dos Citrinos. ISA Press, Lisboa, 158–160.

Ślipiński A, Burckhardt D (2006) Revision of the Australian Coccinellidae (Coleoptera). Part 5. Tribe Serangiini. Annales Zoologici, Warsaw 56: 37–58.

Soares AO, Borges I, Borges PAV, Labrie G, Lucas E (2008) *Harmonia axyridis*: what will stop the invader? BioControl 53(1): 127–145. https://doi.org/10.1007/s10526-007-9141-x

Soares AO, Borges I, Cabral S, Figueiredo H, Resendes R (2006) New records of Coccinellidae (Coleoptera) to the Azores islands. XII Expedição Científica do Departamento de Biologia – Pico 2005. Relatórios e Comunicações do Departamento de Biologia 34: 87–91.

Soares AO, Elias RB, Schanderl H (1999) Population Dynamics of *Icerya purchasi* Maskell (Homoptera: Margarodidae) and *Rodolia cardinalis* Mulsant (Coleoptera: Coccinellidae) in two citrus orchards of São Miguel island (Azores). Boletin de Sanidad Vegetal de Plagas 25: 459–467.

Soares AO, Elias RB, Resendes R, Figueiredo H (2003a) Contribution to the knowledge of the Coccinellidae (Coleoptera) fauna from the Azores islands. Arquipélago. Life and Marine Sciences 20A: 47–53.

Soares AO, Elias RB, Raimundo A (2003b) New Records of Scymnini (Coleoptera: Coccinellidae) to Madeira Island. Boletim do Museu Municipal do Funchal 54(311): 25–29.

Soares AO, Elias RB, Raimundo A (2003c) Approach to the knowledge of Coccinellidade (Coleoptera) species diversity of Madeira and Porto Santo islands. In: Soares AO, Ventura MA, Garcia V, Hemptinne J-L (Eds): Proceedings of the 8th International Symposium on

Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. Arquipélago, Ponta Delgada, 6 pp.

Soares AO, Honěk A, Martinkova Z, Skuhrovec J, Cardoso P, Borges I (2017) *Harmonia axyridis* failed to establish in the Azores: the role of specie richness, intraguild interactions and resource availability. BioControl 62(3): 423–434. https://doi.org/10.1007/s10526-017-9794-z

Soares AO, Honěk A, Martinkova Z, Brown PMJ, Borges I (2018) Can Native Geographical Range, Dispersal Ability and Development Rates Predict the Successful Establishment of Alien Ladybird (Coleoptera: Coccinellidae) Species in Europe? Frontiers in Ecology and Evolution 6: e57. https://doi.org/10.3389/fevo.2018.00057

Stephens JF (1832) In: Illustrations of British entomology or, a synopsis of indigenous insects: containing their generic and specific distinctions;with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata (Vol. IV). Baldwin et Cradock, London, 367–413.

Suffrian CWLE (1843) Entomologische Bemerkungen. *Entomologische Zeitung* (Stettin) 4: 91–95.

Szawaryn K, Bocak L, Ślipiński A, Escalona HE, Tomaszewska W (2015) Phylogeny and evolution of phytophagous ladybird beetles (Coleoptera: Coccinellidae: Epilachnini), with recognition of new genera: Phylogeny and evolution of Epilachnini. Sistematic Entomology 40(3): 547–569. https://doi.org/10.1111/syen.12121

Szawaryn K, Vĕtrovec J, Tomaszewska V (2020) A New Tribe of the Ladybird Beetle Subfamily Microweiseinae (Coleoptera: Coccinellidae) Discovered on an Island in the North Atlantic Ocean. Insects 11: e367. https://doi.org/10.3390/insects11060367

Tarnier MF (1860) Insect Coleóptére. In: Morelet A (Ed.) Iles Açores. Notice sur l'Histoire Naturelle des Açores, suivie dune descriptions des Molusques terrestres de cet archipel. Baillière, Paris, 87–96.

Tavares C, Jactel H, Van Halder I, Branco M (2015a) Reproductive Requirements and Life Cycle of *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), Potential Biological Control Agent of Matsucoccus feytaudi (Hemiptera: Matsucoccidae). Environmental Entomology 44(3): 846–854. https://doi.org/10.1093/ee/nvv042

Tavares C, Jactel H, Van Halder I, Mendel Z, Branco M (2014) A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). Bulletin of Entomological Research 104(3): 367–75. https://doi.org/10.1017/S0007485314000182

Tavares C, Roques A, Courtial B, Branco M, Jactel H, Lopez-Vaamonde C (2015b) Phylogeography of the ladybird *Iberorhyzobius rondensis*, a potential biological control agent of the invasive alien pine bast scale *Matsucoccus feytaudi*. BioControl 60(1): 59–69. https://doi.org/10.1007/s10526-014-9622-7

Thunberg CP (1795) Dissertatio entomologica, sistens Insecta Suecica. IX. Exam. Steno Edvardus Westman. Upsaliae, 105–113.

Tomaszewska W (2010) *Rhyzobius* Stephens, 1829 (Coleoptera, Coccinellidae), a revision of the world species. Fauna Mundi, Vol. 2, Polish Academy of Sciences, Warszawa, 475 pp.

Tomaszewska W, Szawaryn K (2016) Epilachnini (Coleoptera: Coccinellidae)-A Revision of the World Genera. Journal of Insect Science 16(1): 1–91. https://doi.org/10.1093/jisesa/iew082

Uyttenboogaart DL (1930) Contributions to the knowledge of the fauna of the Canary-islands. Tijdschrift voor Entomologie 73: 211–235.

Uyttenboogaart DL (1947) Coleoptera (excl. Staphylinidae et Hydropilidae) von den Azoren und Madeira. Iter entomologicum et botanicum ad insulas Madeiram et Azores anno 1938 a Richard Frey, Ragnar Storå et Carl Cedercreutz factum. Societas Scientiarum Fennica. Commentationes Biologicae 8(12): 1–15.

Weise J (1879) Bestimmungs-Tabellen der europaischen Coleopteren II. Coccinellidae. Zeitschrift fir Entomologie (N. F.) (Breslau) 7: 88–156.

Weise J (1885) Coccinellidae. II. Auflage. Mit Berücksichtigung der Arten aus dem nördlichen Asien. In: Reitter E (Ed.) Bestimmungs-Tabellen der europaischen Coleopteren. II. Heft. Mödling: H. Busing, 83 pp.

Weise J (1910) Coccinellidae von Madagaskar, den Comoren und den Inseln Ostafrikas. Voeltzkow, Reise in Ostafrika in den Jahren 1903–1905 2: 507–520.

Winkler A (1924–1932) Catalogus coleopterorum regionis palaearcticae. A. Winkler, Wien.

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: ecology, evolution and conservation (2nd Edn.). Oxford University Press, New York, 401 pp.

Wollaston TV (1854) Insecta Maderensia; being an account of the insects of the islands of the Madeiran group. Taylor & Francis, London, 634 pp. https://doi.org/10.5962/bhl.title.9060

Wollaston TV (1857) Catalogue of the Coleopterous insects of Madeira in the collection of the British Museum. Taylor & Francis, London, 234 pp.

Wollaston TV (1862) XXXVI. – On Additions to the Madeiran Coleoptera. Annals and Magazine of Natural History 10: 331–342. https://doi.org/10.1080/00222936208681334

Wollaston TV (1864) Catalogue of the Coleopterous Insects of the Canaries in the Collection of the British Museum. Taylor & Francis, London, 648 pp.

Wollaston TV (1865) Coleoptera Atlantidum, Being an Enumeration of the Coleopterous of the Madeiras, Salvages and Canaries. Taylor & Francis, London, 526 pp. https://doi.org/10.5962/bhl.title.29516

Wollaston TV (1867) Coleoptera Hesperidum, Being an Enumeration of the Coleopterous Insects of the Cape Verde Archipelago. London: J. van Voorst, 285 pp. https://doi.org/10.5962/bhl.title.48651

Wollaston TV (1870) On addition to the coleopterous fauna of the Cape-Verde Islands. The Annals and Magazine of Natural History (4) 5: 245–251. https://doi.org/10.1080/00222937008696149

Wollaston TV (1871) On Additions to the Atlantic Coleoptera. Transactions of the Royal Entomological Society of London (4.Ser.): 203–314.

Vandenberg NJ (2002) Coccinellidae. In: Arnett Jr RH, Thomas MC, Skelley PE, Frank JH (Eds) American Beetles (Vol. 2). CRC Press, Boca Raton, 371–389.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science, 277(5325): e494499. https://doi.org/10.1126/science.277.5325.494

Wang X, Ślipiński A, Ren S (2013) The genus *Microserangium* Miyatake (Coleoptera, Coccinellidae) from China. Zookeys 359: 13–33. https://doi.org/10.3897/zookeys.359.6057

ZooKeys 1053: 145–184 (2021)
doi: 10.3897/zookeys.1053.52761
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Review of the Nordic *Gymnocheta* Robineau-Desvoidy (Diptera, Tachinidae) with report of two species new to Europe

Jaakko Pohjoismäki[1], Christer Bergström[2]

[1] *University of Eastern Finland, Department of Environmental and Biological Sciences, P.O. Box 111, FI-80101 Joensuu, Finland* [2] *Säves väg 10, SE-75263 Uppsala, Sweden*

Corresponding author: Jaakko Pohjoismäki (jaakko.pohjoismaki@uef.fi)

Academic editor: P. Cerretti | Received 31 March 2020 | Accepted 18 June 2021 | Published 2 August 2021

http://zoobank.org/BA47DBD9-7A10-47D1-9036-E603CDDCF6C6

Citation: Pohjoismäki J, Bergström C (2021) Review of the Nordic *Gymnocheta* Robineau-Desvoidy (Diptera, Tachinidae) with report of two species new to Europe. ZooKeys 1053: 145–184. https://doi.org/10.3897/zookeys.1053.52761

Abstract

The genus *Gymnocheta* Robineau-Desvoidy, 1830 (Diptera, Tachinidae) has until now been represented by two species in Europe, *G. viridis* (Fallén, 1810) and *G. magna* Zimin, 1958. Two species are newly recorded from Finland and Sweden, *Gymnocheta lucida* Zimin, 1958 and *G. zhelochovtsevi* Zimin, 1958, both previously known only from the Russian Far East and Japan. These four European species are redescribed and illustrated, including the first description of the female of *G. zhelochovtsevi*. A key is provided to seven of the eight described species of Palaearctic *Gymnocheta*. The holotype of *G. viridis* was examined and found to differ from the present concept of the species, instead matching the concept of the more recently described *G. magna*. In the interests of nomenclatural stability, the two names are maintained in their current usage pending a request to the International Commission on Zoological Nomenclature to replace the current holotype of *G. viridis* with a neotype that corresponds to the long-established concept of that species.

Keywords

DNA barcoding, Co1, Ernestiini, Fennoscandia, *Gymnocheta*, new species, species diversity, synonymy, Tachininae, type specimens

Introduction

The genus *Gymnocheta* Robineau-Desvoidy, 1830 constitutes a morphologically homogenous group within the large and multiform tribe Ernestiini and includes medium to large (5.0–13.0 mm), semi-robust tachinids, easily recognisable by their metallic green colouration (Fig. 1), which can convert to hues of metallic blue, purple and red in living as well as in dead specimens. The only other genus of Tachininae in Europe with metallic green members is *Chrysosomopsis* Townsend (Mesnil 1971; Zeegers et al. 2016), which is easily recognised from *Gymnocheta* by their yellow (vs. black) palps and three (vs. four) pairs of postsutural dorsocentral setae. For further diagnostic characters of *Gymnocheta* see Mesnil (1972), Tschorsnig and Richter (1998), and Cerretti et al. (2012).

Gymnocheta is currently known from eight species in the Palaearctic Region (Herting and Dely-Draskovits 1993) and four species in the Nearctic Region (O'Hara and Wood 2004). Interestingly, *G. viridis* (Fallén) was the only Palaearctic species recognised before the work of Zimin (1958). He increased the number of species to seven of which three (*G. flamma* Zimin, *G. mesnili* Zimin and *G. porphyrophora* Zimin) were restricted to China and two (*G. lucida* Zimin and *G. zhelochovtsevi* Zimin) to the Russian Far East. The only widespread species described in the publication was *G. magna* Zimin, with a distribution from Central Europe to Japan (Richter 2004). Only one Palaearctic *Gymnocheta* species has been discovered after Zimin's paper, *G. goniata* Chao, 1979 from China.

During a DNA barcoding study of Finnish Tachinidae (Pohjoismäki et al. 2016), we discovered that the Finnish specimens identified as *Gymnocheta viridis* (Fallén) clustered under two different barcode index numbers (BINs, Ratnasingham and Hebert 2013), BOLD:ACF3891 and BOLD:ACA6555. While some of the specimens had an identical mitochondrial cytochrome oxidase subunit 1 (Co1) gene sequence with the Central European *G. viridis*, some others had a sequence that was distinct from it as well as from that of *Gymnocheta magna* Zimin, the only other known European species of the genus. A closer examination revealed that the differing specimens were also morphologically dissimilar to *G. viridis* and had been collected exclusively from bog habitats, suggesting that the BIN split could be due to a genuine species difference. In fact, once the species difference was realised, additional specimens of this unknown species were recognised from Sweden and originated from similar habitats as in Finland. While investigating specimens in Finnish collections, we also noted the existence of a second unreported and not barcoded species in southern Finland, which differed from the other three species by its wide frons in the male and characteristic shape of the male syncercus.

A survey of the potential species candidates for the two unknown Nordic species among the described Palaearctic species found tentative matches with the descriptions of *G. lucida* and *G. zhelochovtsevi*. The species identities were later confirmed by comparing Nordic specimens with Russian and Japanese material. As an aid to future researchers, redescriptions of both species (originally described in Russian), including also the previously unknown female of *G. zhelochovtsevi*, are provided and full redescriptions of the other European species are given. Also included are notes on the known biology of the species and a key for the identification of the Palaearctic *Gymnocheta* species (not including the little-known *G. goniata*).

An examination of the holotype of *Tachina viridis* Fallén, 1810 (Fig. 1B–F) revealed that it is the same species as *Gymnocheta magna* Zimin, 1958. Normally this synonymy would require the concept of *Gymnocheta viridis* to change to that of *G. magna* and the species currently called *G. magna* would be given a replacement name, in accordance with the provisions of the International Code of Zoological Nomenclature (1999). However, compliance with the Code would cause a great deal of confusion over the identity of the well-established name *G. viridis*. In the interests of nomenclatural stability, we follow Article 75.6 of the Code ("Conservation of prevailing usage by a neotype") in maintaining prevailing usage of the names *G. viridis* and *G. magna* and will request the International Commission on Zoological Nomenclature to set aside under its plenary power the holotype of *Tachina viridis* Fallén and designate in its place a neotype that corresponds to the current interpretation of the species.

Materials and methods

Male and female terminalia were dissected and prepared for examination following the method described by O'Hara (2002). Terminalia are preserved in glycerol in a small plastic vial pinned together with the specimen. External morphological images were taken with a Nikon D2X (Figs 1A, 2B–D) or a Nikon D800 (Figs 1B, 2A, 3A–D) digital camera mounted to a bellow and a macro-optical tube. Helicon Focus, a program that combines the focused areas from the several partially focused images, was used to create one completely focused image. The images were cropped and colour- and contrast-enhanced, but not otherwise manipulated. The material examined is deposited in the following collections (acronyms are used in the text):

AHC	Private collection of A. Haarto, Mietoinen, Finland;
BLKU	Biosystematics Laboratory, Kyushu University, Fukuoka, Japan;
CBC	Private collection of C. Bergström, Uppsala, Sweden;
JPC	Private collection of J. Pohjoismäki, Joensuu, Finland;
MZH	Finnish Museum of Natural History, Zoological Museum, University of Helsinki, Helsinki, Finland;
NHRS	Swedish Museum of Natural History, Stockholm, Sweden;
REC	Private collection of Roger Engelmark, Gubböle, Sweden;
TMNH	Tampere Museum of Natural History, Tampere, Finland;
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia;
ZMLU	Museum of Zoology, Lund University, Lund, Sweden.

Label data are given verbatim using the following symbols: / for the end of a line and beginning of the next; // at the end of a label and beginning of the next (from top to bottom on the same pin).

The classification follows Herting and Dely-Draskovits (1993), apart from using *Chrysosomopsis* Townsend instead of *Chrysocosmius* Bezzi (see Mesnil 1971; Zeegers et al. 2016) and *Panzeria* instead of *Ernestia*, *Appendicia,* and *Eurithia* (Cerretti et al. 2012; O'Hara and Henderson 2020). The morphological terminology used in this study follows Cummin and Wood (2017) and Tschorsnig (1985) for some features of the male terminalia.

Cytochrome oxidase subunit 1 (**Co1**) DNA barcoding was performed as a part of the Tachinidae project of Finnish Barcode of Life initiative (**FinBoL**). The 5′-terminal part of Co1 was amplified using the routine barcoding primers LepF1 and LepR1 (Hebert et al. 2004). The results of the study as well as release of the barcode sequences have been described in detail in Pohjoismäki et al. (2016). All sequences used in this study are available in the GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and the access IDs listed with the listing of each specimen (see above). Other members of the Ernestiini (sensu Herting 1984), *Panzeria puparum* (Fabricius) (GenBank ID KX844044), *P. rudis* (Fallén) (GenBank ID KX844400), *P. truncata* (Zetterstedt) (GenBank ID KX843735), *P. anthophila* (Robineau-Desvoidy) (GenBank ID KX844254), *P. caesia* (Fallén) (GenBank ID KX843746), *P. connivens* (Zetterstedt) (GenBank ID KX843746), *P. vivida* (Zetterstedt) (GenBank ID KX843724), *Cleonice callida* (Meigen) (GenBank ID KX843803), *C. keteli* Ziegler (GenBank ID KX844536), *C. nitidiuscula* (Zetterstedt) (BOLD sample ID JP2016_1), and *Zophomyia temula* (Scopoli) (GenBank ID KX844031), were included for comparison.

Sequence comparisons were performed using MUSCLE alignment (Edgar 2004) and Bayesian inference phylogenetic tree generated using MrBayes 3.2. (Ronquist et al. 2012), applying GTR substitution model with gamma-distributed rate variation across sites and a proportion of invariable sites, and 1,000,000 MCMC generations. The tree was visualised using FigTree 1.4.4. (Rambaut 2009).

Material examined

For clarity, the information for the material on *Gymnocheta lucida*, *G. magna*, *G. viridis*, and *G. zhelochovtsevi* is given under the corresponding species descriptions. In addition to these species, the following non-European species is also included to confirm the identity of the Nordic *G. zhelochovtsevi*.

Gymnocheta porphyrophora Zimin, 1958

China: (1♂, 1♀) 1♂: Сев. предгорье......., Грум-Гржимайло, 14.V.1890 [Northern Foothills....... (not readable), Grum-Grzhimailo, 14.V.1890]; 1♀: р. Сэрг-чу, 13800, близ Желтей, Тибет, Козлов, конец V.1901 [river Sarg-chu, 13800, near Yeltei, Tibet, Kozlov, end V.1901]. Coll. A. Semenov-Tian-Shansky. [ZIN]. Examined from high quality photographs, including the terminalia (Fig. 4D). **Nepal:** (1♂, 1♀) 1♂: (E. NEPAL) / Thurupka (2600 m), 27° 36′ N, 87° 36′ E - - - / Topke Gola (3700 m) / 27° 38′ N, 87° 35′ E // June 12, 1972 / H. Shima leg. / Kyushu Univ. Col. //

Gymnochaetopsis / *porphyrophora* Z. (handwritten) / det. H. Shima 2020 [BLKU]; 1♀: (E. NEPAL) / Thudam (3500 m) / 27° 45′ N, 87° 32′ E / July 8, 1972 / Malaise trap (4) / Kyushu Univ. Col. *Gymnochaetopsis* / *porphyrophora* Z. (handwritten) / det. H. Shima 2020 [BLKU].

Taxonomy

Genus *Gymnocheta* Robineau-Desvoidy, 1830

Gymnocheta Robineau-Desvoidy, 1830: 371 (also subsequently spelled *Gymnochaeta*, unjustified emendation). Type species: *Tachina viridis* Fallén, 1810 (as *viridis* Meigen), by monotypy (see also O'Hara et al. 2009: 142).

Redescription (European species). Male (Figs 1, 2, 4, 5).

***Colouration* (Fig. 1):** The colour described here is based on freshly collected specimens. In older specimens the black or dark brown colour is often changed to brown, red brown, or beige brown. Head to a varying extent covered with microtomentum, which affects how clearly the metallic green ground colour shines through, the latter characteristic of the genal dilation, fronto-orbital plate, and occiput but sometimes hard to recognise, as the interpretation depends on the direction of the incidence of light: the specimens should be viewed from different angles. Facial plate light brown to black with or without a metallic green spot at lower margin. Parafacial black but in older specimens narrowly reddish-brown along the ptilinal fissure. Genal groove reddish brown. Frontal vitta dark brown to black. Occiput and postgena with white to greyish white hairs. Antenna matt dark brown or black due to the greyish microtomentum, pedicel sometimes lighter apically, arista black. Palpus black or dark brown in older bleached specimens. Clypeus (sometimes with a metallic green tint) and prementum black, labella from dark brown to beige brown.

Thorax and abdomen with different shades of metallic green but often also partly blue, purple or red. In our European species *G. magna* and *G. viridis* show a bright metallic ground colour, *G. lucida* an olive green and *G. zhelochovtsevi* a dark green colour, the shine depending on the direction of the light. Scutum, when viewed from the side and slightly from behind, with four black longitudinal stripes of microtomentum, changing from grey to purple depending on the direction of the incident light; presutural area with the medial stripes narrow and widely separated, the lateral stripes are wedge-shaped and reach the level of posthumeral seta. In aged specimens, caught late in the season, the microtomentum can be worn off and give the specimens a polished appearance on scutum. Proepisternum black and densely covered with microtomentum or with the metallic green colour slightly subshiny. Legs normally extensively black or dark brown, which can change to lighter brown in aged specimens; fore coxa in anterodorsal region and sometimes also femora with remnants of metallic green or blue tint, covered with light grey microtomentum. Wing veins black and/or brownish

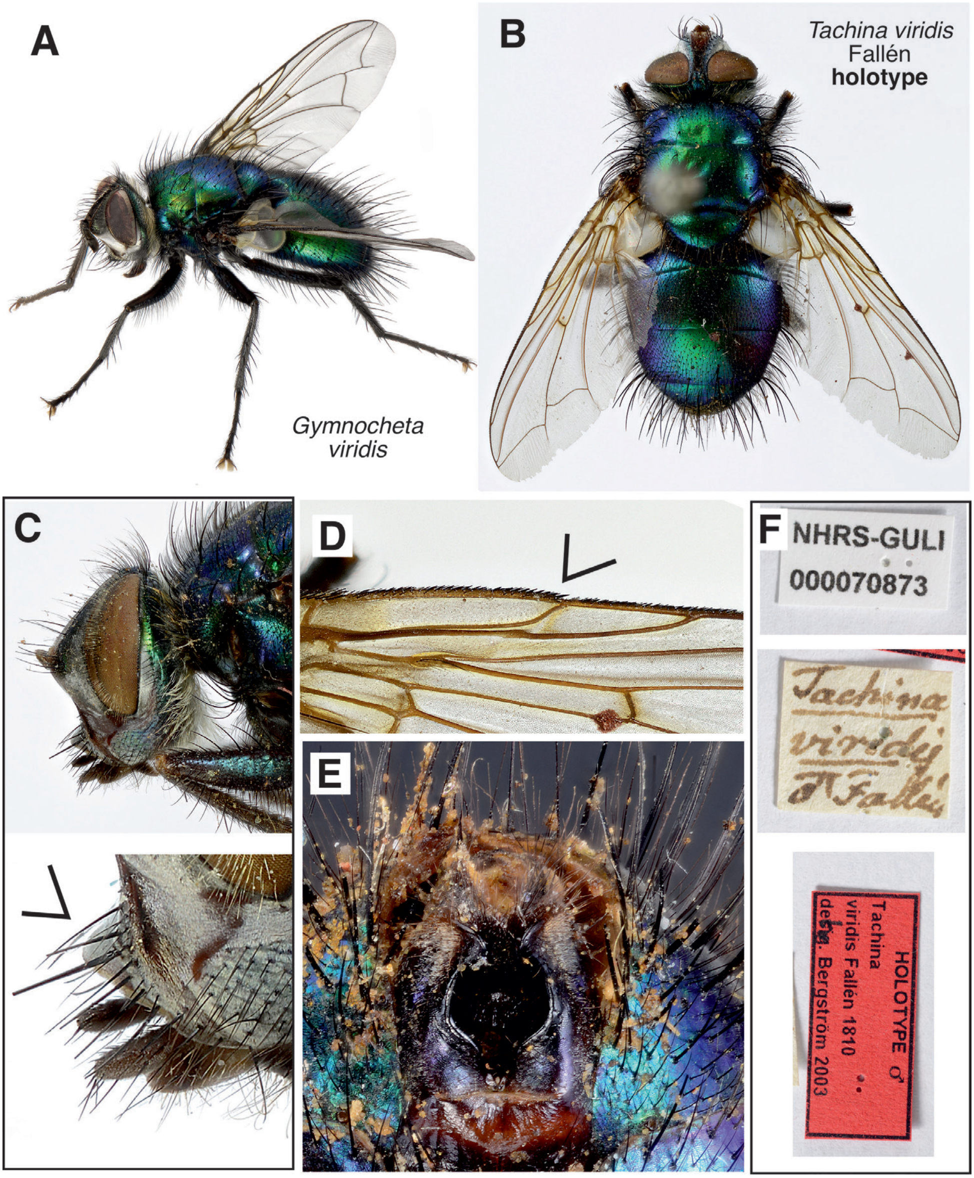

Figure 1. *Gymnocheta* spp. habitus **A** habitus *Gymnocheta viridis* ♂ **B–E** *Tachina viridis* Fallén, holotype specimen **B** dorsal view **C** head in lateral view. Note the protruding lower facial margin (arrowhead) **D** detail of the right wing edge. Note the reduced costal spine (arrowhead) **E** sternite 5 of the holotype **F** labels associated with the holotype. All photographs by Göran Liljeberg.

black, wing membrane with a brownish tinge. Wing membrane around crossvein r-m sometimes narrowly infuscate. Tegula and basicosta dark brown to black. Halteres brown but stalk and knob partly blackish. Calypters greyish white, edge for the most part beige but inner edge distinctly infuscate, with a white fringe.

***Head* (Figs 1, 2):** Head in profile angularly protruding at level of antennal insertion, width of parafacial at this level ca. 0.6–0.8 × the horizontal eye diameter. Frons in dorsal view at narrowest point, 0.3–0.7 × the width of an eye. Frontal vitta gradually tapering toward ocellar tubercle in *G. magna* and *G. viridis*, tapering toward middle (sometimes narrowest here) and then parallel-sided in *G. lucida* or wide and parallel-sided in *G. zhelochovtsevi*. Fronto-orbital plate with a row of 10–14 medioclinate strong frontal setae and some additional setulae, uppermost setula tiny and sometimes slightly reclinate; 3–5 setae extend on upper part of parafacial, reaching the middle of the pedicel with the row curving laterally, and here sometimes accompanied by some setulae; frontal plate outside the frontal row of setae with sparsely short and tiny setulae. Height of face 0.8–0.9 × the length of frons. Gena in profile at narrowest point, 0.3–0.4 × as high as vertical eye diameter. Lower anterior area of genal groove in front of genal dilation bare or rarely with some minute setulae. Vibrissa normally well developed and slightly shorter than height of face, inserted at the level of the lower facial margin. In some specimens of *G. lucida* there is no distinct vibrissa but two or three equally strong supravibrissal setae. Facial plate slightly convex between the antennae and except for *G. magna* hardly visible in profile; lower facial margin protruding particularly in the middle but except for *G. magna* only vaguely visible in profile. Chaetotaxy variable: Facial ridge with 1–4 strong and 0–3 additional thinner supravibrissal setae on lowest quarter (length of them at least equal to narrowest width of parafacial) and 2–5 thin and short setulae. Ridge below vibrissa with 3–7 strong subvibrissal setae continuous with the genal setae, longest 0.5–0.6 × the length of vibrissa. Ocellar tubercle with the ocelli forming a slightly pointed or in some specimens an almost equilateral triangle, two strong lateroproclinate ocellar setae inserted between anterior ocellus and posterior ocelli, accompanied by a tuft of thin setulae (sometimes one or two pairs of additional shorter setae may be present). Inner vertical setae crossed, at least subequal in length to the ocellar setae. Outer vertical setae less developed and subequal with the adjacent postocular setae, except for *G. zhelochovtsevi* where they are almost subequal with the inner vertical. Postocular setae long and thin, apically pronouncedly bending forward over the eyes except for *G. zhelochovtsevi*. Occiput evenly convex, normally with a pair of postocellar setae, rarely missing; in upper part with 2(3) somewhat irregular rows of short black setae behind the postocular row of setae. Palpus slightly clavate at tip, subequal to the length of the antennae, with black setulae. Antenna: Scape erect. Pedicel subtriangular and with one elongate seta. First flagellomere relatively short, in profile usually subrectangular or slightly widened towards apex, but sometimes thick and extended or flat and truncate; maximal width in profile 0.8–1.3 × as wide as parafacial at narrowest point and 1.4–1.8 × as long as pedicel. Arista at first sight bare but at higher magnification pubescence, widened in its proximal 1/4 to almost 2/3, and gradually tapering to apex. Eyes densely covered with long hairs, white with a yellowish tint, hairs slightly shorter in *G. zhelochovtsevi*.

***Thorax* (Fig. 1):** Proepisternum bare. Prosternum bare or with tiny setulae present. Postpronotal lobe with 4(5) strong setae, the three basal arranged in an almost right angle, a slightly weaker anterior seta anterior or anterolateral to the inner basal seta. Chaetotaxy of scutum variable: 3(2)+3 acrostichal, 3(2)+4 dorsocentral and 1+3 intra-

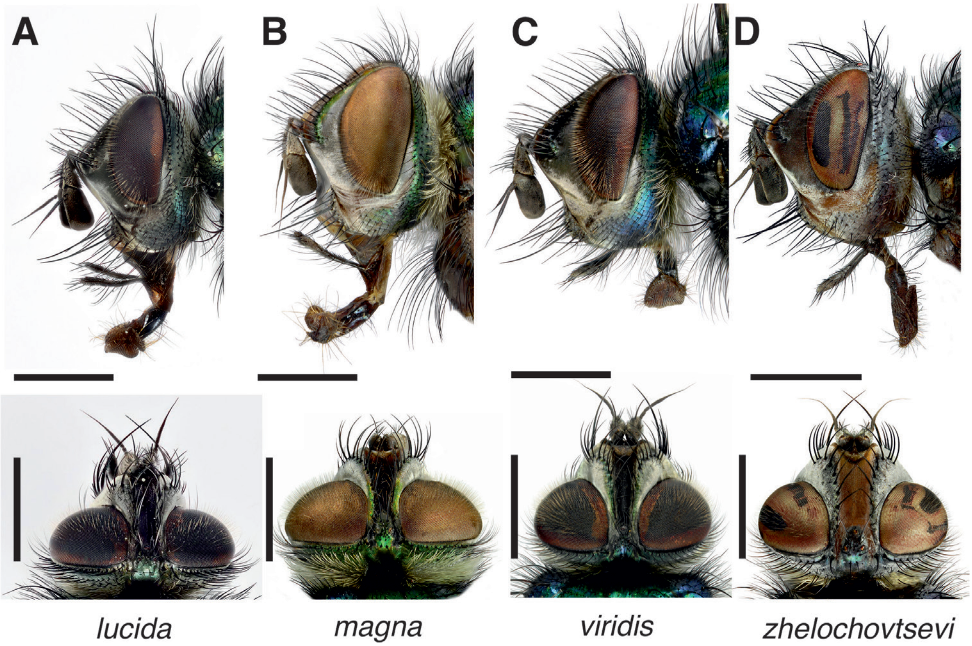

Figure 2. *Gymnocheta* spp. male heads in lateral (upper panels) and dorsal (lower panels) view **A** *Gymnocheta lucida* Zimin **B** *G. magna* Zimin **C** *G. viridis* (Fallén) **D** *G. zhelochovtsevi* Zimin. Note the wide frons and strong outer vertical bristles. Scale bars: 1 mm. All photographs by Göran Liljeberg.

alar setae. Posthumeral seta inside and in front of the presutural intra-alar seta, both close to edge of postpronotum; 1+4 supra-alar setae, presutural supra-alar inserted in the middle between transverse suture and postpronotum; first postsutural supra-alar seta at least subequal with the notopleural setae, shorter than first postsutural intra-alar seta; two notopleural setae, two strong postalar setae. Ground vestiture on scutum (consisting of thin setulae) dense and erect, longest setulae subequal to the shortest setae. Katepisternum with three setae (2+1), rarely four, present. Anepimeron with 2(3) strong setae subequal to the strongest katepisternal setae. Katepimeron bare or with up to five tiny setulae in anterior 1/2. Scutellum also with a rather variable chaetotaxy; normally with four or five pairs of strong marginal setae, sometimes mixed with some shorter and weaker marginal setae/setulae, almost horizontal with the plane of scutellum, apical setae missing, one subapical pair, sometimes very close to apex, parallel or slightly diverging, 2(3) lateral pairs and one basal pair; apart from this often with a tiny pre-basal seta at least present on one side; 2–4 strong suberect preapical discal setae, together with some setulae forming a row in front of the marginal setae, the strongest pair in the middle sometimes subequal to the lateral setae, mixed with numerous tiny setulae.

Legs **(Fig. 1):** Claws and pulvilli on fore legs equal to or slightly longer than tarsal segment 5, the latter ca. 2 × as long as tarsal segment 4. Chaetotaxy variable and it is sometimes difficult to distinguish between seta and setula (seta here accepted if its length is subequal with the width of tibia at middle): Fore tibia with 4–7 anterodorsal setae, 2–5 posterodorsal setae in an irregular row and two or three posterior setae; preapical anterodorsal seta well developed, subequal with the preapical dorsal and preapical posterior setae.

Wing **(Fig. 1):** Wing veins apart from costal vein and vein R_{4+5} bare. Usually two costal spines (rarely one or three), the strongest lower spine 1.5–3 × as long as the surrounding costal setulae. Fourth and fifth costal section 1.8–2.4 (n = 6) × as long as sixth costal sector. Vein R_{4+5} at node with ventral and dorsal setulae. Bend of vein M acute, length of appendix 0.3–0.5 × the shortest distance from bend to wing edge. Cell r_{4+5} open at wing edge or rarely almost closed (according to Zimin normally short-stalked or closed in *G. mesnili*). Apical section of vein M concave reaching wing margin in front of wingtip.

Abdomen **(Figs 1, 4):** Domed, ground-vestiture erect or at least semierect on tergites 3 and 4, also ventrally. Syntergite 1+2 with middorsal depression reaching to the end of the segment. Chaetotaxy variable: Tergite 2 without a pair of median marginal setae, with 2(1)–3 lateral setae on each side. Tergite 3 with 2–4 pairs of unequally often irregularly set strong median discal setae, with a pair of median marginal setae and (1)2–3 lateral setae on each side. Tergite 4 with 2–3(4) pairs of unequally and likewise irregularly set strong median discal setae, in dorsal view with a full row of 10–14 marginal setae. Tergites 3 and 4 frequently with one median discal seta missing or set more laterally. Tergite 5 with two or three irregular rows of unequally strong discal setae and a row of medium strong marginal setae.

Male terminalia **(Figs 1E, 4, 5):** Tergite 6 completely reduced. Sternite 6 strongly asymmetrical, with the broader left arm articulating with segment 7+8. Segment 7+8 large and convex, slightly larger than epandrium, separated from tergite 5 by a wide membrane. Epandrium in profile with a subquadrate appearance, with numerous setulae (the longest placed dorsally). Sternite 5 (Fig. 1E, 4E) in ventral view with distinct posterolateral lobes and a broad medial cleft that anteriorly narrows to a small U-shaped indentation; length of cleft (measured from the tip of the posterolateral lobes, including the U-shaped cleft) 1.8–2.5 × its width (measured at the anteriormost incision). Lobes with widespread setulae, rounded or triangular at apex; along the inner edge towards the cleft distinctly concave, from inner dorsomedial surface showing a long narrow or backwards expanding process; U-shaped median incision in posterior medioventral region with a pair of densely spinulose wart-like lobes; basal plate bare (without setulae) ca. 0.40–0.45 × the length of the sternite itself, and 2.2–2.7 × as wide as long, anterior margin distinctly concave; transversal membranous stripe wide and narrow, almost touching the U-shaped indentation. Tergite 6 completely reduced. Sternite 6 strongly asymmetrical, with the broader left arm articulating with syntergosternite 7+8, the latter large and convex slightly larger than epandrium. Epandrium arched trough-shaped, in lateral view with a subtriangular appearance, with numerous setulae (the longest placed dorsally). Syncercus in lateral view (Fig. 5A) smoothly curved at apex; in caudal view (Fig. 5B) triangular, narrowed to a blunt or rounded apex, with long basal lobes; 1.7–2.1 × as long as maximal width (length measured from base of membranous median suture to apex), slightly incurved at middle and close to

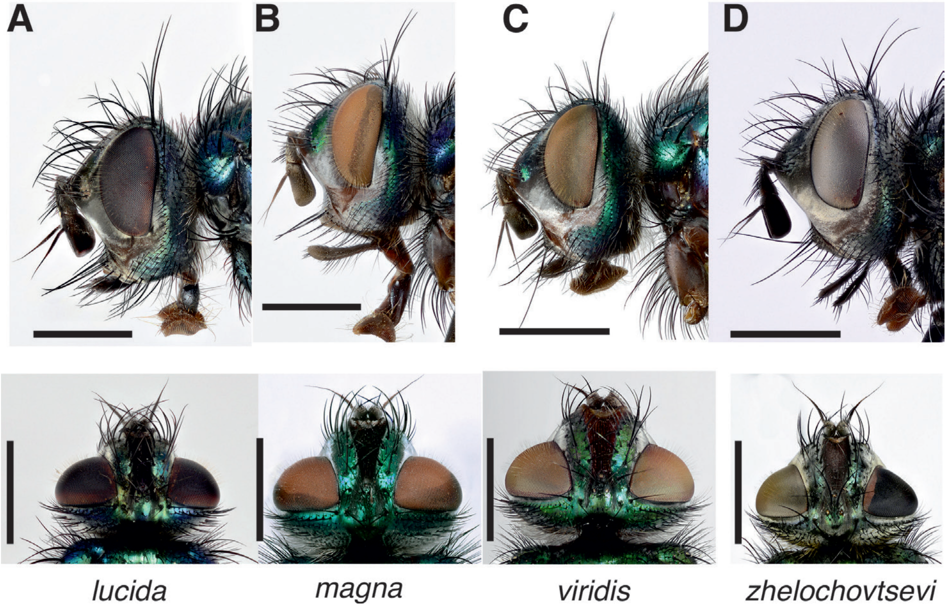

Figure 3. *Gymnocheta* spp. female heads in lateral (upper panels) and dorsal (lower panels) view **A** *Gymnocheta lucida* Zimin **B** *G. magna* Zimin **C** *G. viridis* (Fallén) **D** *G. zhelochovtsevi* Zimin. Scale bars: 1 mm. All photographs by Göran Liljeberg.

apex; numerous black setae/setulae laterally give *G. lucida* a characteristic appearance. Surstylus in lateral view (Fig. 5A) slightly curved (*G. lucida*) or arch-like bent (*G. magna*, *G. viridis*, and *G. zhelochovtsevi*), at least proximally along posterior margin with some tiny setulae, otherwise with numerous spread sensory pores; separated from epandrium by a very narrow membranous succession. Pregonite lance-like in caudal view; lobe-like in lateral view (Fig. 5C) with a hook-like projection apically and some sensorial hairs along its posterior margin. Postgonite quite narrow, broadly membranous apically and therefore with a hook-like appearance.

Aedeagus: Basiphallus with a basal projection and a distinct digitiform epiphallus. Distiphallus in lateral view (Fig. 5C) with the dorsal sclerite as two narrow separate arms extending from apex of basiphallus, close to the posterior edge of the distiphallus all the way to the anterior tip; i.e., not fused dorsomedial and consequently without a median projection; basis of ventral sclerite prominent, lateroventral region with a row of numerous spines; medioventral ridge in lateral view narrow and weakly sclerotised, in ventral view resembling X, with base directed towards the ventral sclerite and apex to the end of the dorsal sclerite.

Female (Figs 3, 6): Differs from male as follows:

***Colouration*:** Fronto-orbital plate with a more widespread metallic green colour; the metallic ground colour continues down on the upper part of parafacial; in large parts covered by greyish microtomentum in *G. zhelochovtsevi*.

***Head* (Fig. 3):** Frons wider, at its narrowest point 0.8–1.0 × as wide as an eye in dorsal view. Frontal vitta either progressively tapering towards ocellar tubercle and at this level

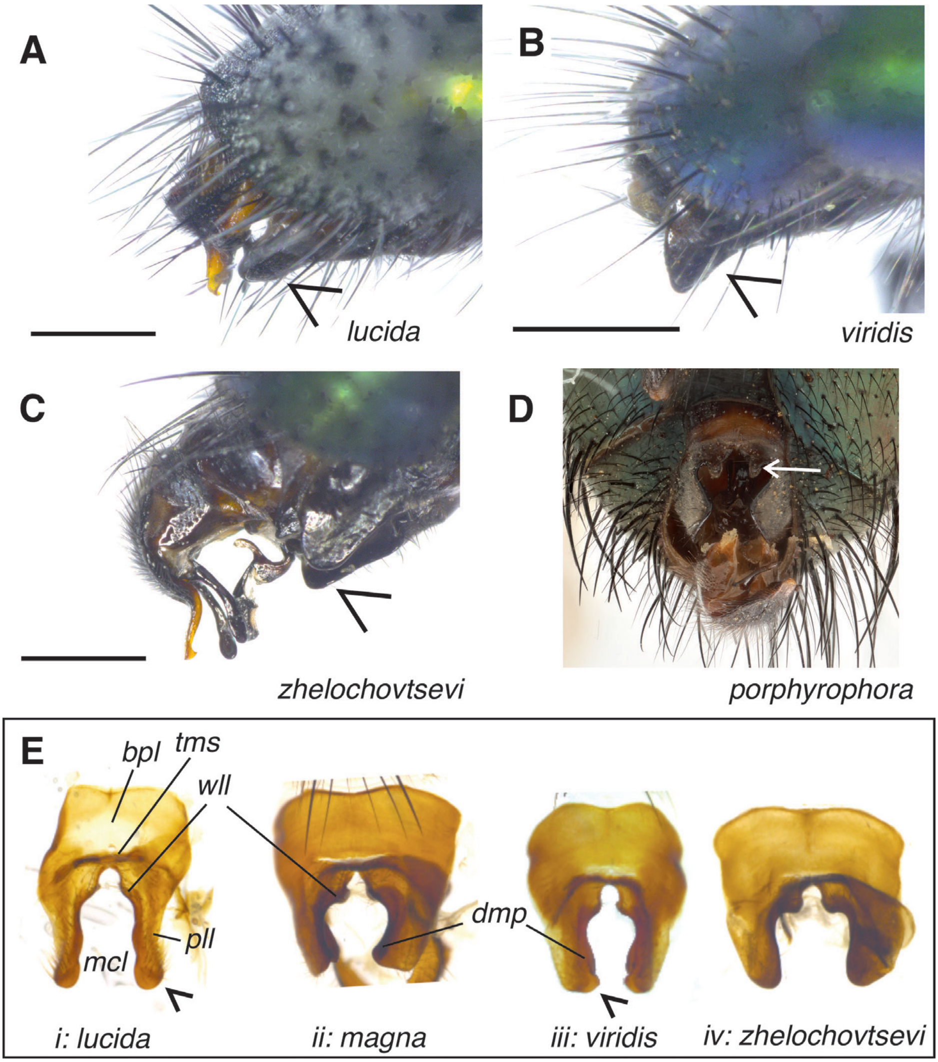

Figure 4. Fifth sternites of *Gymnocheta* spp. males **A** *Gymnocheta lucida* male abdomen. Note the narrow profile of the posterior edge of the fifth sternite (arrow) **B** the edge of the fifth sternite in *G. viridis* is bulky and protruding beyond the tip of the abdomen, clearly recognisable from the side **C** the posterolateral lobe of *G. zhelochovtsevi* is somewhat subrectangular as in *G. magna*, but more rounded in profile. Note the apical hook of the syncercus **D** in contrast to *G. zhelochovtsevi*, posterior edge of fifth sternite in *G. porphyrophora* with well-developed median lobes (arrow) **E** dissected fifth sternites of Nordic *Gymnocheta* spp. in comparison: i) *G. lucida*, ii) *G. magna*, iii) *G. viridis* and iv) *G. zhelochovtsevi*. A distinct dorsomedial process present in *G. magna* and *G. viridis* Abbreviations: **bpl**–basal plate; **dmp**–dorsomedial process; **mcl**–median cleft; **pll**–posterolateral lobe; **tms**–transversal median stripe; **wll**–wart-like lobe (or median lobe). Photograph **D** by V. Neimorovets, rest by J. Pohjoismäki.

mostly narrower than width of fronto-orbital plate (*G. magna* and *G. viridis*), narrowest close to middle (*G. lucida*) or with almost parallel edges in anterior 1/2 or more and the narrowing (*G. zhelochovtsevi*). Fronto-orbital plate normally with fewer, 6–11 moderately strong medioclinate frontal setae. Ocellar tubercle with a pair of strong proclinate ocellar setae as in male but with shorter and more sparsely set setulae. Fronto-orbital plate with 2(3) strong proclinate orbital setae, the anterior one stronger, one upper, slightly lateroclinate, orbital seta at level of anterior ocelli. Inner vertical setae strong and crossed. Outer vertical setae strong and at least 0.6 × the length of the inner vertical setae. Postocular setae short and insignificantly bending forward. First flagellomere 1.3–1.8 × as long as pedicel.

***Legs*:** Legs black. Claws and pulvilli on fore legs shorter ca. 0.7–0.8 × as long as tarsal segment 5, the latter 1.5–1.7 × longer than tarsal segment 4.

***Abdomen*:** Tergite 5 trapezoid, along anterior margin ca. 2 × as wide as long.

***Female terminalia* (Fig. 6):** Ovipositor short, deeply drawn into the lumen of the sternite 5. Uterus present, 3 equally sized spermathecae. Species are ovolarviparous; dissected females of *G. lucida* and *G. viridis* sometimes contained > 200 first instar larvae in different state of development. The first instar larvae are known to search actively for the host.

Tergite 6 reduced into narrow and somewhat elongated hemitergites, widely separated, in the membranous region accompanied by 0–3 tiny setulae posterior to the seventh spiracle and sometimes also one or two setulae in a more apical position, sixth spiracle in lateral margin of tergite 6. Sternite 6 shorter 0.5–0.7 × as long as, but slightly wider (1.1–1.2 ×) than sternite 5, 1.5–2 × as wide as long with 4–8 strong setae along the posterior margin accompanied by numerous setulae in posterior 1/5. Tergite 7 strongly reduced, divided into two widely separated small hemitergites located close to the lingulae, with 0–3 setulae in the adjacent membranous area, left and right seventh spiracles displaced in membrane between tergites 6 and 7, sometimes close to sixth spiracles. Sternite 7 ca. as long but slightly narrower than sternite 6, with numerous tiny setulae most of them restricted to the posterior margin, anterior 4/5 bare. Tergite 8 missing (fully reduced). Sternite 8 strongly reduced, hidden between hypoproct and sternite 7; covered by sensory pores (sensilla trichodea). Hypoproct in ventral view semi-circular to almost triangular, with a middorsal depression, densely covered with setulae, in lateral view (Fig. 6) with dorsal side straight or slightly bent towards the cerci, lingulae present. Epiproct strongly reduced (no sclerotising visible) but in caudal view indicated by the presence of 3–10 setulae inserted above the cerci. Cerci with numerous setulae of varying length, in lateral view the strongest setulae at least subequal in length with sternite 7.

The European species of *Gymnocheta* are treated in alphabetical order. All Finnish records are stored in the Finnish species database, www.laji.fi.

Gymnocheta lucida Zimin

Gymnocheta lucida Zimin, 1958: 60. Lectotype ♂ [ZIN], by designation of Richter (1981: 917) (see below).

Material. Russia: ***Lectotype*** ♂, by designation of Richter (1981: 917). Label: Майхэ близ Шкотова, Уссур. кр., 5.VI.1927, Штакельберг (Mayhe near Shkotov, Ussur.

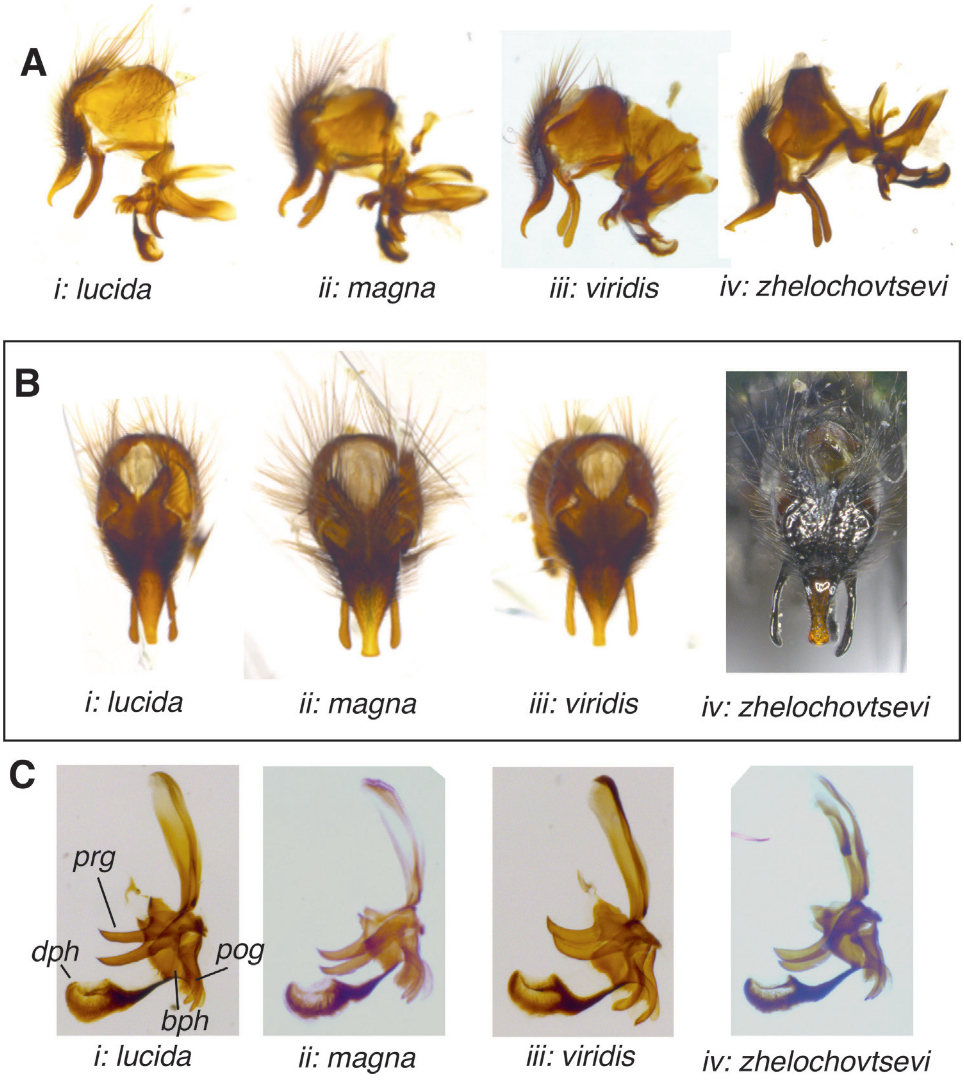

Figure 5. Comparison of *Gymnocheta* spp. male terminalia **A** lateral view of the terminalia: **i** *G. lucida* **ii** *G. magna* **iii** *G. viridis* and **iv** *G. zhelochovtsevi* – note the apical hook of the syncercus **B** dorsal view of the terminalia: **i** *G. lucida* **ii** *G. magna* **iii** *G. viridis* and **iv** *G. zhelochovtsevi*, same specimen as in Fig. 4C **C** aedeagus and gonites of **i** *G. lucida* **ii** *G. magna* **iii** *G. viridis* and **iv** *G. zhelochovtsevi*. Abbreviations: **bph**–basiphallus; **dph**–distiphallus; **prg**–pregonite; **pog**–postgonite. All photographs by J. Pohjoismäki.

kr., 5.VI.1927, Stackelberg) – [Russia, Primorsky Krai, Ussuri district] [ZIN]. Examined from high quality photographs. **Japan:** (2♂♂, 1♀) 1♂: Honshu / 3. V. 1967 / H. Kurahashi // *Gymnochaeta* / *lucida* Mesn. (handwritten) / det. H. Shima, 1982 [BLKU]; 1♀: Honshu / 3. V. 1967 / H. Kurahashi [BLKU]; 1♂: [Aomori, Japan] / Inekari River, Koguriyama, / Hirosaki City / May 28, 2013 / D. Katô leg. // *Gymnocheta* / *viridis* Fall. ? (handwritten) / det. T. Tachi 2020 [BLKU]. **Finland:** (5♂♂, 5♀♀) 1♂:

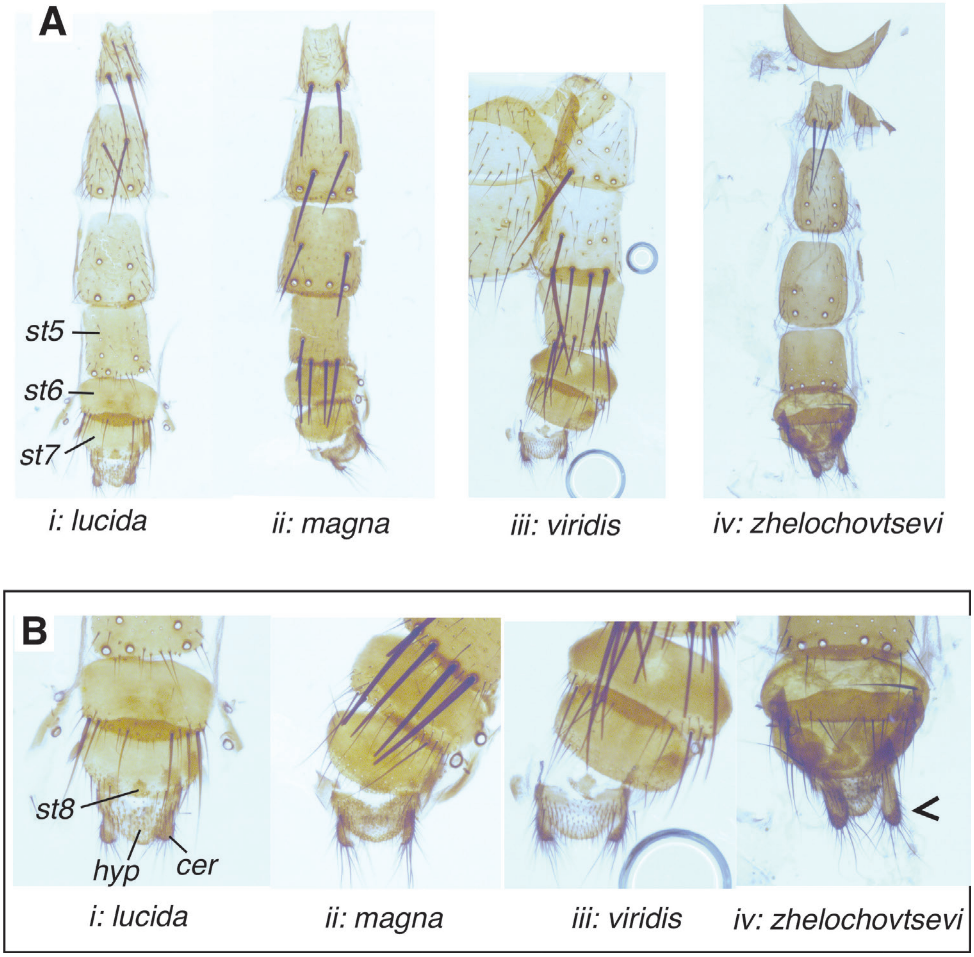

Figure 6. Comparison of *Gymnocheta* spp. female sternites and terminalia **A** ventral view of the sternites and terminalia of **i** *G. lucida* **ii** *G. magna* **iii** *G. viridis* and **iv** *G. zhelochovtsevi* **B** detail of the female terminalia of **i** *G. lucida* **ii** *G. magna* **iii** *G. viridis* and **iv** *G. zhelochovtsevi*. Note the long cerci in *G. zhelochovtsevi*. All photographs by J. Pohjoismäki.

Finland, Tavastia australis, Tammela, Torronsuo, 60.74, 23.58, 13.vi.2004, K. Mattila leg. (BOLD Sample-ID JP00605, GenBank accession number KX843924) [TMNH]; 1♂: Finland, Karelia borealis, Ilomantsi, Pirhunvaara, 62.973; 31.406, 24.vi.2008, J. Kahanpää leg. (BOLD Sample-ID jka08-00018, GenBank accession number KX844119); 1♂: Finland, Ostrobottnia borealis borealis, Rovaniemi, Kivalo, 66.325; 26.854, 13.–25.vi.2014, I. Gonzales leg. [JPC]; 1♀: Finland, Lapponia Kemensis pars occidentalis, Kittilä, Vuotsonperän jänkä, 67.617; 25.45, 24.vii.2007, J. Salmela leg. (BOLD Sample-ID JP00603, GenBank accession number KX843771) [TMNH]; 1♀: Finland, Tavastia australis, Juupajoki, Lakkasuo, 61.798; 24.317, 12.vii.2007, J. Pohjoismäki leg. (BOLD Sample-ID JP00604, GenBank accession number KX843828)

[TMNH]; 1♂: Finland, Karelia borealis, Lieksa, Lahnasuo, 63.118; 30.6144, 20.v.–11.vi.2015, J. Pohjoismäki leg. (BOLD Sample-ID JP2019005) [JPC]; 1♂: ibid. Dissected. [JPC]; 2♀♀: Finland, Karelia borealis, Lieksa, Lahnasuo, 63.118; 30.6144, 12.vi.–3.vii.2015, J. Pohjoismäki leg. [JPC]; 1♀: Finland, Karelia borealis, Polvijärvi, Tiaissuo, 62.950233; 29.424098, 7.–27.vii.2014, J. Pohjoismäki leg. [JPC]. For the boundaries of the Finnish geographical provinces see https://laji.fi/theme/emk). **SWEDEN:** (64♂♂, 33♀♀) 1♀: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 18.vi.1978, leg. R.&T-B. Engelmark [REC]; 1♀: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 22.vi.1978, leg. R.&T-B. Engelmark [REC]; 1♀: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 27.vi.1978, leg. R.&T-B. Engelmark [REC]; 1♀: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 02.vii.1978, leg. R.&T-B. Engelmark [REC]; 1♂: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 06.vii.1978, leg. R.&T-B. Engelmark [REC]– 1♀: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 02.vii.1979, leg. R.&T-B. Engelmark [REC]; 1♂: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 01.vi.1981, leg. R.&T-B. Engelmark [REC]; 1♀: Lu. Lpm, Jokkmokk, Keutatjape, O1667053 N7383578, 18.vi.1981, leg. R.&T-B. Engelmark [REC]; 1♂: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 29.vi.1981, leg. R.&T-B. Engelmark [REC]; 1♂: Lu. Lpm, Jokkmokk, Kallkällmyran, O1677655 N7384113, 30.vi.1981, leg. R.&T-B. Engelmark [REC] Dissected.; 1♂: Lu. Lpm, Jokkmokk, Sasnekape, O1677032 N7380533, 13.vii.1981, leg. R.&T-B. Engelmark [REC]; 1♀: Lu. Lpm, Jokkmokk, Vaimat, ”Stormyren”, O1664900 N7384200, 16.vii.2008, leg. C. Bergström [CBC]; 1♀: Hls, Nordanstig, Ilsbo, Sörängsberget, O1564037 N6863588, 17.vii.1987, leg. C. Bergström [CBC]; 1♀: SE, Vrm, Kristinehamn, Flymossen, O1404043 N6580966, 14.vii.1985, leg. C. Bergström [CBC]; 4♂♂: SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 30.v.1999, leg. C. Bergström [CBC], 1♂ dissected; 2♂♂: SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 03.vi.1999, leg. C. Bergström [CBC]; 2♀♀: SE, UP, Huddunge sn. Evighetsmossen, O1572550 N6657230, 16.vi.2003, leg. C. Bergström [CBC] Dissected; 1♂: 30 / 220 // SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 29.v.2020, leg. C. Bergström [CBC]; 2♂♂: 61–62 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 04.vi.2020, leg. C. Bergström [NHRS]; 2♂♂: 70–71 / 2020// SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 05.vi.2020, leg. C. Bergström [CBC]; 3♂♂, 2♀♀: 72–76 / 2020 // SE, UP, Huddunge sn. Öjemossarna, O1571242 N6657364, 09.vi.2020, leg. C. Bergström [CBC]; 1♂: 82 / 2020 // SE, UP, Huddunge sn. Öjemossarna, O1571242 N6657364, 10.vi.2020, leg. C. Bergström [BLKU]; 1♂: 83–92 / 2020 // SE, UP, Huddunge sn. Öjemossarna, O1571242 N6657364, 10.vi.2020, leg. C. Bergström [CBC]; 6♂♂: 111–116 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572270 N6657616, 15.vi.2020, leg. C. Bergström [CBC]; 15♂♂: 117–131 / 2020 // SE, UP, Järlåsa sn. Ramsmossen, O1574877 N6649254, 18.vi.2020, leg. C. Bergström [CBC]; 2♀♀: 138–139 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572270 N6657616, 21.vi.2020, leg. C. Bergström [CBC]; 1♀: 141–142 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572270

N6657616, 21.vi.2020, leg. C. Bergström [BLKU]; 2♀♀: 141–142 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572270 N6657616, 21.vi.2020, leg. C. Bergström [NHRS]; 1♂♀: in copula, 9♂♂: 144–145, 154–162 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 21.vi.2020, leg. C. Bergström [CBC]; 1♂♀: in copula, 2♂♂,10♀♀: 183, 165-175,184-185 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 23.vi.2020, leg. C. Bergström [CBC]; 1♂, 2♀♀: 194–195, 200 / 2020 // SE, UP, Huddunge sn. Evighetsmossen, O1572552 N6657235, 29.vi.2020, leg. C. Bergström [CBC]

Diagnosis. *Gymnocheta lucida* Zimin is a dark metallic olive to bronze-green tachinid, often with a matt appearance due to a dense microtomentum, which also gives the genal dilation a greyish white appearance.

Redescription. Body length: 7.2–9.5 mm (n = 29).

Male (Figs 2A, 4A, Ei, 5A:i, B:i, C:i).

Colouration**:** Head covered with dense greyish white microtomentum. The metallic ground colour of the genal dilation shines through weakly, compared to *G. magna* and *G. viridis*. However, this difference is sometimes hard to recognise, as the interpretation depends on the direction of the incidence of light, and the specimens should be viewed from different angles. Facial plate black normally without a metallic green spot. Occiput, postgena, genal dilation dark metallic bronze-green in ground colour, frontal plate sometimes narrowly metallic bronze-green along the frontal setae, ocellar triangle mostly black. Palpus deeply black (charcoal) or dark brown in older bleached specimens. Prementum black, labella brown. Thorax and abdomen metallic dark olive green in ground colour, shine depending on the direction of the incidence of light; covered with greyish white microtomentum. The intensity of the microtomentum varies, some specimens having more matt appearance than others and in general the microtomentum in males is more dominant than in females. The intensity of the green colouration is variable, some specimens are more lucid green while others, especially from cooler locations, are very dark, almost blackish green. Scutum, when viewed from the side and slightly from behind, with four longitudinal stripes of microtomentum, changing from grey to purple depending on the direction of the incident light. In aged specimens, caught late in the season, the microtomentum can be worn out and give the specimens a polished appearance for the most dorsal part of scutum and postpronotum. Proepisternum black and densely covered with microtomentum. Fore coxa in anterodorsal region and sometimes also femora with remnants of metallic shine, covered with light grey microtomentum. Wing membrane around crossvein r-m narrowly (sometimes somewhat indistinctly) infuscate. Tegula and basicosta black.

Head **(Fig. 2A):** Frons at its narrowest point, 0.43–0.51 (n = 19) × as wide as an eye in dorsal view. Frontal vitta tapering toward middle (sometimes narrowest at this point) and then parallel-sided towards the ocellar tubercle. Head in profile somewhat protruding at level of antennal insertion, width of parafacial at this level ca. 0.55–0.65 × (n = 17) the horizontal eye diameter. Fronto-orbital plate with a row of 10–12 medioclinate moderately strong frontal setae and some additional setulae, uppermost setula tiny sometimes slightly reclinate, four or five setae descending on upper part of parafacial, reaching the middle of the pedicel with the row curving laterally, and here sometimes attended by some setulae; fronto-orbital plate outside the frontal row of setae with sparsely, spread, short and tiny setulae. Height of face slightly shorter than the length of frons (n = 17). Gena in profile at narrowest point, 0.29–0.38 (n = 14) × as high as vertical eye diameter. Vibrissa normally well-developed but in some specimens there is no distinct vibrissa but two or three equally strong supravibrissal setae. Facial plate slightly convex but hardly visible in profile, but lower facial margin protruding especially in the middle but in profile hardly below the subvibrissal setae. Facial ridge on less than lower 1/5 with 2–4 strong and 0–2 additional thinner supravibrissal setae (length of them at least equals narrowest width of parafacial) and 2–4 thin and short setulae. Ridge below vibrissa with 3–5 strong subvibrissal setae continuous with the genal setae, longest ca. 0.5 × the length of vibrissa. Inner vertical setae strong and crossed, longer than the ocellar setae, outer vertical setae less developed, subequal with the adjacent postocular setae. Postocular setae long and thin, apically pronouncedly bending forward over the eyes. Occiput with a pair of postocellar setae mostly subequal with the outer vertical setae, but sometimes missing. Palpus slightly clavate at tip, subequal to the length of the antenna and densely covered with short black setulae 2 strong preapical setulae and four or five irregular ventral setulae. Antenna: First flagellomere in profile 1.10–1.32 ×) (n = 15) wider than parafacial at narrowest point, and 1.39–1.56 (n = 15) × as long as pedicel. Arista widened in at least its basal 1/2 (sometimes almost in basal 2/3) and gradually tapering to apex.

***Thorax*:** Prosternum bare. Scutum with 3(2)+3 acrostichal, 3(2)+4 dorsocentral and 1+3 intra-alar setae. Ground vestiture on scutum (consisting of thin setulae) dense and erect, longest setulae subequal to the shortest setae. Scutellum normally with four (rarely five) pairs of strong marginal setae, the subapical pair sometimes inserted close to apex, a tiny pre-basal seta present at least on one side; normally four suberect preapical discal setae, forming a row in front of the marginal setae, the strongest pair in the middle sometimes subequal to the lateral setae, mixed with numerous tiny setulae the longest at least 1/5 as long as the strong preapical setae.

***Legs*:** Claws and pulvilli on fore legs ca. 1.1–1.2 (n = 5) × as long as tarsal segment 5, the latter 2.0–2.1 (n = 5) × as long as tarsal segment 4. Fore tibia with a row of 4–6 anterodorsal setae and two or three thin setulae, 4–7 setae/setulae in an irregularly posterior or posterodorsal position (often two or three of them representing setae but sometimes only five tiny setulae present): preapical anterodorsal seta well developed, subequal with the preapical dorsal and preapical posterior setae. Mid tibia with a row of 4–6 anterodorsal setae the strongest in the middle, 2–4 posterodorsal setae (at least two are strong), two posterior setae, one ventral seta often accompanied by a tiny setula. Hind tibia with equally long preapical anterodorsal and posterodorsal setae, apical posteroventral seta ca. 1/2 length of the anterioventral seta; a continuous irregular row of 8–11 anterodorsal setae / setulae of which 4–6 represent strong setae, three or four posterodorsal setae and two or three anteroventral setae.

***Wing*:** Usually two costal spines (rarely one or three), the strongest lower spine ca. 3 × as long as the surrounding costal setulae, normally only somewhat shorter than crossvein r-m. Fourth and fifth costal section 1.8–2.1 (n = 6) × as long as sixth costal sector. Vein R_{4+5} with 3–7 ventral and 2–9 dorsal setulae (in one deviating specimen with nine setulae almost reaching r-m). Cell r_{4+5} often somewhat narrowly open at wing edge, 0.50–0.75 × the length of crossvein r-m.

Abdomen **(Fig. 4A):** Domed, ground-vestiture erect or at least semierect on tergites 3 and 4, also ventrally. Tergite 2 with two (rarely one) lateral setae on each side. Tergite 3 with two or three pairs of unequally often irregularly set strong median discal setae, with a pair of median marginal setae and 2(3) lateral setae on each side. Tergite 4 with two or three pairs of unequally and likewise irregularly set strong median discal setae, in dorsal view with a full row of 10–12 marginal setae. Tergites 3 and 4 frequently with one median discal seta missing or set more laterally. Tergite 5 with two or three irregular rows of unequally strong discal setae and a row of medium strong marginal setae.

Terminalia (4 dissections) (Figs 4A, Ei, 5A:i, B:i, C:i): Sternite 5 (Fig. 4A, Ei) in ventral view with finger-like lobes; length of cleft (measured from the anteriormost indentation) 2.5 × its width. Lobes with widespread setulae, rounded at apex. Dorsomedial process narrow and somewhat indistinct. Basal plate bare (without setulae) ca. 0.4 × as long as sternite 5 and 2.2–2.3 × as wide as long. Syncercus in profile (Fig. 5A:i) smoothly curved before apex, in caudal view (Fig. 5B:i) rounded at apex; 2 × as long as its maximal width (measured from base of membranous median suture to apex); vaguely curved inwards at middle and close to apex; numerous dorsolateral setulae at middle gives a characteristic dense and fur-like appearance. Surstylus (Fig. 5A:i) bacilliform with some tiny setulae most prominent along posterior margin in the proximal region, otherwise with numerous spread sensory pores, straight in caudal view, in profile gradually tapering at base, smoothly curved, evenly thick apart from an indicated widening at apex, bent towards syncercus. Pregonite lance-like in caudal view; lobe-like in profile (Fig. 5C:i) with a narrow hook-like projection apically, shortly tapering at apex, with short sensorial hairs along its posterior margin, anterior margin to some extent incurved. Aedeagus: distiphallus in profile compact and widest close to apex (Fig. 5C:i).

Female (Figs 3A, 6A:i, B:i): Differs from male as follows:

Colouration**:** Fronto-orbital plate almost entirely metallic bronze-green when viewed from behind and slightly from above; the metallic ground colour at least partly interrupted on the upper part of parafacial, sometimes in patches reaching the level of the lowermost frontal setae. However, most of the metallic ground colour on upper part of parafacial and anterior 1/3 of fronto-orbital plate is covered by greyish white microtomentum, dense especially along eye margin and frontal setae, but when viewed from side and slightly from above with golden reflections. Thorax and abdomen dark metallic green to bronze-green, microtomentum normally thinner than in males, most intense on the pleura and episternum.

Head **(Fig. 3A):** Frons wider, at its narrowest point 0.78–0.93 (n = 10) × as wide as an eye in dorsal view. Frontal vitta tapering toward middle (sometimes narrowest at this point) and then gradually widening towards the ocellar tubercle, its width at ocellar tubercle exceeding the width of fronto-orbital plate at this point. Fronto-orbital plate normally with fewer, 7–11 moderately strong medioclinate frontal setae. Outer vertical setae strong 0.65–0.75 × the length of inner vertical setae; subequal with the ocellar setae and the posterior proclinate orbital setae, distinctly stronger than the lateroclinate orbital setae and at least twice the length of the adjacent postocular setae. Postocellar setae short, tiny and subequal with the upper postocular setae. First flagellomere 1.29–1.46 (n = 10) × as long as pedicel, normally ca. as wide as parafacial at narrowest point.

***Legs*:** Claws and pulvilli on fore legs shorter, ca. 0.7–0.8 (n = 5) × as long as tarsal segment 5, the latter 1.5–1.6 (n = 5) × as long as tarsal segment 4.

***Abdomen*:** Ground vestiture dorsolateral on tergites 3 and 4 distinctly prone contrasting to the erected setulae between the median discal setae. Tergites 3 and 4 with two or three pairs of median discal setae. Sternite 5 somewhat elongated, 1.1–1.2 × as long as its maximal width (Fig. 6A:i), with 5–8 strong setae in posterior 1/2, three or four of them along the posterior margin, in posterior 2/3 accompanied by numerous (50–60) irregularly spread setulae of varying size.

Terminalia (2 dissections) (Fig. 6A:i, B:i): Tergite 6 divided into narrow and somewhat elongated hemitergites, widely separated, each closely accompanied by 0–3 tiny setulae in the posterior membranous area (and sometimes indicated by a pair of setulae in a more apical position). Sternite 6 shorter 0.6–0.7 × as long as but slightly wider (1.2 ×) than sternite 5, 1.5–1.6 × as wide as long with 8 setae (n = 3) along the posterior margin and with numerous tiny setulae in posterior 1/5. Tergite 7 with 0–3 setulae in the adjacent membranous area. Sternite 8 with 6–8 sensory pores (sensilla trichodea). Hypoproct (Fig. 6B:i) in ventral view almost triangular, apex only slightly rounded (studied in ventral and somewhat caudal position pointed at apex): with a quite poorly developed medioventral depression, densely covered with setulae that laterally are longer; in profile slightly bent towards the cerci, apex of hypoproct hardly reaching tip of cerci, lingulae well developed. Epiproct in caudal view indicated by the presence of three or four setulae inserted above the cerci. Cerci short with numerous setulae of varying length, the strongest setulae in profile subequal to the length of sternite 7.

DNA. The Co1 DNA barcode sequence of *G. lucida* differs markedly from the other European species of *Gymnocheta* (Fig. 7). It has been assigned a species-specific Barcode Index Number (BIN): BOLD:ACF3891.

Distribution. *Gymnocheta lucida* was previously known only from the Russian Far East and Japan (Richter 2004) and we report it here for the first time as also common and widespread in Finland and northern Sweden. In the Barcode of Life Database (BOLD), there is one match for the species-specific BIN from Norway. This species likely occurs also elsewhere in Europe but has been confused with the common *G. viridis*, and may have a continuous range throughout the Central Palaearctic.

Biology. Almost all Finnish records of *G. lucida* are from ombrotrophic raised bogs. The only exception is the record from Rovaniemi, Lapland (Finland), collected from a pine forest habitat. However, it is typical that insect species that are specific

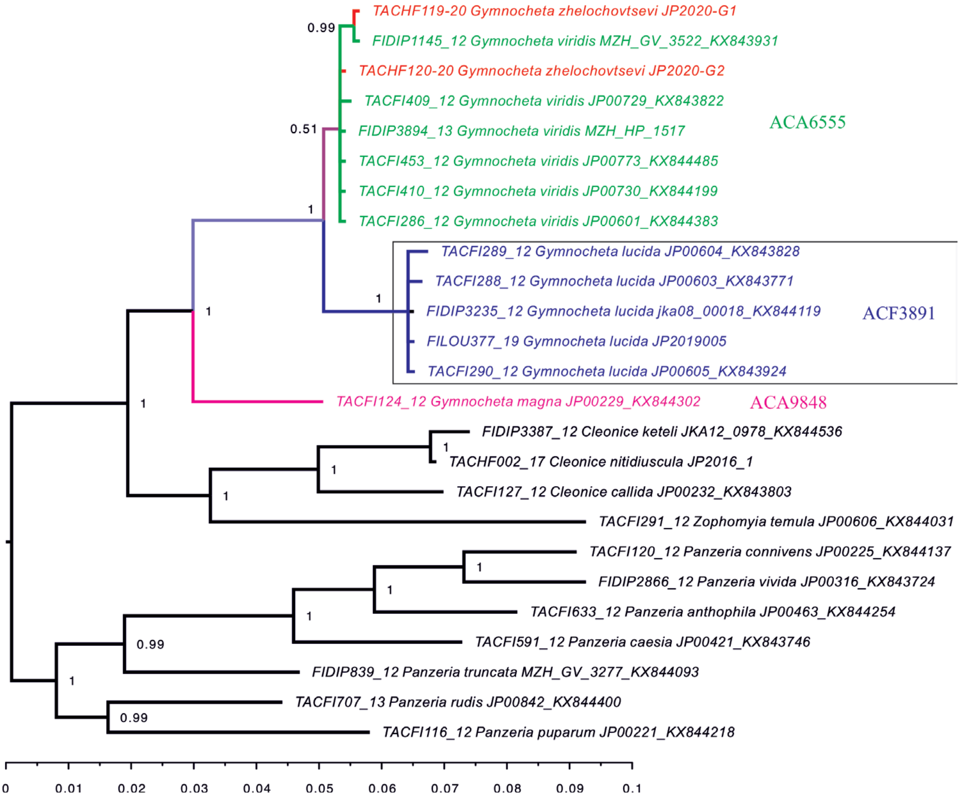

Figure 7. Maximum likelihood tree of the *Co1* sequences of the Nordic *Gymnocheta* spp. and related Ernestiini. Numbers at nodes indicate posterior probabilities and scale bar the relative sequence divergence. BOLD progress ID given before the species name and sample ID as well as GenBank access number given after it. The DNA barcodes do not differ between the Nordic *G. zhelochovtsevi* and *G. viridis* (BOLD:ACA6555) but differ significantly from *G. lucida* (BOLD:ACF3891) and *G. magna* (BOLD:ACA9848).

to bogs or moorlands in the south extend their habitat preferences to open forests or heathlands in the north. *Gymnocheta viridis* is also sometimes recorded from bogs, so the habitat is not a reliable indicator for the species. Similarly, the habitats in Upland are best described as ombrotrophic bogs separated by different types of coniferous woodlands. The bogs partly covered with dwarfed pine trees, and a scrub layer dominated by *Vaccinium uliginosum*, *Rhododendron tomentosum*, *Myrica gale*, *Calluna vulgaris*, and *Betula nana*. The coniferous area surrounding the bogs consists discontinuously of rocky outcrops densely covered by different lichens, i.e., *Cladonia* sp. and *Cetraria islandica*, and old pine trees, and sinks also with old pine trees and single spruces; the scrub layer here is dominated by *Vaccinium myrtillus* but also with elements of *Vaccinium vitis-idaea*, *Rhododendron tomentosum*, and *Vaccinium uliginosum*. The three collection sites of Kallkällmyran, Keutatjape, and Sasnnekape are located just south of the Arctic Circle in Jokkmokk, Lule Lappmark (Sweden). They have been described as rich to medium rich fens in the coniferous zone near Jokkmokk (Engelmark and Engelmark 1989). These minerotrophic fens are fed with ferriferous groundwater and the complex vegetation is characterised by *Saxifraga hirculus*.

Males appear in late May and individuals are first and foremost observed in small sunlit clearings in the sinks between the rocky outcrops, sitting on leaves and twigs of blueberries apparently watching for approaching females. Some of these clearings likely represent hot spots for aggregation. These are frequently attended by males that fly out sporadically from time to time in response to another passing male, but in one of these hot spots mating was observed on two occasions. One male was collected when visiting the flowers of *Rhododendron tomentosum*. Females appear around second week of June and they are, apart from the ones observed *in copula*, found on the edge of the bogs close to the rocky outcrops. They have been observed between late June to mid-July in characteristic slow, searching flight, low in the vegetation often just a couple of inches above the moss layer, examining tufts of sedges and shrubs, such as *Vaccinium uliginosum* and *Betula nana*. The hosts are currently unknown but concealed larvae of Noctuidae or Erebiidae (Lepidoptera), living in the habitats described above, are most likely.

Gymnocheta magna Zimin

Gymnocheta magna Zimin, 1958: 53. Lectotype ♂ [ZIN], by designation of Richter (1981: 917) (see below).

Material. Russia: ***Lectotype*** ♂, by designation of Richter (1981: 917). Type locality: Ущ. Суцэуктз, ю.-а. Кентей, Монголия, конец V. 1924 (Козлов). Mongolia, Hentiy Aimag [as “Kentei” in Russian], Sutszukte. Not examined. **Sweden:** (4♂♂, 6♀♀) 1♀: SE, UP, Årsta/Slavsta, O1606484 N6639427, 16.vi.1980, leg. C. Bergström [CBC]; 2♀♀: SE, UP, Kvarnbo, O1598600 N6637685, 6.vi.1982, leg. C. Bergström [CBC]; 1♀: SE, UP, Ekebydalen, O1600268 N6637514, 6.vii.1983, leg. C. Bergström [CBC]; 1♂: SE, UP, Skogsängen, Nåsten, O6636152 N1597099, 11.vi.1986, leg. C. Bergström [CBC]; 2♂♂, 1♀: SE, UP, Skogsängen, Nåsten, O6636152 N1597099, 22.vi.1987, leg. C. Bergström [CBC]; 1♀: SE, UP, Skogsängen, Nåsten, O6636152 N1597099, 27.vi.1987, leg. C. Bergström [CBC]. **Finland:** (2♂♂, 3♀♀) 1♂: Ostrobottnia media, Raahe, Hakotauri, 64.7002; 24.4736, 3.vii.2006, K. Varpenius leg. (BOLD Sample-ID JP00229, GenBank accession number KX844302) [TMNH]–1♂: Finland, Karelia borealis, Ilomantsi, Ilajansuo, 62.915455; 31.201721, 20.vi.2013, J. Pohjoismäki leg. [JPC]; 1♀: Ostrobottnia kajanensis, Kuhmo, Ulvinsalo, 63.973506; 30.319950, 22.vi.2019, J. Pohjoismäki leg. [JPC]; 1♀: Regio Aboensis, Mietoinen, Perkko, 6733:3222, 9.v.-16.vi.2004, A. Haarto leg. [AHC]; 1♀: Tavastia australis: Pälkäne, 6807:3353, 27.vi.1993, Y. Ranta leg. [AHC]. **Japan:** (2♂♂, 1♀) 1♂: [KYUSHU] / Takachiho-mine / Kagoshima pref. // VI–7–1960 / H. Shima leg. (handwritten) // *Gymnochaetopsis* / *magna* Zimin / det. H. Shima 2020 [BLKU]; 1♂: [KYUSHU] / Mt. Takachiho / Kagoshima // 16.vi.1968 / A. Nakanishi (handwritten) //

Gymnochaetopsis / *magna* Zimin / det. H. Shima 2020 [BLKU]; 1 ♀: [HONSHU] / Niigata / Myôkôkgen-sho / Sasagamine / 22.vi.1996 / T. Tachi [BLKU].

Diagnosis. A lucid green *Gymnocheta* species with a notably protruding lower facial margin and green femora. This is also the only European *Gymnocheta* species with short costal spines.

Redescription [values in brackets refer to the holotype of *T. viridis* Fallén]. Body length: 7.8–12.1 [12.1] mm (n = 10).

Male (Figs 1B–E, 2B, 4Eii, 5A:ii, B:ii, C:ii).

***Colouration*:** Head covered with a greyish white microtomentum. The metallic ground colour subshiny on the genal dilation but the shine/intensity is depending on the direction of the incident light. Facial plate with a greyish white microtomentum; lower protruding area however with a distinct mint metallic green tint. Occiput, postgena, genal dilation, ocellar tubercle metallic green in ground colour. Fronto-orbital plate narrowly but mostly distinctive mint metallic green along the frontal row of setae. Palpus, clypeus (sometimes with a metallic green tint) and prementum dark brown to black, labella brown beige. Thorax and abdomen bright mint metallic green in ground colour, contrasting with gilt or purple lustre depending on the direction of the incident light, with an indistinct greyish white microtomentum. Scutum when viewed from the side and slightly from behind with four longitudinal stipes changing from grey to gilt or purple depending on the direction of the incident light. Proepisternum normally with the metallic green ground colour subshiny, but less so in dwarfish specimens. Fore coxa in anterior region and femur posteriorly mostly with a metallic green shine. Wing membrane around crossvein r-m rarely infuscated. Tegula and basicosta dark brown or black.

***Head* (Figs 1C, 2B):** Frons narrower than in *G. lucida*, at its narrowest point 0.31–0.38 [0.37] (n = 6) × as wide as an eye in dorsal view. Frontal vitta gradually tapering toward ocellar tubercle. Frons in lateral view somewhat protruding, width of parafacial at level of antennal insertion 0.59–0.72 [0.72] × (n = 6) the horizontal eye diameter. Fronto-orbital plate with a row of 10–14 [11] medioclinate frontal setae, mixed with some setulae, three to five setae descending on upper part of parafacial, reaching the middle of the pedicel with the row curving laterally, uppermost tiny setulae sometimes reclinate; orbital plate at level of ocellar tubercle with numerous moderately long and tiny setulae, frontal plate with more sparsely spread short and tiny setulae. Height of face 0.79–0.85 [0.80] × the length of frons (n = 6). Gena in profile at narrowest point, 0.35–0.39 [0.38] (n = 6) × as high as vertical eye diameter. Facial plate bulged medially and slightly visible in lateral view, lower facial margin distinctly protruding, in strict lateral view visible in front and below the vibrissa. Facial ridge on lower 0.20–0.25 with 1–3 [2] strong and 0–3 [2] additional thinner supravibrissal setae (length of them at least subequal to narrowest width of parafacial) and 2–5 thin and short setulae. Below the vibrissa 4–7 [7] strong subvibrissal setae continuous in front of the genal setae, the posteriormost subvibrissal seta close to the foremost lower genal margin. Inner vertical setae crossed, thin and weaker or at most subequal in length with the ocellar setae, outer vertical setae at most subequal with the adjacent postocular setae. Postocular setae long and thin, apically pronouncedly bending forward over the eyes. Occiput and postgena both with white to greyish white hairs. Antennae: First flagellomere in profile 0.90–1.06 (n = 5) × the actual width of parafacial; at narrowest point; 1.52–1.79 (n = 5) as long as than pedicel. Arista widened in its proximal ¼–1/3, gradually tapering towards apex.

***Thorax* (Fig. 1B):** Prosternum frequently with tiny setulae [without]. Scutum with 3(4)+3 [3+3] acrostichal, 3–4 dorsocentral and 1+3 intra-alar setae. Scutellum with 4(5) [5] pairs of strong setae along margin, apical and subapical pairs slightly diverging; 2–4 [3] suberect dorsal scutellar setae, in front of the subapical setae, the strongest subequal to the lateral setae, rarely with an additional pair of medium strong median dorsal setae; tiny dorsal setulae numerous, the longest at least 1/2 length of the strongest dorsal seta.

***Legs*:** Claws and pulvilli on fore legs slightly longer than fifth tarsal segment, the latter 1.7–2.0 (n = 3) × as long as the fourth. Fore tibia with a row of 5–6 anterodorsal setae, and an irregular row of 2–4 posterodorsal and 2 posterior setae; preapical anterodorsal seta subequal with the preapical dorsal seta, preapical posterodorsal seta short, its length rarely exceeding 1/3 of the dorsal seta. Mid tibia with three or four anterodorsal setae, the strongest in the middle of row, five or six posterior (pd and p) setae, one ventral seta often accompanied by an additional tiny setula. Hind tibia with a continuous row of nine or ten unequally strong anterodorsal setae / setulae of which four or five represent strong setae, three or four posterodorsal setae, the lowest one the strongest, and two or three anteroventral setae.

***Wing*:** (Fig. 1B, 1D) Usually two costal spines, both short and the strongest ventral spine at most 1.5 × as long as the strongest surrounding costal setulae, normally only slightly exceeding 1/2 the length of crossvein r-m. $CS_4 + CS_5$ 2.0–2.3 (n = 3) × as long as CS_6. Vein R_{4+5} at base with 2–4 ventral and 3–5 dorsal setulae.

***Abdomen* (Fig. 1B):** Tergite 2 without a pair of median marginal setae, with 1(2) lateral marginal setae on each side. Tergites 3 and 4 with two or three unequally strong and often irregularly set pairs of median discal setae (sometimes two pairs and one unmatched seta). Tergite 3 with a pair of medial marginal setae, tergite 4 in dorsal view with a full row of 10–12 [10] marginal setae, tergite 5 with two or three irregular rows of strong and medium strong discal setae and a dense row of weak marginal setae.

Terminalia (two dissections) (Figs 1E, 4Eii, 5A:ii, B:ii, C:ii): Sternite 5 (Figs 1E, 4Eii) in ventral view with short and wide lobes; length of cleft 1.7–1.8 × its maximal width. Lobes with widespread tiny setulae, curved inward at apex (posteriormost region in ventral and slightly lateral view with a subtriangular appearance); Dorsomedial process black and expanding backwards, strong, and very characteristic in part separated from sternite 5. Basal plate bare (without setulae) ca. 0.45 × as long as sternite 5 and 2.2–2.3 × as wide as long. Syncercus in lateral view (Fig. 5A:ii) smoothly curved at apex, similar to *G. lucida*; in caudal view (Fig. 5B:ii) somewhat resembling a pointed triangle with long basal lobes; 1.7–1.8 × as long as its maximal width (measured from base of membranous median suture to apex), slightly incurved at middle and close to a characteristic wide and blunt apex, dorsolateral at middle with numerous relatively long setulae. Surstylus (Fig. 5A:ii) slender, straight in caudal view; in lateral view slightly arch-like bent at ca. middle, almost evenly thick apart from apex that is slightly widening, bent towards syncercus. Pregonite lobe-like in lateral view with a wide hook-like projection, with short sensorial hairs along its proximal posterior margin, anterior margin slightly more curved than in *G. lucida*. Aedeagus: Distiphallus (Fig. 5C:ii) in lateral view compact but not widening close to apex.

Female (Figs 3B, 6A:ii, B:ii): Differs from male as follows:

Colouration**:** Fronto-orbital plate vivid mint metallic green when viewed from behind and slightly from above; the metallic ground colour continues down on the upper part of parafacial reaching the level of the lowermost frontal setae; the upper part of parafacial and anterior 1/3 of fronto-orbital plate with a thin greyish white microtomentum, visible along eye margin and as a slim line at the edge of frontal vitta. Thorax and abdomen vivid metallic green, at most with thin whitish microtomentum.

Head **(Fig. 3B):** Frons wider, at its narrowest point 0.75–0.83 (n = 5) × as wide as an eye in dorsal view. Frontal vitta gradually tapering towards ocellar tubercle, at this level often narrower than width of fronto-orbital plate. Fronto-orbital plate normally with fewer, 8–11 moderately strong medioclinate frontal setae. Outer vertical setae fairly stronger than the ocellar setae, shorter than the posteriormost proclinate orbital setae, at least twice the length of the adjacent postocular setae. Postocellar setae short and tiny and subequal with the upper postocular setae. One female with a long and slender first flagellomere otherwise not deviating from the situation in males 1.55–1.88) (n = 5) × as long as pedicel; its maximum width 0.94–1.08 (n = 5) × the actual width of parafacial at narrowest point.

Legs**:** Claws and pulvilli on fore legs shorter ca. 0.7–0.8 × as long as tarsal segment 5, the latter 1.5–1.7 × as long as tarsal segment 4.

Abdomen**:** Ground vestiture dorsolateral on tergites 3 and 4 distinctly prone contrasting to the erected setulae between the median discal setae. Tergites 3 and 4 normally with two or three pairs of median discal setae, tergites 3 and 4 occasionally devoid of one seta. Sternite 5 (Fig. 6A:ii) somewhat elongated, 1.1–1.2 × as long as its maximal width, with four strong setae along posterior margin accompanied by numerous irregularly spread setulae of varying size and one to two additional strong seta in posterior 4/5.

Terminalia**:** (two dissections) (Fig. 6B:ii)Tergite 6 divided into narrow and somewhat elongated hemitergites, widely separated, each in the membranous area accompanied by 3 tiny setulae posterior to the seventh spiracle and one or two setulae in a more apical position. Sternite 6 shorter, 0.5–0.6 × as long as but slightly wider (1.2 ×) than sternite 5, 2 × as wide as long with four setulae along the posterior margin and with numerous tiny setulae in posterior 1/5. Tergite 7 with three setulae in the adjacent membranous area close to lingulae. Sternite 8 strongly reduced, hidden between hypoproct and sternite 7; compared with *G. lucida* and *G. viridis* rather well developed; possesses at least 20 sensorial pores of which some are provided with tiny setulae; laterally on both sides with a long setula. Hypoproct (Fig. 6B:ii) in ventral view semicircle-shaped, with a distinct middorsal depression, densely covered with setulae, laterally on both sides with one longer setula, in lateral view not bent towards the cerci, apex of hypoproct reaching tip of cerci, lingulae well developed. Epiproct strongly reduced (no sclerotising visible) but in caudal view indicated by the presence of up to ten setulae inserted above the cerci. Cerci with numerous setulae of varying length, in lateral view the strongest setulae are at least subequal in length with sternite 7.

DNA. *Gymnocheta magna* has a unique Co1 barcode sequence, BOLD:ACA9848 (Fig. 7).

Distribution. Widely distributed in the Palaearctic Region (O´Hara et al. 2009). *Gymnocheta magna* is a relatively rare but widespread species in northern Europe. It was recorded as new to Sweden in Hedström (1985) and to Norway in Haraldseide (2012). It was listed from Finland in the checklist by Hackman (1980). The oldest specimen in MZH is from 1865, from Finland.

Biology. The biology of *Gymnocheta magna* is poorly known. This is a summer species in the Nordic countries with a flight time from early June to mid-July. It is not a heathland specialist as suggested by some sparse records from Central Europe (Tschorsnig and Herting 1994), but has also been caught from meadows, forest margins and gardens (see also Fallén's notes below). Both sexes visit flowers, especially those of cow parsnip, *Anthriscus sylvestris* (L.) and caraway, *Carum carvi* L. Females have been observed basking on aspen leaves. Hosts are unknown but are likely to be concealed larvae of Erebidae (Lepidoptera); see *G. viridis*.

Gymnocheta viridis (Fallén)

Material. ***Holotype*** ♂ with a Fallén faded handwritten ink label reading (Fig. 1F): *Tachina* / viridis / ♂ Fallén. It also bears the following labels: Holotype ♂ / *Tachina* / *viridis* Fallén, 1810 / det. Bergström 2003 // *Gymnocheta* ♂ / *viridis* (Fallén) / = *magna* Zimin SYN. N. / det. Bergström 2003. [NHRS, catalogue number NHRS-GULI000070873]. **Sweden:** (53♂♂, 16♀♀): ♂ (Fig. 1A): 3 / 2007 (red frame) // SE, UP, Uppsala, / Flogsta, Ekebydalen / O1600393 N6637642 / 2007-04-30/ leg. Christer Bergström // *Gymnocheta viridis* (Fallén) / J. Pohjoismäki & / C. Bergström 2021 [NHRS]. 3♂♂: SE, SÖ, Katrineholm, / Warbro, Hammarvik / O15405 N65458 1983-05-30 / leg. C. Bergström [CBC]; 5♂♂, 2♀♀: SE, SÖ, Katrineholm, / Warbro, Hammarvik / O15405 N65458 1985-05-25 / leg. C. Bergström [CBC]; 6♂♂: SE, SÖ, Katrineholm, / Warbro, Hammarvik / O15405 N65458 1985-05-26 / leg. C. Bergström [CBC]; 2♂♂: SE, SÖ, Katrineholm, / Warbro, Hammarvik / O15405 N65458 1985-05-27 / leg. C. Bergström [CBC]; 1♂, 3♀♀: SE, SÖ, Katrineholm, / Warbro, Hammarvik / O15405 N65458 1986-05-17 / leg. C. Bergström [CBC]; 1♀: SE, SÖ, Katrineholm, / Warbro, Hammarvik / O15405 N65458 1987-06-21 / leg. C. Bergström [CBC]; 1♀: SE, UP, Flogsta / Ekebydalen, / O16007 N66375 2000-06-15 / leg. C. Bergström [CBC]; 1♂: SE, UP Flogsta / Ekebydalen, / O16007 N66375 2000-05-11 / leg. C. Bergström [CBC]; 1♂: SE, UP, Enköping, / Fånö herrgård / O15890 N66069 2001-05-13 / leg. C. Bergström [CBC]; 5♂♂: SE, UP, Uppsala näs fg. / Sätrasjön / O1594026 N6634171 2001-05-10 / leg. C. Bergström [CBC]; 8♂♂: SE, UP, Enköping, / Fånö herrgård / O15890 N66069 2001-05-27 / leg. C. Bergström [CBC]; 2♂♂: UP, Uppsala näs fg. / Sätrasjön / O1594026 N6634171 2001-06-01 / leg. C. Bergström [CBC]; 1♂, 2♀♀: SE, UP, Uppsala näs fg. / Sätrasjön / O1594026 N6634171 2001-06-03 / leg. C. Bergström [CBC]; 3♂♂: 1381,1384, 1387 (red labels) // SE, UP, Uppsala näs fg. / Sätrasjön / O1594300 N6634400 2001-06-03 / leg. C. Bergström [CBC]. 3♂♂: 1♀, SE, UP, Nåsten / Skogsängen / O1597099 N6636152 2001-06-07 / leg. C. Bergström [CBC] (2 dissected); 2♂♂: SE, UP, Nåsten / Skogsängen / O1597099 N6636152 2005-05-13 / leg. C. Bergström [CBC]; 3♂♂: 4, 6, 7 / 2007 (red frame) // SE, UP, Uppsala, / Flogsta, Ekebydalen / O1600393 N6637642 / 2007-04-30/ leg. Christer Bergström [NHRS]; 4♂♂: 2, 5, 8, 9 / 2007 (red frame) // SE, UP, Uppsala, / Flogsta, Ekebydalen / O1600393 N6637642 / 2007-04-30/ leg. Christer Bergström [CBC]; 2♂♂: SE, VRM, Kristinehamn / O1401300 N6583100 1980-06-13 / leg. C. Bergström [CBC]; 2♀♀: SE, ÖL, S. Möckleby / ”Kalkstensbrottet” / O1537800 N6245300 2000-06-03 / leg. C. Bergström [CBC]; 1♀: SE, ÖL, Segerstad / Seby strand / O1545800 N6245500 2002-05-18 / leg. C. Bergström [CBC]; 1♂: SE, ÖL, Smedby sn. / Eckelsudde / O1537100 N6254400 2002-05-18 / leg. C. Bergström [CBC]; 4♂♂, 3♀♀: SE, ÖL, Kastlösa sn. / Bredäng / O1535100 N6260300 2002-05-19-20 / leg. C. Bergström [CBC]. **Finland:** 6♂♂, 6♀♀, including GenBank accession numbers: KX84393[MZH], KX844485, KX844383 [TMNH, rest of the specimens JPC]. **Germany:** 4♂♂, 6♀♀, Hessen and Nordrhein-Westfalen, including GenBank accession numbers: KX844199, KX843822 [both TMNH, rest of the specimens JPC].

Tachina viridis Fallén, 1810: 276.

Notes. The identity of *Tachina viridis* Fallén, 1810: 276. *Gymnocheta viridis* (Fallén, 1810) is the oldest described *Gymnocheta* and represents the type species of the genus. The Fallén collection, drawer 13 (4), contains a single type specimen (formally the holotype) (Fig. 1B–E) mounted on an old thick pin and is in good condition except for the missing antennae and broken vibrissae. There are also some missing frontal setae and median discal setae on tergites 3 and 4. The protruding lower facial margin (Fig. 1C), metallic green femora (Fig. 1C), indistinct costal spines (Fig. 1D) and the shape of sternite 5 (Fig. 1E) make it obvious that the specimen represents the species until now known as *Gymnocheta magna* Zimin, 1958. When Fallén (1820: 25) wrote “Linea vertices subferruginea, utrinque viridi nitens. Femora virida; tibiae tarsique nigra.” [Frontal stripe brownish, both sides lustrous green. Femora green; tibiae and tarsi black.], he surely must have been looking at this specimen, as the femora of the represented species are notably green compared to the other European *Gymnocheta*. It is also obvious that the name *viridis* used by Fallén, Zetterstedt, Wahlberg, and many subsequent authors until the work of Zimin has concealed at least two different species as shown by the examination of old Swedish specimens (see below).

As a further confirmation of the type specimen identity, the original description in Swedish also refers to a single male: "♂ Denna lysande art, funnen på kummin midsommartiden i Maltesholms trädgård i Skåne, …". [This brilliant species, found on caraway [*Carum carvi*] in midsummer time in Maltesholms garden in Skåne, ….] (Fallén 1810: 276). In later work Fallén (1820: 25) notes records by Zetterstedt while referring to his own previous work: "Mas et Fem. In paludosis Abusa, mense Majo, utrumque sexum legit Zetterstedt. In floribus Cari Carvi in horto praedii Maltesholm mense Junio, unicum marem Muscae caesaris magnitudine vidimus ipsi." [Males and Females. Zetterstedt collected both sexes in May [from] mires/bogs in Abusa [a place in Skåne]. In June on flowers of caraway in Maltesholm garden, a unique male observed, size of *Musca* [= *Lucilia*] *caesar*]. Zetterstedt (1844: 1190) himself writes later about *Tachina viridis*: "Hab. in foliis fruticum & herbarum, etiam in floribus umbellatarum, locis paludosis mihi praesertim obbvia, per hortos & prata Sueciæ, 30 Maj.–15 Jun., minus frequens; scilicet in Scania ad Lund, Abusa, Maltesholm &c., passim; in templo Upsaliæ antiquæ semel a D. Prof Wahlberg capta; e Dania a D Stæger missa". [On foliage of shrubs and herbs as well as flowers of Apiaceae, on bogs/mires [and] I especially [have observed] in gardens and meadows in Sweden. May 30–June 15, less abundant; namely from Skåne to Lund, Abusa, Maltesholm etc., infrequent; in the old Uppsala collection of D. Prof. Wahlberg; many from Denmark by D. Staeger].

Two of these aforementioned non-type specimens are in the NHRS main collection: 1♀: Labels: Hlm / P.Wg. This is apparently the specimen mentioned by Zetterstedt (1844: 1190) "in templo Upsaliae antiquae semel a D. Prof. Wahlberg capta". This specimen, like that of the holotype, represents *Gymnocheta magna* Zimin; 1♂: Labels: Sc. // Z (on a small white tag). In contrast to the previous, this specimen represents the current concept of *Gymnocheta viridis*.

Three additional non-type specimens are present in the Diptera Scandinaviae Collection, drawer 22 in ZMLU: 1♂: Labels: lemon yellow tag // *T. viridis* / ♂. Abusa (handwritten by Zetterstedt). Identity: *Gymnocheta viridis*. This specimen is apparently one of those mentioned by Fallén (1820: 25) and by Zetterstedt (1844: 1190); 1♂: Labels: 9. // Staeger. Identity: *Gymnocheta viridis*. Zetterstedt 1844: 1190 mentioned this specimen; 1♀: Label: purple red tag // *T. viridis* / ♀. Lund. (handwritten by Zetterstedt). Identity: *Gymnocheta magna* (= *viridis sensu* Fallén). This specimen is apparently the one from Lund mentioned by Zetterstedt (1844: 1190).

For the sake of nomenclatural stability, we propose maintaining the current usage of the names *G. viridis* and *G. magna*. Neotype specimen for *Gymnocheta viridis* will be assigned later if ICZN accepts the petition for the replacement of the holotype. The following redescription represents *G. viridis* in its prevailing concept.

Diagnosis. A common, vivid metallic green *Gymnocheta* with strong costal spines and narrow frons in male.

Redescription. Body length: 7.2–10.8 mm (n = 19).

Male (Figs 1A, 2C, 4C, Eiii, 5A:iii, B:iii, C:iii).

***Colouration*:** Head covered with a greyish white microtomentum. The metallic ground colour subshiny at least partly on the genal dilation but the intensity of the shine depends on the direction of the incident light. Facial plate brown, in lower part sometimes with an indistinct metallic green tint. Occiput, postgena, genal dilation, ocellar tubercle metallic green in ground colour, frontal plate narrowly metallic green along the frontal setae. Palpus, clypeus (sometimes with a metallic green tint) and prementum dark brown to black, labella brown beige. Thorax and abdomen bright metallic green in ground colour, in varying degrees depending on the direction of the incident light with an indistinct light grey microtomentum. Scutum when viewed from the side and slightly from behind with four longitudinal stripes changing from grey to gilt or purple depending on the direction of the incident light. Proepisternum normally black, and densely covered with microtomentum, in larger specimens partly with a metallic green tint. Fore coxa in anterior region and femur posteriorly often with weak metallic green shine. Wing membrane around crossvein r-m not infuscated. Tegula and basicosta dark brown or black.

Head **(Fig. 2C):** Frons intermediate in width between *G. magna* and *G. lucida* at its narrowest point 0.35–0.45 [0.40] (n = 20) × as wide as an eye in dorsal view. Frontal vitta gradually tapering toward ocellar tubercle. Head in lateral view somewhat protruding, width at level of antennal insertion 0.60–0.77 [0.71] × (n = 14) the horizontal eye diameter. Fronto-orbital plate with a row of 10–14 [11] medioclinate moderately strong frontal setae, and some additional setulae; three or four [three to the left four to the right] of them extending to the middle of the pedicel with the row curving laterally, uppermost tiny setula sometimes reclinate; fronto-orbital plate outside the frontal row of setae with sparsely spread short and tiny setulae. Height of face 0.76–0.88 [0.85] × the length of frons (n = 13). Gena in profile at narrowest point, 030–0.42 [0.40] (n = 14) × as high as vertical eye diameter. Lower facial margin normally slightly protruded; in strict lateral view normally not visible in front of vibrissa. Facial ridge on lower 0.2–0.25 of its length with 2–3 [3] strong and 0–2 [2] additional thinner supravibrissal setae, length of which at least subequal to narrowest width of parafacial, and 2–5 [5] thin and short setulae. Below the vibrissa 4–7 [5] strong subvibrissal setae continuous to the row of genal setae, the posteriormost subvibrissal seta close to the foremost lower genal margin. Inner vertical setae crossed, thin and normally just slightly longer than the ocellar setae, outer vertical setae poorly developed, subequal with or even shorter than the adjacent postocular setae. Postocular setae long and thin, apically pronouncedly bending forward over the eyes. Occiput with a pair of postocellar setae subequal with the ocellar setae. Occiput and postgena with white to greyish white hairs. Antennae: First flagellomere subrectangular, short and evenly curved posteriorly at apex, maximal width in lateral view 0.76–0.91 [0.87] (n = 15) × the actual width of parafacial, at narrowest point; 1.47–1.73 [1.56] (n = 14) × as long as pedicel. Arista widened in proximal 2/5, rarely ½, and gradually tapering towards apex.

***Thorax*:** Prosternum bare. Scutum with 3(2)+3 [3+3] acrostichal, three or four dorsocentral and 1+3 intra-alar setae. Scutellum with 4(5) pairs of strong almost horizontal setae along margin, apical and subapical pairs slightly diverging; 2–4 [2] suberect discal setae, forming a row in front of the marginal setae, the strongest subequal to the lateral setae, rarely with an additional pair of strong median discal setae; tiny dorsal setulae numerous, the longest measuring 1/2 the length of the strongest dorsal seta.

***Legs*:** Claws and pulvilli on fore legs subequal in length with fifth tarsal segment, the latter 1.8–2.0 (n = 6) × as long as tarsal segment 4. Fore tibia with a row of 5–8 [five and six] anterodorsal setae, and an irregular row of 4–8 [6] posterior setae. Preapical anterodorsal seta subequal with the preapical dorsal and preapical posterior setae; preapical posterodorsal seta short, its length rarely exceeding 1/3 of the dorsal seta. Mid tibia with 4–6 [4] anterodorsal setae, the strongest in the middle of row, 5–8 [7] posterior setae, one ventral seta often accompanied by an additional tiny setula. Hind tibia with a continuous row of 9–12 unequally strong anterodorsal setae / setulae, of which 4–6 represent strong setae, four or five posterodorsal setae and three (rarely four) anteroventral setae.

***Wing*:** Usually two costal spines, the lower (ventral) spine strongest and ca. 2–3 × as long as the surrounding costal setulae, normally somewhat shorter than crossvein r-m. CS_4 + CS_5 2.1–2.4 (n = 12) × as long CS_6. Vein R_{4+5} at base with 3–6 [three and four] ventral and 3–8 [4] dorsal setulae.

***Abdomen* (Fig. 4B):** Tergite 2 with 3(2) lateral setae on each side. Tergite 3 with (2)3–4 [2 pairs and one unpaired] unequally strong and often irregularly set pairs of median discal setae; a pair of median marginal setae and 3(2) [3] lateral setae on each side. Tergites 4 with 2–3(4) [2] pairs of unequally strong and likewise irregularly set median discal setae; in dorsal view with a full row of 10–14 [10] marginal setae; tergite 5 with two or three irregular rows of strong and medium strong discal setae and a dense row of weak marginal setae.

Terminalia (five dissections) (Figs 4B, Eiii, 5A:iii, B:iii, C:iii): Sternite 5 (Fig. 4B, Eiii) in ventral view with long and wide lobes; length of medial cleft ca. twice its maximal width. Lobes with widespread setulae, slightly curved inwards at apex. Dorsomedial process black and prominent, expanding backwards partly separated from the lobes. Basal plate bare, ca. 0.4 × as long as sternite 5 and 2.6–2.7 × as wide as long. Syncercus in lateral view (Fig. 5A:iii) smoothly curved at apex, in dorsal view (Fig. 5B:iii) triangular, with long basal lobes and rounded apex; 1.6–1.7 × as long as maximal width (measured from base of membranous median suture to apex), marginally incurved at middle and close to apex; numerous dorsolateral setulae at middle gives a dense and fur-like appearance similar to *G. lucida* but the setulae are slightly longer. Surstylus slender, straight in caudal view; in lateral view tapering at base and distinctly arch-like bent in proximal 1/2, apex clavate and bent towards syncercus. Pregonite (Fig. 5C:iii) in caudal view rodlike; in lateral view lobe-like, with a characteristic wide and curved hook-like projection.

Aedeagus: Distiphallus in lateral view of almost uniform width.

Female (Figs 3C, 6A:iii, B:iii): Differs from male as follows:

***Colouration*:** Fronto-orbital plate vivid metallic green when viewed from behind and slightly from above; the metallic ground colour continues down on the upper part of parafacial reaching the level of the lowermost frontal setae; the upper part of parafacial and anterior 1/3 of fronto-orbital plate with a thin greyish white microtomentum, visible along eye margin and as a slim line at edge of frontal vitta. Thorax and abdomen vivid metallic green at most with a thin whitish microtomentum.

Head (Fig. 3C): Frons wider, at its narrowest point 0.76–0.93 (n = 12) × as wide as an eye in dorsal view. Frontal vitta gradually tapering towards ocellar tubercle, at this level often narrower than width of fronto-orbital plate. Fronto-orbital plate normally with fewer, 8–11 moderately strong medioclinate frontal setae. Outer vertical setae subequal with the ocellar setae, shorter than the posteriormost proclinate orbital setae, at least 2 × the length of the adjacent postocular setae. Postocellar setae short and tiny and subequal with the upper postocular setae. First flagellomere 1.38–1.62 (n = 8) × as long as pedicel; its maximum width 0.82–0.93 of the width of the parafacial at narrowest point.

***Legs*:** Claws and pulvilli on fore legs shorter ca. 0.7–0.8 × as long as tarsal segment 5, the latter 1.5–1.7 × as long as tarsal segment 4.

***Abdomen*:** Tergites 3 and 4 normally with two pairs of median discal setae, tergite 3 rarely missing one seta or with one additional seta, tergite 4 occasionally devoid of one seta. Ground vestiture dorsolateral on tergites 3 and 4 distinctly prone contrasting to the erect setulae between the median discal setae. Tergite 5 trapezoid, along anterior margin ca. 2 × as wide as long. Sternite 5 ca. as long as its maximal width, with 6–10 strong setae in posterior 1/3, four of them along the posterior margin and one or two pairs of median setae, in posterior 1/2 accompanied by numerous (60–70) irregularly spread setulae of varying size.

Terminalia (four dissections) (Fig. 6A:iii, B:iii): Tergite 6 in form of widely separated hemitergites; without tiny setulae in the adjacent posterior membranous area. Sternite 6 (Fig. 6A:iii) shorter 0.6–0.7 × as long as wide, slightly wider (1.1–1.2 ×) than sternite 5 and 1.8–1.9 × as wide as long, with 6–8 relatively strong setae along the posterior margin, accompanied by numerous (>20) tiny setulae. Tergite 7 strongly reduced, without tiny setulae in the adjacent membranous area. Sternite 7 slightly narrower than sternite 6, with numerous tiny setulae most of them restricted to the posterior margin. Sternite 8 reduced to a small faintly sclerotised plate with 6–12 sensory pores (sensilla trichodea). Hypoproct (Fig. 6B:iii) in ventral view distinctly rounded at apex (studied in ventral and somewhat caudal position somewhat blunt at apex): with a prominent depression, densely covered with short and tiny setulae, only a few in lateral position longer than the hypoproct itself; in lateral view not curved towards the cerci, apex of hypoproct reaching tip of cerci, lingulae well developed. Epiproct strongly reduced but in caudal view normally indicated by the presence of 2–4 setulae inserted between the cerci and above the hypoproct. Cerci reminiscent of a short-shafted paddle, weakly sclerotised with numerous setulae of varying length, in lateral view with some setulae that are subequal to the length of sternite 7 (twice the length of cerci itself).

DNA. The European specimens of *G. viridis* share the Co1 DNA barcode sequence (BOLD:ACF3891) with Finnish *G. zhelochovtsevi* (Fig. 7).

Distribution. A widely distributed and common species in the Palaearctic Region, including all of Europe, Japan (Hokkaido, Honshu), Middle East, all of Russia and Transcaucasia (Richter 2004; O'Hara et al. 2009). It is possible that at least some northern records of the species, at least from the Taiga region in the Nordic countries, represent *G. lucida*.

Biology. *Gymnocheta viridis* is a common spring–early summer species, often numerous at the right locations. Typical habitats include forest margins and meadows, but the species is frequently seen also in gardens. The males start their flight in early April in Central Europe and around end of April to early June in the north. The last female records in Finland are from mid-July. Males are frequently observed basking on tree trunks and watching for passing females. Both sexes can be collected from flowers, especially on cow parsnip (*Anthriscus sylvestris*), but also from other Daucaceae. The species is a known parasitoid of Erebidae (Lepidoptera) living in grass tufts, such as *Mesapamea secalis* Linnaeus and *Photedes minima* Haworth (Tschorsnig 2017). The females can be frequently seen in meandering flight in the low vegetation and investigating tufts of grass or sedges in search for a host.

Gymnocheta zhelochovtsevi Zimin

Gymnocheta zhelochovtsevi Zimin, 1958: 62. Holotype ♂ [ZIN] (see below).

Material. **Russia:** ♂: Южные Курилы, Итуруп, Рыбаки, 5 км SW Курильска, В. Рихтер, 23. VI.1968 [Southern Kurils, Iturup, Ribaki, 5 km SW Kurilsk, V. Richter, 23. VI.1968], det. V. Richter. Dissected by V. Richter [ZIN]. Examined from high quality photographs, including the terminalia. **Japan:** ♂: JAPAN / Mt. Muine / Sapporo / HOKKAIDO / 20 Jun.1974 / K. Nishida // *Gymnochaeta* / *zhelochovtsevi* ? / Zimin (handwritten) / det. H. Shima 1982 [BLKU]; ♂: JAPAN / Hokkaido / Churui Vil. Haruyama / 1 Jul.1993 / A. Kuromoto // *Gymnocheta* ♂ / *zhelochovtsevi* Zimin / det. C. Bergström 2020 [BLKU]. Dissected. **Finland:** ♂: Regio aboensis, Salo, Halikko, Perkko, 67158-60:32853-8, 12.vi.2020, A. Haarto leg. [AHC], BOLD Sample-ID JP2020-G1; ♂: Karelia australis, Vehkalahti, 18.vi.1966, L. Tiensuu leg. Dissected. [MZH]; ♀: Regio aboensis, Korppoo, 66840:31958, malaise, 19.vi.–22.vii.2003. A. Haarto leg. Dissected. BOLD Sample-ID JP2020-G2; 2♀♀: Regio aboensis, Salo, Halikko, Perkko, 671604:328551, 12.-28.vi.2020, malaise, Haarto leg. [AHC]; 1♀: Regio aboensis, Salo, Halikko, Perkko, 67158-60:32853-8, 28.vi.2020, A. Haarto leg. [AHC]. **Sweden:** 1♀: S. Vb: Umeå: Tavelån: / Östra Tjälamark; malaise / RT 90 70952, 17177 / 10.v.-16.vi.2016 / S. Hellqvist 14947 // *Gymnocheta* ♀ / *zhelochovtsevi* Zimin / det. C. Bergström 2020 [CBC].

Diagnosis. *Gymnocheta zhelochovtsevi* is characterised by a dark, almost black metallic green, wide frons in both sexes, and a hooked syncercus in the male.

Redescription. Body length: 9.2–10.4 mm (n = 7).

Male (Figs 2D, 4C, Eiv, 5A:iv, B:iv, C:iv).

***Colouration*:** Head covered with dense greyish or yellowish white microtomentum. The metallic ground colour is only weakly shining through, similar as is seen with *G. lucida*. Facial plate black without a metallic green spot. Occiput, postgena, genal dilation, ocellar triangle and frontal plate almost black in ground colour, although a hint of dark metallic bronze-green shine can be seen with changing light incidence. Palpus clypeus and prementum black, labella dark brown. Thorax and abdomen dark metallic green in ground colour, not as lucid as in *G. magna* or *G. viridis* and covered with indistinct greyish white microtomentum. Scutum, when viewed from the side and slightly from behind, with four pronounced longitudinal stripes of microtomentum, changing from grey to purple depending on the direction of the incident light. Proepisternum black and with thin grey microtomentum. Legs extensively black, but fore coxa in anterodorsal region and sometimes also femora with remnants of metallic shine, covered with light grey microtomentum. Wing membrane around crossvein r-m not infuscated.

Head **(Fig. 2A):** Frons at its narrowest point, 0.53–0.68 (n = 5) × as wide as an eye in dorsal view. Frontal vitta almost parallel-sided in anterior part hardly tapering until closely before ocellar tubercle. Head in profile protruding at level of antennal insertion, width of parafacial at this level ca. 0.65–0.75 × (n = 2) the horizontal eye diameter. Fronto-orbital plate with a row of 10–12 medioclinate moderately strong frontal setae and some additional setulae, uppermost setula tiny and sometimes slightly reclinate, four or five setae extend to the middle of the pedicel with the row curving laterally; fronto-orbital plate outside the frontal row of setae with 4–10 sparsely spread, short and tiny setulae. Height of face 0.8–0.9 × the length of frons (n = 2). Gena in profile at narrowest point, 0.4–0.5 (n = 2) × as high as vertical eye diameter. Facial plate and lower facial margin not visible in profile. Facial ridge on less than lower 1/5 with one or two strong, two additional thinner supravibrissal setae, and four or five setulae. Ridge below vibrissa with 3–5 strong subvibrissal setae continuous with the genal setae, longest ca. 0.6 × the length of vibrissa. Inner vertical setae strong and crossed, longer than the ocellar setae; outer vertical setae subequal with inner vertical setae, distinctly stronger than the postocular setae. Postocular setae short and barely bending forward over the eyes. Occiput with a pair of postocellar setae, weaker that the outer vertical setae, thinner but longer than the postocular setae. Palpus slightly clavate at tip, subequal to the length of the antenna and densely covered with short black setulae, two strong preapical setulae and 4–5 irregular ventral setulae. Antenna: Pedicel subtriangular and with one elongate seta, 1.2–1.5 × as long as wide at apex (n = 4). First flagellomere 1.5–1.7 × (n = 5) as long as the pedicel, in profile subrectangular, rounded at apex; maximal width in profile as wide (0.9–1.1) (n = 2) as parafacial at narrowest point. Eyes sparsely covered with, compared with the other species, relatively short whitish hairs with a yellowish tint.

***Thorax*:** Prosternum bare. 2(3)+3 acrostichal, 3+4 dorsocentral and 1+3 intra-alar setae. Ground vestiture on scutum (consisting of thin setulae) sparse and erect, longest setulae 0.5–0.6 × as long as the shortest setae, anteriorly shorter, at most 0.3 × the length of the setae. Scutellum with four pairs of strong marginal setae, mixed with some shorter and weaker marginal setae/setulae, almost horizontal with the plane of scutellum, apical setae missing; subapical setae close to the apex, parallel or slightly diverging, two lateral pairs and one basal pair; four suberect preapical discal setae, forming a row in front of the marginal setae, the strongest pair in the middle sometimes subequal to the lateral setae, mixed with numerous tiny setulae the longest at least 1/2 as long as the strong preapical setae.

***Legs*:** Claws and pulvilli on fore legs ca. 1.0 (n = 3) × as long as tarsal segment 5, the latter 2.0 (n = 3) × as long as tarsal segment 4. Fore tibia with a row of 5–7 anterodorsal setae, 3–5 setae in an irregular posterodorsal row and two posterior setae; preapical anterodorsal seta well developed, subequal with the preapical dorsal and preapical posterior setae. Mid tibia with a row of five anterodorsal setae the strongest in the middle, four or five posterodorsal setae, two or three posterior setae, one strong ventral seta accompanied by a shorter seta above. Preapical anterodorsal seta of the hind tibia subequal to the preapical dorsal seta, preapical anteroventral seta 1/2 the length of anterodorsal seta; a continuous irregular row of 8–10 anterodorsal setae, three or four posterodorsal setae and three or four anteroventral setae.

***Wing*:** One or two costal spines, the strongest lower spine 2–3 × as long as the surrounding costal setulae. Fourth and fifth costal section ca. 2 × as long as sixth costal sector. Vein R_{4+5} at node with four ventral and three or four dorsal setulae. Cell r_{4+5} often somewhat narrow at wing edge, 0.8 × the length of crossvein r-m.

***Abdomen* (Fig. 4C):** Domed, ground-vestiture prone or semierect on tergite 5, also ventrally. Tergite 2 with two lateral setae on each side. Tergite 3 with two pairs of median discal setae; with a pair of median marginal setae and two or three lateral setae on each side. Tergite 4 similarly with two or three pairs of unequally and irregularly set strong median discal setae, in dorsal view with a full row of 10–12 marginal setae. Tergite 5 with two or three irregular rows of unequally strong discal setae and a row of strong marginal setae.

Terminalia (three dissections) (Figs 4C, Eiv, 5A:iv, B:iv, C:iv):

Sternite 5 (Fig. 4C, Eiv) in ventral view with long and wide lobes; length of medial cleft 1.3–1.4 × its maximal width. Lobes with numerous setulae, apex in ventral view rounded in a ventral and slightly lateral view with a subtriangular appearance. Dorsomedial process long and narrow, indistinct, and visible only as a callosity, along its length connected with the lobes. Basal plate bare, ca. 0.4 × as long as sternite 5 and 2.6–2.7 × as wide as long. Syncercus in profile (Fig. 5A:iv) dorsally strongly bowed in the middle and with a characteristic tooth-like hook at the apex, reminiscing of the situation in *Gymnocheta porphyrophora* Zimin (1958); in caudal view (Fig. 5B:iv) subtriangular with long basal lobes and a widened apex; dorsolateral with numerous long setulae that generate a dense and fur-like hairiness. Surstylus (Fig. 5A:iv) bacilliform, straight in caudal view, in profile gradually tapering at base, then slightly arch-like bent at middle; evenly thick apart from an indicated widening at apex, bent towards syncercus. Pregonite rodlike in caudal view; lobe-like in profile (Fig. 5C:iv) with a wide hook-like projection apically, shortly tapering at apex. Aedeagus: Basiphallus with a basal projection and a distinct digitiform epiphallus, resembling the preceding species. Distiphallus (Fig. 5C:iv) in profile compact and evenly wide.

Female (Figs 3D, 6A:iv, B:iv): Differs from male as follows:

***Colouration*:** Fronto-orbital plate almost entirely metallic dark green when viewed from behind and slightly from above; the metallic ground colour at least partly interrupted on the upper part of parafacial. However, most of the metallic ground colour on upper part of parafacial and anterior 1/3 of fronto-orbital plate is covered by greyish white microtomentum, which is dense especially along eye margin and frontal setae.

Head **(Fig. 3D):** Frons wider, at its narrowest point 0.8–1.0 (n = 4) × as wide as an eye in dorsal view. Frontal vitta wide and with parallel edges in anterior 1/2 and then slightly tapering towards ocellar tubercle, its width at ocellar tubercle exceeding the width of fronto-orbital plate at this point. Fronto-orbital plate normally with fewer, 6–9 moderately strong medioclinate frontal setae. Outer vertical setae strong and 0.6–0.7 × the length of inner vertical setae, stronger than ocellar setae. Postocellar setae subequal with the upper postocular setae. First flagellomere 1.3–1.5 (n = 4) × as long as pedicel, normally as wide as, or slightly wider than the parafacial at narrowest point.

***Thorax*:** Whitish grey microtomentum normally thinner than in males, most intense on the pleura and episternum.

***Legs*:** Claws and pulvilli on fore legs shorter ca. 0.7–0.8 (n = 5) × as long as tarsal segment 5, the latter 1.5–1.6 (n = 5) × as long as tarsal segment 4.

***Abdomen*:** Tergites 3 and 4 with one or two pairs of median discal setae. Tergite 5 trapezoid, along anterior margin ca. 2 × as wide as long, posterior edge concave (blunt or pointed in *G. lucida*). Sternite 5 slightly wider than long, with 4 strong setae along posterior margin (Fig. 6A:iv).

Terminalia (one dissection) (Fig. 6A:i, B:i): Tergite 6 divided into narrow and somewhat elongated hemitergites, widely separated, each closely accompanied by a pair of setulae at posterior margin. Sternite 6 shorter, 0.5 × as long and 1.2 × as wide as sternite 5 (n = 1), with ca. 10 tiny setulae along the posterior margin. Tergite 7 strongly reduced. Sternite 7 semi-spherical, ca. as long but slightly narrower than sternite 6, with numerous setulae most of them tiny, restricted to the posterior margin. Sternite 8 strongly reduced, partly hidden below sternite 7. Hypoproct (Fig. 6B:iv) in ventral view almost triangular, pointed, apex only slightly rounded, densely covered with setulae that are longer laterally; in profile slightly bent towards the cerci, apex of hypoproct not reaching the tip of cerci. Cerci elongated, with numerous setulae of varying length, the strongest setulae in profile subequal to the length of sternite 7.

DNA. Despite the morphological differences, *G. zhelochovtsevi* shares Co1 DNA barcode sequence with *G. viridis* (Fig. 7). DNA barcode sharing is not uncommon in Tachinidae (Pohjoismäki et al. 2016).

Distribution. Like *G. lucida*, *G. zhelochovtsevi* had been thought to be an Eastern Palaearctic species (Richter 2004). So far, the only records from Europe are the ones listed here from the southern and southwestern coast of Finland and from Sweden.

Biology. The specimens from Halikko were collected from a flood meadow adjacent to a meandering stream. The meadow is characterised mainly by tall grass and sedges, surrounded by shrub of willows (*Salix* spp.) and bird cherry (*Prunus padus* L.). One male and one female were hand netted from the flowers of *Anthriscus sylvestris* (L.) and two females were collected with a Malaise trap. The female specimen from Korppoo was caught in a Malaise trap in a seashore meadow, surrounded by shrub of meadowsweet (*Filipendula ulmaria* (L.)) and alders (*Alnus* spp.). The Swedish specimen was collected in a Malaise trap, placed close to the calmly flowing, slightly meandering, ca.

5 m wide Tavelån River. The trap was placed in overgrowth known as "raningsmark"; i.e., grassland long ago used as a hay meadow or grazing but now characterised by bush wood with meadow glades between the shrubbery.

Notes. Lauri Tiensuu mentioned on page 138 of his unpublished notes that a specimen identified by him as a female of *G. viridis*, but actually a male of *G. zhelochovtsevi*, was collected around (on?) aspen (*Populus tremula* L.) trunks near the village of Salmenkylä in the former municipality of Vehkalahti. The original description by Zimin was based on one male specimen, whose fifth sternite was poorly illustrated and the epandrium not illustrated at all in the original publication. The tip of the syncercus of the species has a characteristic hook (Figs 4C, 5A:iv), somewhat resembling that of *Gymnocheta porphyrophora*, which caused us some confusion. However, the median lobes at the posterior edge of the sternite of *G. porphyrophora* are well developed (Fig. 4D), unlike in any of the other species discussed here.

Revised key to the Palaearctic *Gymnocheta* species

This identification key is based on the ones provided by Zimin (1958) and Richter (2004) with some modifications. The extent of microtomentum at the orbits and upper part of the frons as described by Zimin (1958) and Mesnil (1975) differentiating *Gymnocheta magna* and *G. viridis* is not reliable on its own, especially in females. Although on average specimens of *G. lucida* and *G. zhelochovtsevi* can be differentiated from *G. magna* and *G. viridis* by their colouration, we do not regard the colour alone an important diagnostic feature as it can be influenced by the developmental conditions as well as by the age and condition of the specimen. However, the colour difference can be useful when sorting out specimens for closer inspection. At first glance, the colouration of *G. lucida* appears quite matt, olive metallic green and that of *G. zhelochovtsevi* very dark green compared to the bright, almost golden metallic green of *G. magna* and *G. viridis*. As we do not have much knowledge of *G. goniata*, apart from the rather short description (Chao 1979), it is not included in the key. Based on the figures in Chao (1979: figs 6, 7), the species seems to be closely related to *G. flamma*, when comparing the shape of sternite 5 and the hooked syncercus (not broadened dorsally at the tip as in *G. zhelochovtsevi*). The species is bright green in contrast to the cherry-red *G. flamma*.

1 Cell r_{4+5} short-stalked, closed, or rarely narrowly open at wing margin; appendage at bend of vein M equal to or slightly shorter than distance between crossvein dm-cu and bend; body slender, shining, dark olive green; length of external costal spine equal to length of crossvein r-m, width of frons > 1/2 as wide as an eye [Not seen. Female unknown] ..... ***Gymnocheta mesnili* Zimin**

– Cell r_{4+5} open, other combinations of features **2**

2 Abdomen cherry-red or wine red **3**

– Abdomen green **4**

3 Scutum with 4 brownish black, distinct narrow longitudinal vittae separated by wide areas of thin white microtomentum, distinct in the presutural part of scutum. Frons in dorsal view 0.25–0.33 × the width of an eye in males and 0.66 × in females. Lower facial margin in lateral view distinctly protruding between the vibrissae. Male sternite 5 as in Fig. 4D, syncercus with an apical hook similar to Fig. 5A:iv .... ***Gymnocheta porphyrophora*** **Zimin**

– Frons in male narrow, 0.20–0.25 × the width of an eye. Apex of syncercus not wider than apex of surstylus (caudal view), labella small-sized [Not seen. Female unknown] .... ***Gymnocheta flamma*** **Zimin**

4 Males **5**

– Females **8**

5 Frons in dorsal view 0.5–0.7 × the width of an eye (Fig. 2D). Frontal vitta wide, at level of ocellar tubercle 3.0–3.5 × the width of the orbital plate. Fronto-orbital plate, parafacial, genal dilation and occiput coated by a dense greyish white microtomentum. Outer vertical seta almost as strong as the inner vertical seta, much stronger than the postocellar setae. Thorax and abdomen of a dark metal green colour. Terminalia as in Figs 4C, E:iv, 5A:iv, B:iv, C:iv .... ***Gymnocheta zhelochovtsevi*** **Zimin**

– Frons in dorsal view either not exceeding 0.4 × the width of an eye, and frontal vitta gradually narrowing towards ocellar tubercle (*G. magna* and *G. viridis*), or frons wider (*G. lucida*), but then frontal vitta narrowing towards middle. Frontal vitta at level of ocellar tubercle at most twice the width of the orbital plate. Occiput at least mediodorsally with a shiny metallic green colour. Outer vertical seta weaker than the inner, subequal to the postocellar setae **6**

6 Frons in dorsal view at its narrowest point, 0.43–0.51 × width of an eye (Fig. 2A). Frontal vitta narrowing towards middle, then edges parallel reaching ocellar tubercle. Fronto-orbital plate, parafacial, and genal dilation with a rather dense greyish white microtomentum, the metallic green colour almost not shining through. Thorax and abdomen olive green. Scutum with thin microtomentum, when viewed from above and slightly from behind with distinct greyish white longitudinal stripes. Arista widened in at least its basal 1/2, sometimes almost in basal 2/3 and gradually tapering to apex. Proepisternum always black and densely covered with microtomentum Terminalia as in Figs 4A, E:i, 5A:i, B:i, C:i .... ***Gymnocheta lucida*** **Zimin**

– Frons in dorsal view rarely exceeding 0.4 × width of an eye. Frontal vitta gradually narrowing towards ocellar tubercle. Fronto-orbital plate, parafacial, and genal dilation with a thin greyish white or white microtomentum but the metallic green colour subshiny at least at the fronto-orbital plate. Thorax and abdomen more bright green, sometimes with a golden- or blue green lustre. Scutum with thin microtomentum. Arista normally widened in less than proximal 1/2. Proepisternum usually partly metallic green 7

7 Lower facial margin slightly protruding (Fig. 2C), normally without areas of a green shine. Costal spine distinct, at least 0.7 × the length of crossvein r-m. Arista widened in proximal 2/5, rarely 1/2 of its length. Terminalia as in Figs 4C, E:iii, 5A:iii, B:iii, C:iii...................... ***Gymnocheta viridis* (Fallén)**

– Lower facial margin strongly or moderately protruding (Figs 1C, 2B). Costal spine short, 0.5 × the length of crossvein r-m. Arista widened in its proximal 1/4–1/3. Terminalia as in Figs 4E:ii, 5A:ii, B:ii, C:ii.................................... ....***Gymnocheta magna* Zimin**

8 Frons in dorsal view 0.8–1.0 × as wide as an eye (Fig. 3D). Frontal vitta wide**,** with almost parallel edges in ca. anterior 1/2, then gradually tapering towards ocellar tubercle; width at level of ocellar tubercle subequal to the orbital plate. Scutum with 4 greyish white longitudinal stripes due to the dense microtomentum covering the dark stripes, present also behind the transverse suture. Postpronotum and scutellum also with distinct greyish white microtomentum. Occiput covered with a dense greyish microtomentum. Parafacial, genal dilation and fronto-orbital plate in anterior 1/3 and along eye margin with greyish white microtomentum. Thorax and abdomen dark metallic green. Terminalia as in Figs 6A:iv, B:iv.................................. ....***Gymnocheta zhelochovtsevi* Zimin**

– Frons normally not exceeding 0.9 × the width of an eye. Frontal vitta either gradually tapering towards ocellar tubercle or narrowest at ca. middle. Scutum either with 4 greyish white longitudinal stripes or when viewed from different directions with 4 dark stripes covered by thin microtomentum. Occiput in upper part behind the row of postocular setulae and fronto-orbital plate at least in their upper part metallic green, without microtomentum..**9**

9 Thorax and abdomen metallic olive green; viewed from different directions notably scutum with a bronze or golden lustre. The greyish white microtomentum in anterior part of fronto-orbital plate shifting into a bronze or golden lustre when viewed from different directions. Frontal vitta tapering towards middle, then slightly widening towards ocellar tubercle. Width of first flagellomere normally wider than parafacial at narrowest point. Arista widened in at least its basal 1/2, sometimes almost in proximal 2/3 and gradually tapering to apex. Cell r_{4+5} narrowly open, or (as an exception) closed at wing margin. Terminalia as in Figs 6A:i, B:I.............................. .... ***Gymnocheta lucida* Zimin**

– Thorax and abdomen bright metallic green; viewed from different directions with purple lustre. The greyish white microtomentum in anterior part of fronto-orbital plate sometimes shifting into a silvery lustre. Frontal vitta gradually tapering towards ocellar tubercle. Width of first flagellomere not exceeding width of parafacial at narrowest point. Arista normally widened in less than proximal 1/2. Cell r_{4+5} wide open at wing margin.......................**10**

10 Lower facial margin hardly protruding between vibrissae (Fig. 3C). Costal seta at least 0.7 × the length of crossvein r-m. Prosternum without setulae. Arista widened in proximal 2/5 (or rarely 1/2) and gradually tapering towards apex. Terminalia as in Figs 6A:iii, B:iii .... ***Gymnocheta viridis*** **(Fallén)**

– Lower facial margin distinctly protruding between vibrissae (Fig. 3B). Costal seta short, at most 0.5 × the length of crossvein r-m. Prosternum sometimes with setulae. Arista widened in its proximal 1/4–1/3, gradually tapering towards apex. Terminalia as in Fig. 6A:ii, B:ii....... **Gymnocheta magna Zimin**

Acknowledgements

We are grateful to Dr. Takuji Tachi (BLKU) for his generous loan of Japanese *Gymnocheta* specimens. We are indebted to Dr. Olga G. Ovtshinnikova (ZIN) for her kind help with the type specimens and to Dr. Vladimir Neimorovets (All-Russian Research Institute of Plant Protection, St. Petersburg-Pushkin, Russia) for the high-quality photographs of the specimens in ZIN. Dr. Antti Haarto (Mietoinen, Finland) is thanked for the generous loan of specimens in his personal collection and Dr. Marko Mutanen (University of Oulu, Finland) for his excellent work managing the Finnish Barcode of Life (FinBoL) project. Sincere thanks are due to Göran Liljeberg (Västerljung) for technical support preparing Figs 1–3 for this paper and to Yngve Brodin (NHRS) who enabled us to study the holotype of *Tachina viridis* and also helped us obtain the original description of *G. goniata*. We would also like to thank Mr. Jere Kahanpää (ZMH) and Jim O'Hara (Agriculture and Agri-Food Canada, Ottawa) for their help with obtaining some of the relevant references. Dr. Pierfilippo Cerretti (Sapienza Università di Roma) is thanked for the smooth editorial process and Drs. Hans-Peter Tschorsnig (Stuttgart) and Jim O'Hara for their constructive reviews as well as help in solving the nomenclatural issues.

References

Cerretti P, Tschorsnig H-P, Lopresti M, Di Giovanni F (2012) MOSCHweb – a matrix-based interactive key to the genera of the Palaearctic Tachinidae (Insecta, Diptera). ZooKeys 205: 5–18. https://doi.org/10.3897/zookeys.205.3409

Chao C-M (1979) New species of Tachinidae (Diptera) from Mount Tomuer, Xinjiang, China. Entomotaxonomia 1(2): 79–82. [In Chinese with English summary]

Cumming JM, Wood DM (2017) Adult morphology and terminology. In: Kirk-Spriggs A, Sinclair BJ (Eds) Afrotropical Diptera, vol. 1. South African National Biodiversity Institute, Pretoria, South Africa, 89–133.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797. https://doi.org/10.1093/nar/gkh340

Engelmark R, Engelmark T-B (1989) The calyptrate fly fauna (Diptera, Calyptratae) of three fens near Jokkmokk in Swedish Lapland. Entomologisk Tidskrift 110: 81–95.

Fallén CF (1810) Försök att bestämma de i Sverige funne Flugarter, som kunna föras till Slägtet Tachina. Kongl. Vetenskaps Academiens Nya Handlingar, Serie 2, 31: 253–287. [in Swedish]

Fallén CF (1820) Monographia Muscidum Sveciae. Part 3., Lund, Sweden, 25–40. [in Swedish]

Hackman W (1980) A check list of the Finnish Diptera. Notulae entomologicae 60: 117–162.

Haraldseide H (2012) Contributions to the knowledge of Norwegian Tachinidae (Diptera, Oestroidea) – Part 1, including an updated checklist. Norwegian Journal of Entomology 59: 43–58.

Hebert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. Proceedings of the National Academy of Sciences of the United States of America 101: 14812–14817. https://doi.org/10.1073/pnas.0406166101

Hedström L (1985) Svenska insektsfynd – rapport 1. [Swedish insect records – report 1.]. Entomologisk Tidskrift 106: 147–153. [in Swedish]

Herting B (1984) Catalogue of Palaearctic Tachinidae (Diptera). Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 369:, 1–228.

Herting B, Dely-Draskovits Á (1993) Tachinidae. In: Soós Á, Papp L (Eds) Catalogue of Palaearctic Diptera, vol. 13. Anthomyiidae—Tachinidae. Hungarian Natural History Museum, Budapest, Hungary, 118–458.

Herting B, Tschorsnig H-P, O'Hara JE (1999) Case 3084. *Musca geniculata* De Geer, 1776 and *Stomoxys cristata* Fabricius, 1805 (currently *Siphona geniculata* and *Siphona cristata*; Insecta, Diptera): proposed conservation of usage of the specific names by the replacement of the lectotype of *M. geniculata* by a neotype. Bulletin of Zoological Nomenclature 56: 235–239. https://doi.org/10.5962/bhl.part.23084

International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature. 4th edition adopted by the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London, [xxix +] 306 pp.

ICZN [International Commission on Zoological Nomenclature] (2001) Opinion 1975. *Musca geniculata* De Geer, 1776 and *Stomoxys cristata* Fabricius, 1805 (currently *Siphona geniculata* and *Siphona cristata*; Insecta, Diptera): specific names conserved by the replacement of the lectotype of *M. geniculata* by a neotype. Bulletin of Zoological Nomenclature 58: 154–155.

Mesnil LP (1971) 64g. Larvaevorinae (Tachininae). Die Fliegen der Palaearktischen Region 10 (Lieferung 286): 977–1024. [in German]

Mesnil LP (1972) 64g. Larvaevorinae (Tachininae). Die Fliegen der Palaearktischen Region 10 (Lieferung 293): 1065–1112. [in German]

O'Hara JE (2002) Revision of the Polideini (Tachinidae) of America north of Mexico. Studia Dipterologica, Supplement 10: 1–170.

O'Hara JE, Wood DM (2004) Catalogue of the Tachinidae (Diptera) of America north of Mexico. Memoirs on Entomology, International 18, 410 pp.

O'Hara JE, Shima H, Zhang C (2009) Annotated catalogue of the Tachinidae (Insecta: Diptera) of China. Zootaxa 2190: 1–236. https://doi.org/10.11646/zootaxa.2190.1.1

O'Hara JE, Henderson SJ (2020) World genera of the Tachinidae (Diptera) and their regional occurrence. Version 11.0. http://www.nadsdiptera.org/Tach/WorldTachs/Genera/Gentach_ver11.pdf [accessed May 2021]

Pohjoismäki JL, Kahanpää J, Mutanen M (2016) DNA Barcodes for the Northern European Tachinid Flies (Diptera: Tachinidae). PLoS ONE 11: e0164933. https://doi.org/10.1371/journal.pone.0164933

Rambaut A (2009) Computer program distributed by the author. http://tree.bio.ed.ac.uk/software/figtree/ [accessed January 4, 2020]

Ratnasingham S, Hebert PD (2013) A DNA-based registry for all animal species: the barcode index number (BIN) system. PLoS ONE 8: e66213. https://doi.org/10.1371/journal.pone.0066213

Richter VA (1981) Novie i maloizvestnie vidi tahin (Diptera, Tachinidae) Fauni SSSR [New and little known species of Tachinids (Diptera, Tachinidae) of the USSR fauna]. Entomologicheskoe Obozrenie [Entomological Review], LX, 4: 917–933. [In Russian]

Richter VA (2004) 124. Sem. Tachinidae – Tahini. In: Lehr PA (Ed.) Opredelitel nasekomih Dalnego Vostoka Rosii, Tom VI-oi, Dvukrilie i blohi, chast 3. [Key to the insects of Russian Far East, Vol. VI, Diptera and Siphonaptera, Part 3.]. Dalnauka, Vladivostok, 148–398. [in Russian]

Robineau-Desvoidy AJB (1830) Essai sur les Myodaires. Mémoires présentés par divers savants a l'Académie des Sciences de l'Institut de France et imprimés par son ordre, v. 2, Imprimé par autorisation du Roi a l'Imprimerie Royal, Paris, 371–372. [in French]

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Tschorsnig H-P (1985) Taxonomie forstlich wichtiger Parasiten: Untersuchungen zur Struktur des männlichen Postabdomens der Raupenfliegen (Diptera, Tachinidae). Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 383: 1–137. [in German]

Tschorsnig H-P, Herting B (1994) Die Raupenfliegen (Diptera: Tachinidae) Mitteleuropas: Bestimmungstabellen und Angaben zur Verbreitung und Ökologie der einzelnen Arten. Stuttgarter Beiträge zur Naturkunde 506: 1–170. [in German]

Tschorsnig H-P, Richter VA (1998) Family Tachinidae. In: Papp L, Darvas B (Eds) Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance). Vol. 3. Higher Brachycera. Science Herald, Budapest, 691–827.

Tschorsnig H-P (2017) Preliminary host catalogue of Palaearctic Tachinidae (Diptera). [First version, provided online on:] http://www.nadsdiptera.org/Tach/WorldTachs/CatPalHosts/Home.html [Accessed 27 April 2021]

Zeegers T, Ziegler J, Tschorsnig H-P (2016) Tachinidae. Part 3. A new Palaearctic species of the genus *Chrysosomopsis* Townsend (Diptera, Tachinidae) from Central Europe and the Altai Mountains. In: Ziegler J (Ed.) Diptera Stelviana. A dipterological perspective on a changing alpine landscape. Results from a survey of the biodiversity of Diptera (Insecta) in the Stilfserjoch National Park (Italy). Vol 2 Studia Dipterologica. Supplement 21: 276–282.

Zetterstedt JW (1844) Diptera Scandinaviae disposita et descripta 3, Lundae [Lund], Sweden, 895–1280. [in Latin]

Zimin LS (1958) Kratkii obzor vidov podtribi Chrysocosmiina fanui SSSR i sopredelnih stran (Diptera, Larvaevoridae) [Summary of the subtribe species Chrysocosmiina of the faunas of the USSR and nearby countries (Diptera, Larvaevoridae)]. Sbornik Rabot Instituta Prikladnoi Zoologi i Fitopathologii, Leningrad 5: 40–66. [in Russian]

ZooKeys 1053: 185–195 (2021)
doi: 10.3897/zookeys.1053.67326
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Rediscovery of *Orientotlos iishibai* Sakai, 1980 (Crustacea, Decapoda, Brachyura, Leucosiidae) in Taiwan

Peter K. L. Ng[1], Tin-Yam Chan[2]

[1] *Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Singapore* [2] *Institute of Marine Biology and Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung 202301, Taiwan*

Corresponding author: Tin-Yam Chan (tychan@mail.ntou.edu.tw)

Academic editor: Sameer Pati | Received 14 April 2021 | Accepted 25 June 2021 | Published 2 August 2021

http://zoobank.org/6C907A4B-5874-40D1-881E-18BA380D9C21

Citation: Ng PKL, Chan T-Y (2021) Rediscovery of *Orientotlos iishibai* Sakai, 1980 (Crustacea, Decapoda, Brachyura, Leucosiidae) in Taiwan. ZooKeys 1053: 185–195. https://doi.org/10.3897/zookeys.1053.67326

Abstract

The leucosiid crab *Orientotlos iishibai* Sakai, 1980 was described from one female collected off western Japan and had never been reported since. The species is now recorded from southwestern Taiwan for the first time, and is redescribed and figured at length. Although Sakai argued that *Orientotlos* Sakai, 1980, is closely related to *Oreophorus* Rüppell, 1830 and *Atlantotlos* Doflein, 1904, the genus is actually morphologically most similar to *Merocryptus* A. Milne-Edwards, 1873. The two genera, however, still differ markedly in a number of key carapace and cheliped characters.

Keywords

East Asia, Leucosioidea, new record, redescription, rubble crab, taxonomy

Introduction

Sakai (1980) described an unusual new genus and new species of leucosiid crab, *Orientotlos iishibai* Sakai, 1980, from a single female obtained from trawl bycatch from off Kumano-nada, Mie Prefecture, on the Pacific side of central Japan. Sakai (1980) commented that it was closely related to *Oreophorus* Rüppell, 1830, and *Atlantotlos* Doflein, 1904, but differed in carapace and cheliped features. The genus had never been reported since its description. We here report a specimen of *Orientotlos iishibai* recently collected in southern Taiwan. The species is redescribed and figured, and its taxonomic position is discussed.

Material and methods

The terminology used follows Tan and Ng (1996), with amendments by Davie et al. (2015). Measurements provided are of the maximum carapace width and length, respectively. The specimen is deposited in the National Taiwan Ocean University (**NTOU**), Keelung, Taiwan.

Taxonomy

Family Leucosiidae Samouelle, 1819

Genus *Orientotlos* Sakai, 1980

Type species. *Orientotlos iishibai* Sakai, 1980, by original designation.

Diagnosis. Carapace subhexagonal in outline; dorsal surfaces between plates and bosses with numerous, well-spaced boletiform and rounded tubercles; subhepatic region forming a distinct obtuse angle visible in dorsal view; hepatic plate distinct, separated from first anterolateral tooth by wide cleft; anterolateral margin with 3 large lobiform teeth; posterolateral margin concave, with median triangular tooth; posterior carapace margin with 2 large lozenge-shaped bosses; postfrontal median keel prominent, high, extending posteriorly to cardiac region as raised row of rounded tubercles; postorbital region without deep depression; large boletiform plates on protogastric, epibranchial and metabranchial regions; cardiac region with raised, vaguely T-shaped ridge formed of fused granules; intestinal region inflated, with a large subtriangular boletiform plate; antennule with basal segment occupying lower two-thirds of fossa; basal antennal article large, subquadrate, fused with epistome, forming most of suborbital margin; third maxilliped with merus, ischium and exopod paved with numerous flattened rounded tubercles, basal parts with boletiform tubercles, exopod stout, broad, reaching to about half length of merus; palm of cheliped short, stout, without ridges, lobes or teeth, fingers shorter than palm; ambulatory legs short, merus, carpus and propodus covered with slender and boletiform tubercles along upper and lower margins, dactylo-propodal lock present; anterior thoracic sternites (1–4) strongly compressed, surface of sternite 3 with numerous boletiform tubercles; female thoracic sternite 4 forming keel around distal part of sternopleonal cavity; vulvae relatively small, round, positioned distinctly apart; female pleon ovate, shield-like, covered with rounded tubercles, somites 1 and 2 free, somites 3–6 fused, telson narrowly triangular with distal part linguiform.

Remarks. The concept of *Oreophorus* Rüppell, 1830 has changed substantially since 1980, with several revisions clarifying the identities of allied genera (*Tlos* Adams & White, 1849, and *Oreotlos* Ihle, 1918) and the establishment of several new ones: *Dolos* Tan & Richer de Forges, 1993, *Alox* Tan & Ng, 1996, and *Cateios* Tan & Ng, 1996. *Orientotlos* can nevertheless be easily distinguished from these genera by the anterolateral margin of carapace not expanded posteriorly and sometimes reaching level of the posterior carapace margin, the anterolateral margin is distinctly lobiform or dentiform, dorsal carapace surface without regions distinctly raised to form bosses, with depressed areas never eroded and no obvious postocular depression or groove, cardiac region not large or strongly inflated, and the palm of cheliped is short ovate, with fingers short and relatively slender and cutting edges lined with low teeth (cf. Tan and Richer de Forges 1993; Tan and Ng 1996).

The carapace of *Orientotlos* only superficially resembles that of *Atlantotlos* (type and only species *Atlantotlos rhombifer* Doflein, 1904), described from off the Congo in West Africa, in general shape (Doflein 1904: 51). The latter genus differs markedly from *Orientotlos* in possessing a smooth carapace, without inflated bosses, boletiform, or rounded tubercles, an entire posterior carapace margin, and less prominently armed pereopods (cf. Doflein 1904: pl. 15, figs 7, 8).

Orientotlos is actually most similar to *Merocryptus* A. Milne-Edwards, 1873 in having the anterolateral margin of the carapace with three large lobiform teeth (Figs 1, 2A, C, D) (versus margin with low lobes or spines but never clearly dentiform); a prominent lobe on posterolateral margin of carapace (Figs 1, 2A, C, D) (versus lobe absent or undiscernible in *Merocryptus*, although margin may be uneven or spiniform); median keel on gastric, cardiac and intestinal regions high and strongly inflated (Figs 1, 2A, C, D) (versus much lower in *Merocryptus*); intestinal region formed by a pair of distinct, fused subtriangular bosses (Figs 1, 2A, C, D) (versus more coniform or evenly rounded in *Merocryptus*); posterior carapace margin with two broad truncate, lozenge-shaped bosses (Figs 1, 2C, D) (versus entire or with dentiform projections in *Merocryptus*); female cheliped palm and fingers proportionately shorter and stouter (Figs 1, 2A, B, 3F) (versus more elongate and slender in *Merocryptus*); and vulvae widely spaced (Fig. 4E) (versus proportionately larger and closer to the midline in *Merocryptus*) (cf. A. Milne-Edwards 1873; Yokoya 1933; Serène 1955; Sakai 1976; Zarenkov 1994; Chen and Sun 2002; Galil 2019; Galil and Ng in press).

Orientotlos iishibai Sakai, 1980

Figs 1–4

Orientotlos iishibai Sakai, 1980: 74, text-fig. 1. – Ng et al. 2008: 92 (list).

Material examined. Taiwan • 1 ♀ ovigerous (7.8 × 6.5 mm); station CP4210, off southwestern Taiwan coast; 22°18.94'N, 120°20.57'E; depth 116–159 m; 14 Nov. 2020; T.-Y. Chan leg.; hard bottom substrate; NTOU B00125.

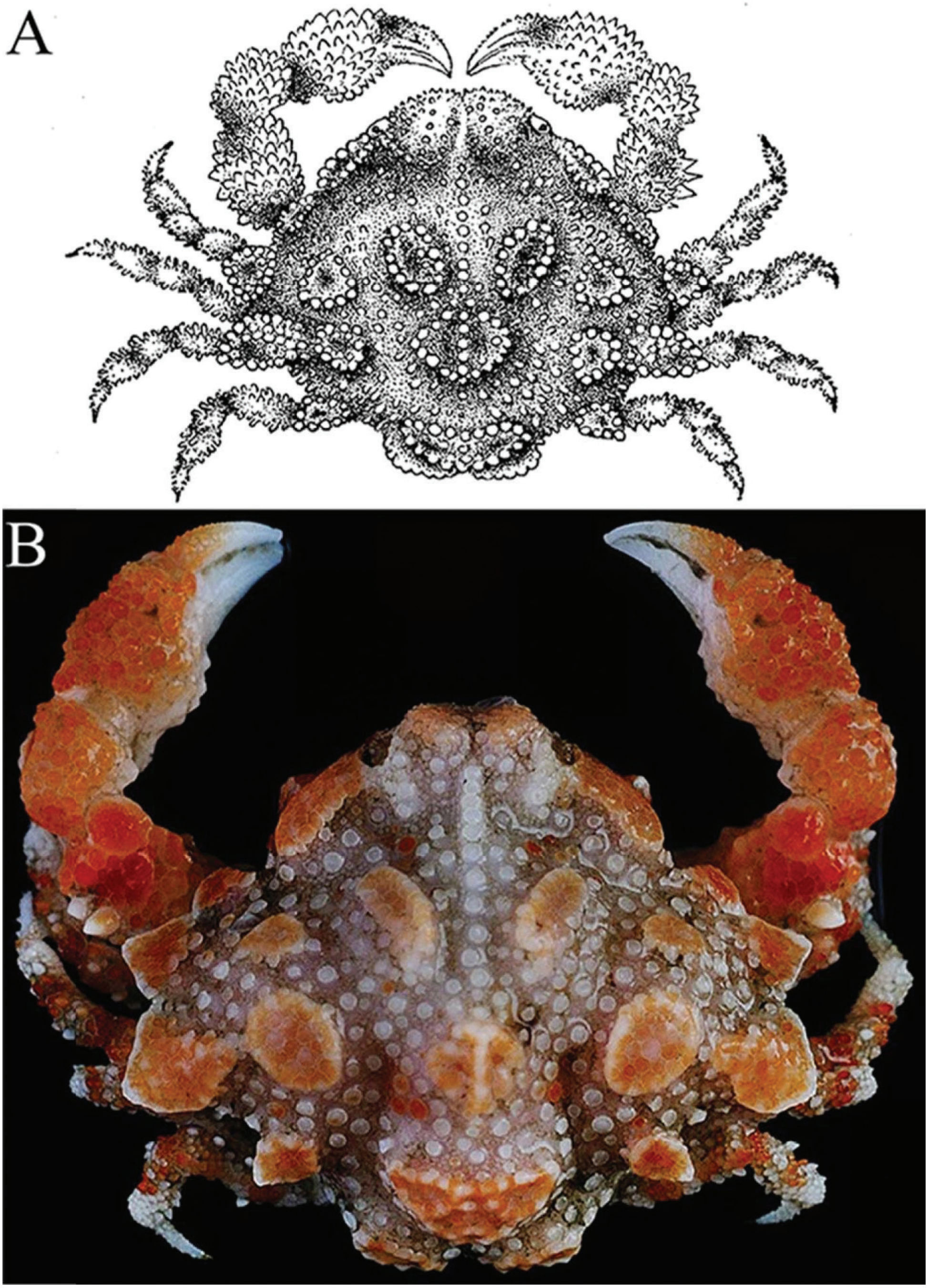

Figure 1. *Orientotlos iishibai* Sakai, 1980 **A** holotype female (7.0 by 5.5 mm) (repository unknown), Japan [after Sakai 1980: text-fig. 1] **B** color in life, female (7.8 × 6.5 mm) (NTOU B00125), Taiwan.

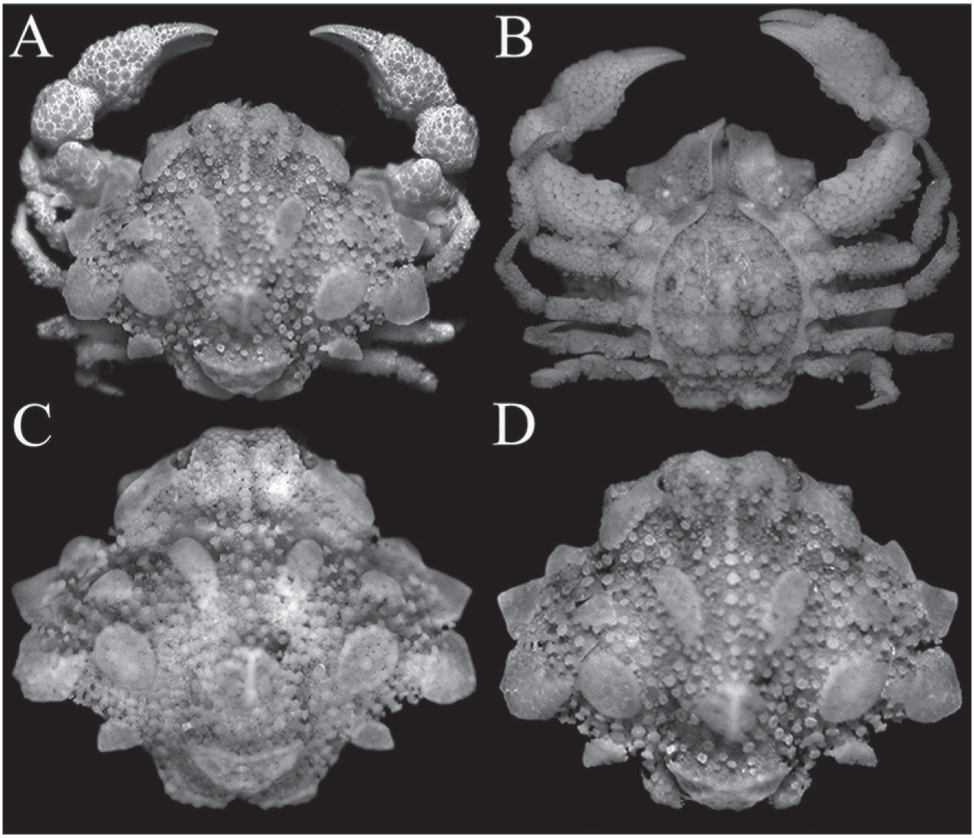

Figure 2. *Orientotlos iishibai* Sakai, 1980, female (7.8 × 6.5 mm) (NTOU B00125), Taiwan **A** overall dorsal view **B** overall ventral view **C, D** dorsal view of carapace from different angles.

Diagnosis. As for genus.

Description. Female. Carapace subhexagonal in outline, 1.2× as wide as long; upper surface (between plates and bosses) paved with numerous, well-spaced boletiform and rounded tubercles of varying sizes (Figs 1, 2A–D). Front produced, upturned, margin weakly bilobed with shallow median concavity; frontal margin gently confluent with concave supraorbital margin; hepatic region plate-like, formed by coalesced granules; subhepatic region swollen, forming a distinct obtuse angle visible in dorsal view; hepatic plate separated from first anterolateral tooth by a wide, deep cleft; anterolateral margin with 3 large lobiform teeth increasing in size posteriorly, third tooth directed obliquely, surface paved with flattened granules, margins lined with low granules; posterolateral margin concave, with median triangular tooth, margin with rounded granules; posterior carapace margin with 2 large lozenge-shaped bosses, directed posteriorly, margin flattened, surface and margins lined with rounded and flattened granules (Figs 1, 2A–D). Suborbital region substantially compressed; subhepatic region

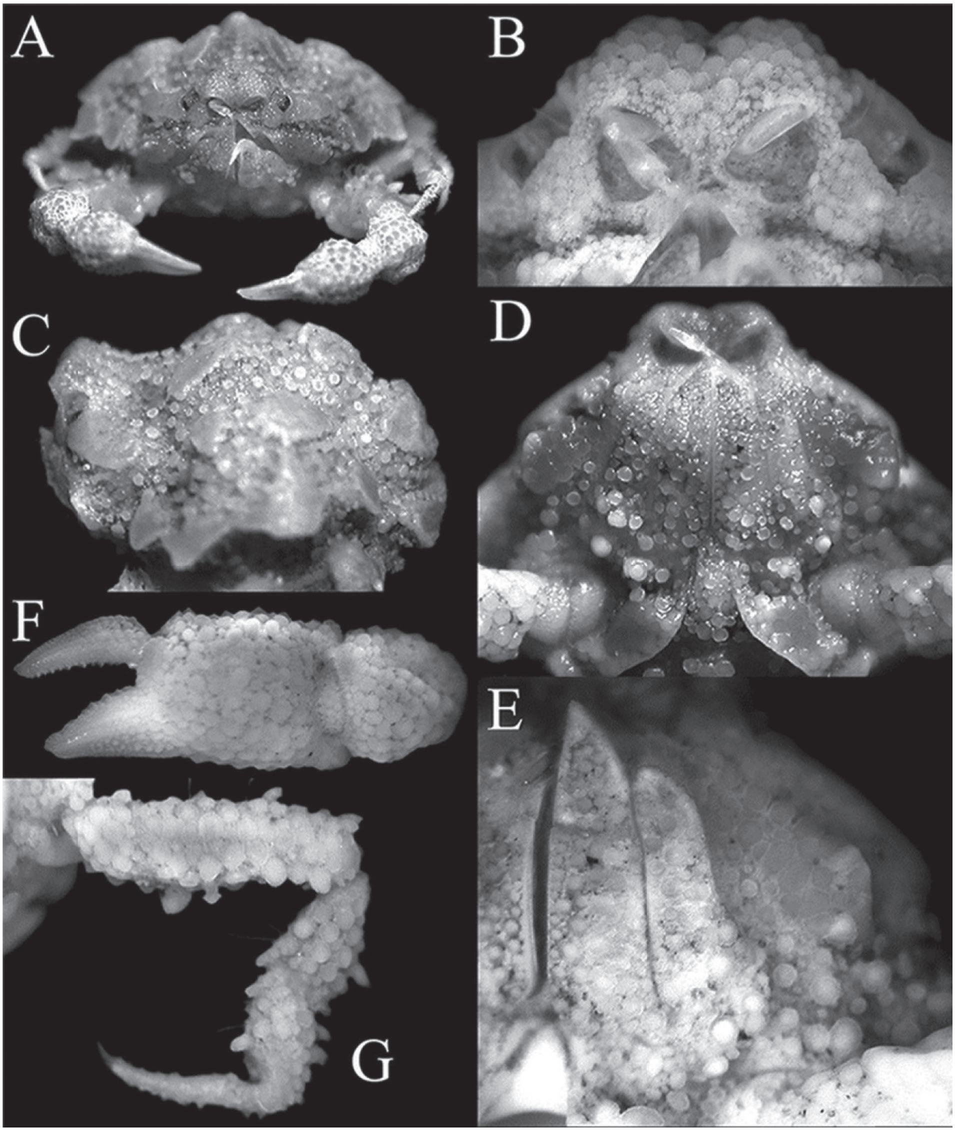

Figure 3. *Orientotlos iishibai* Sakai, 1980, female (7.8 × 6.5 mm) (NTOU B00125), Taiwan **A** frontal view of cephalothorax **B** frontal view showing antennules, antennae and orbits **C** lateral view of cephalothorax **D** pterygostomial region, buccal cavity, third maxillipeds and anterior part of sternopleonal cavity **E** left third maxilliped **F** outer view of left chela **G** right fourth ambulatory leg.

swollen, surface with large, flattened tubercles, margins of subhepatic and pterygostomial regions covered with numerous boletiform tubercles (Fig. 3D, E); subhepatic and hepatic regions separated by distinct groove lined with granules, inner edge leading to just before tip of efferent branchial channel, outer edge joining cleft between hepatic lobe and first anterolateral tooth (Fig. 3A, B). Postfrontal median keel on gastric region prominent, high, extending posteriorly to cardiac region as raised row of rounded tubercles; postorbital region gently concave, without deep depression; median part of carapace dome-shaped, protogastric region with ovate boletiform plate, obliquely positioned, margin granulated; cardiac region swollen, with raised, vaguely T-shaped ridge formed of fused granules surrounded by rounded granules; epibranchial region with a small, subovate, transversely positioned boletiform plate, margin lined with small granules; mesobranchial region with large ovate boletiform plate, margin lined with granules; intestinal region strongly inflated, with a large subtriangular boletiform plate, directed posteriorly, margin with distinct granules (Figs 1, 2A, C, D, 3A, C). Orbital margin not clearly marked, gradually merging with granules from frontal margin and hepatic region; cornea visible in dorsal view, peduncle short with small sharp granules (Fig. 2C, D). Antennule folded into an oblique fossa; basal segment finely granulate, occupying lower two-thirds of fossa (Fig. 3B). Basal antennal article large, subquadrate, fused with epistome, forming most of suborbital margin, covered with rounded tubercles; antennae small, slender, inserted in orbital hiatus (Fig. 3B). Anterior margin of efferent branchial channel produced, reaching to just before proepistome, slightly notched (Fig. 3B).

Third maxilliped with merus, ischium and exopod paved with numerous flattened, rounded tubercles of varying sizes, those on proximal parts generally larger; merus triangular, about half length of ischium; palp (carpus, propodus and dactylus) shorter than merus, inserted on inner surface; dactylus distinctly longer than propodus; ischium subrectangular, with no visible median sulcus; basis-ischium and coxa not expanded, covered with numerous large rounded tubercles and some boletiform tubercles; exopod stout, broad, reaching to about half length of merus, basal part with large rounded, boletiform tubercles (Fig. 3D, E).

Chelipeds subequal, closely covered with tubercles of varying sizes and shapes; merus trigonal in cross-section, surface covered with closely-packed low, rounded granules, posterior margin with 3 or 4 large conical tubercles, inner margin with low, broad tubercles and granules; carpus rounded, surface covered with closely-packed low, rounded granules, inner distal angle with low tooth; palm short, stout, upper and outer surfaces with low, conical tubercles, relatively densely packed, inner surface prominently swollen, covered with large, rounded granules; fingers short, shorter than palm, dorsal margin of dactylus with row of low, short granules, outer surface with low, flattened granules, cutting edge with small sharp denticles, pollex relatively broader, outer surface with small rounded granules, submarginal ones arranged in approximate rows, cutting edge with low denticles (Figs 1, 2A, B, 3A, F).

Ambulatory legs short, decreasing in size posteriorly; merus, carpus and propodus covered with slender and boletiform tubercles along upper and lower margins, outer surface with large, rounded granules and tubercles; dactylo-propodal lock present; dactylus slender, glabrous, lined with granules, tip curved, corneous (Figs 2A, B, 3G).

Anterior thoracic sternites (1–4) strongly compressed; sternites 1 and 2 completely fused to form small plate; sternites 3 and 4 appearing fused but vaguely demarcated by arrangement of granules, surface of sternite 3 with numerous boletiform tubercles,

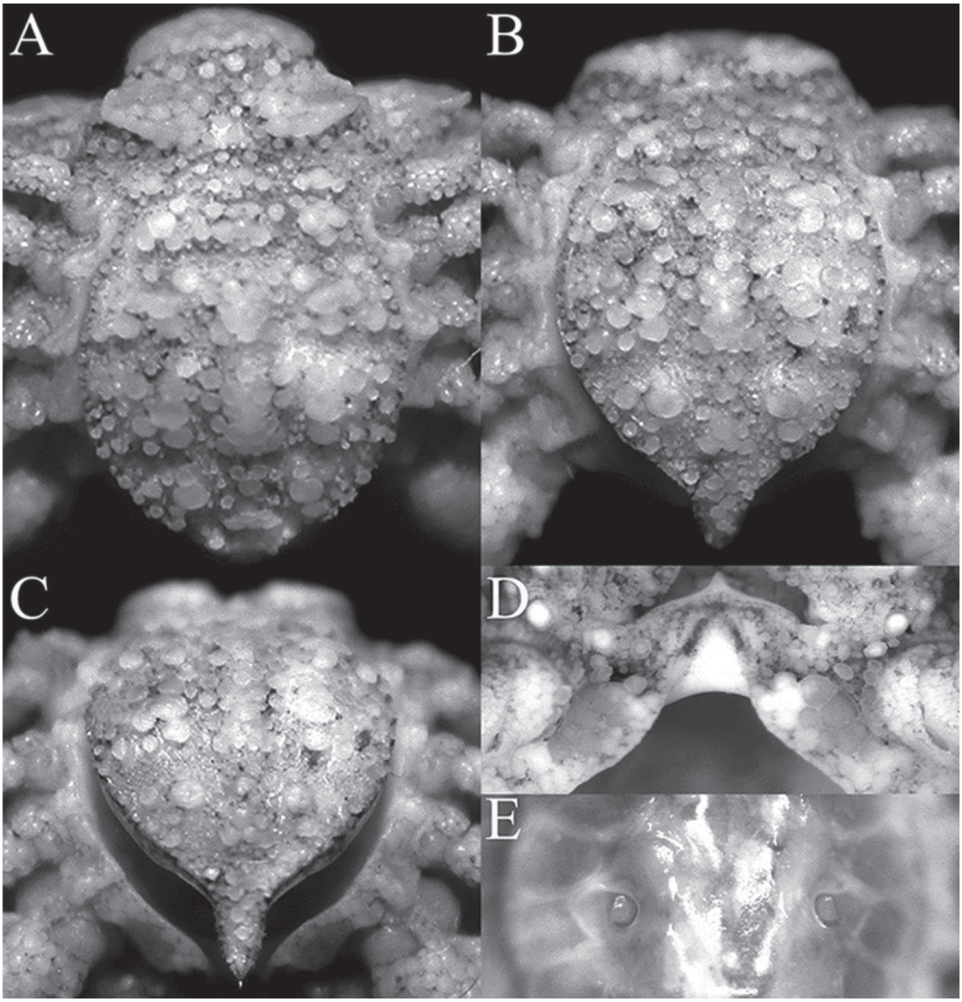

Figure 4. *Orientotlos iishibai* Sakai, 1980, female (7.8 × 6.5 mm) (NTOU B00125), Taiwan **A** intestinal region, posterior carapace lobes and pleonal somites 2–6 **B** posterior carapace lobes, pleonal somites 2–6, and telson **C** pleonal somites 4–6 and telson **D** anterior thoracic sternites and sternopleonal cavity **E** sternopleonal cavity and vulvae.

larger on lateral surfaces; surfaces of sternites 4–7 with flattened and low, rounded tubercles (Figs 2B, 4A–D). Sternite 4 forming keel around distal part of sternopleonal cavity, occupying anterior third of overall cavity (Figs 3D, 4D). Sternopleonal cavity subovate, deeply excavated, glabrous, reaching buccal cavity anteriorly; sutures between sternites 4/5, 5/6, 6/7, and 7/8 interrupted medially (Figs 3D, 4D, E). Vulvae relatively small, round, positioned distinctly apart, with opening directed laterally (Fig. 4E).

Pleon ovate, shield-like, entirely covered with closely packed, rounded tubercles of varying sizes, larger ones partially coalescing; somite 1 very narrow, girdle-like, not visible when pleon closed, free; somite 2 narrow, semicircular, free; somites 3–6 completely fused, sutures not clearly visible in dorsal view, distinct in ventral view, margins lined with rounded granules; telson narrowly triangular, with proximal part broad, distal part linguiform, lateral margins deeply concave (Figs 2D, 4A–C).

Remarks. Sakai (1980: 74) described the genus and species on the basis of only one 7.0 by 5.5 mm female, and no depth information was indicated with the provenance data. The description is relatively short and only one figure was provided. The whereabouts of the holotype is not known. We have checked the various museums in Japan, Germany, Netherlands and the USA where Sakai is known to have deposited material, but we could not locate the holotype in any of these countries. Sakai (1980: 73) commented that the source of his material was from the collection of Eiji Iishiba, a member of the Japanese Carcinological Society, and it is likely that the material was returned to Iishiba after study. Where the holotype is today is not known.

At 7.8 by 6.5 mm, the present ovigerous female from Taiwan is larger than the type but closely resembles it, except that the hepatic lobe is more plate-like (Figs 1B, 2A, C, D) (versus prominently granuliform); and the anterolateral lobes are more dentiform, the margins of each lobe less distinctly granuliform (Figs 1B, 2A, C, D) (versus lobes more rounded and distinctly lined with rounded granules) (cf. Fig. 1A; Sakai 1980: text-fig. 1).

Not considering the generic characters, the carapace of *Orientotlos iishibai* superficially most closely resembles that of *Alox ornatum* (Ihle, 1918), which also has many rounded granules on its surface. However, in *A. ornatum* the granules are arranged very differently, being more closely packed and sometimes coalescing (cf. Tan and Ng 1996: pl. 5A; Galil and Ng 2007: fig. 1C; Galil and Ng 2020: fig. 1A).

No males of *Orientotlos iishibai* have been collected, so the important characters of the male pleon and gonopods are unknown.

Biology. Station CP4210 is a hard bottom habitat and the trawl net was seriously damaged, though its cod end was intact. That same haul contained many sponges and crinoids and their associated fauna, including a new species of stenopodid shrimp of the genus *Odontozona* Holthuis, 1946, often associated with sponges (Chen and Chan, in press). The hard substrate may explain the rarity of *Orientotlos iishibaii* in collections, as this habitat is very hard to sample, especially in deeper waters (see Mendoza et al. 2010). In fact, the rare deep-water western Pacific leucosiid *Galilia* Ng & Richer de Forges, 2007 originates from a similar habitat (see Ng and Richer de Forges 2007; Komai and Tsuchida 2014; Shih et al. 2015).

Acknowledgements

Sincerely thanks are extended to Tohru Naruse and an anonymous reviewer for providing constructive comments. This work was supported by research grants from the Ministry of Science and Technology, Taiwan and the Center of Excellence for the Oceans (National Taiwan Ocean University), which is financially supported from the Featured Areas Research Center Program within the framework of the Higher Education Sprout Project by the Ministry of Education (MOE) in Taiwan.

References

Adams A, White A (1849) Crustacea. In: Adams A (Ed.) The zoology of the voyage of H.M.S. Samarang, under the command of Captain Sir Edward Belcher, C.B., F.R.A.S., F.G.S. during the years 1843–1846. Reeve, Benham and Reeve, London, 33–66. [+ pls 7–13] https://doi.org/10.5962/bhl.title.120169

Chen C-L, Chan T-Y (in press) A new shrimp species of the genus *Odontozona* Holthuis, 1946 (Crustacea: Decapoda: Stenopodidea) from Taiwan. Arthropoda Selecta, in press.

Chen H, Sun H (2002) Arthropoda Crustacea. Brachyura. Marine primitive crabs. Fauna Sinica. Invertebrata 30, Science Press, Beijing, 597 pp. [+ color pls 1–4, pls 1–16]

Davie PJF, Guinot D, Ng PKL (2015) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR, Von Vaupel Klein JC (Eds) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea (Vol. 9C–I): Decapoda: Brachyura (Part 1). Brill, Leiden, 11–163. https://doi.org/10.1163/9789004190832_004

Doflein F (1904) Brachyura. In: Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer “Valdivia” 1898–1899. Verlag von Gustav Fischer, Jena 6, [1–6 + i–xiv +] 1–314. [Atlas (pls 1–58)]

Galil BS (2019) Re-description and new records of a poorly known leucosiid crab, *Merocryptus boletisculpta* Zarenkov, 1994 (Crustacea, Decapoda, Brachyura). Western Indian Ocean Journal of Marine Science 18(2): 93–97. https://doi.org/10.4314/wiojms.v18i2.11

Galil BS, Ng PKL (2007) Leucosiid crabs from Panglao, Philippines, with descriptions of three new species (Crustacea: Decapoda: Brachyura). Raffles Bulletin of Zoology, Supplement 16: 79–94.

Galil BS, Ng PKL (2020) New and rare leucosiid crabs (Crustacea: Decapoda: Brachyura) from Papua New Guinea. In: Corbari L, Ahyong ST, Chan T-Y (Eds) Deep-Sea Crustaceans from Papua New Guinea. Tropical Deep-Sea Benthos, Paris 31: 403–444. [Mémoires du Muséum national d’Histoire naturelle 213]

Galil BS, Ng PKL (in press) New and rare leucosiid crabs (Crustacea: Decapoda: Brachyura) from Madagascar. In: Richer de Forges B, Corbari L (Eds) Deep-Sea Crustaceans from Madagascar. Tropical Deep-Sea Benthos, in press.

Holthuis LB (1946) Biological results of the Snellius Expedition. XIV. The Decapoda Macrura of the Snellius Expedition. I. The Stenopodidae, Nephropsidae, Scyllaridae and Palinuridae. Temminckia 7: 1–178.

Ihle JEW (1918) Die Decapoda Brachyura der Siboga-Expedition. III. Oxystomata: Calappidae, Leucosiidae, Raninidae. Siboga Expeditie Monografie 39b2: 159–322.

Komai T, Tsuchida S (2014) Deep-sea decapod crustaceans (Caridea, Polychelida, Anomura and Brachyura) collected from the Nikko Seamounts, Mariana Arc, using a remotely operated vehicle “Hyper-Dolphin”. Zootaxa 3764: 279–316. https://doi.org/10.11646/zootaxa.3764.3.3

Mendoza JCE, Naruse T, Tan SH, Chan T-Y, Richer De Forges B, Ng PKL (2010) Case studies on decapod crustaceans from the Philippines reveal deep, steep underwater slopes as prime habitats for ‘rare’ species. Biological Conservation 19: 575–586. https://doi.org/10.1007/s10531-009-9744-x

Milne-Edwards A (1873) Descriptions des quelques crustacés nouveaux ou peu connus provenant du Musée de M. C. Godeffroy. Journal du Muséum Godeffroy 1: 77–88. [pls 12, 13] https://doi.org/10.5962/bhl.title.10644

Ng PKL, Guinot D, Davie PJF (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology, Supplement 17: 1–286.

Ng PKL, Richer de Forges B (2007) A new genus and new species of leucosiid crab from New Caledonia, with a note on the validity of *Tanaoa serenei* (Richer de Forges, 1983) (Crustacea: Decapoda: Brachyura). Zootaxa 1662: 15–24.

Rüppell E (1830) Beschreibung und Abbildung von 24 Arten Kurzschwänzigen Krabben, als Beitrag zur Naturgeschichte des rothen Meeres. H. L. Brönner, Frankfurt am Main, 28 pp. [+ pls 1–6]

Sakai T (1976) Crabs of Japan and the Adjacent Seas. In three volumes: English text, [xxix +] 773 pp., Japanese text, 461 pp., Plates volume, 16 pp. [pls 1–251]. Kodansha Ltd., Tokyo.

Sakai T (1980) On new and rare crabs taken from Japanese and Central Pacific waters. Researches on Crustacea 10: 73–84. [figs 1–3, pl. 5, frontispiece 2] https://doi.org/10.18353/rcustacea.10.0_73

Serène R (1955) Sur quelques espèces rares de Brachyures (Leucosidae) de l'Indo-Pacifique (2è partie). Treubia 23(1): 137–218. [figs 1–11, pls 6–11]

Shih Y-J, Ho P-H, Chan T-Y (2015) Leucosiid crabs (Crustacea: Decapoda: Brachyura) from Taiwan, with three new records. Zootaxa 4052: 127–134. https://doi.org/10.11646/zootaxa.4052.1.7

Tan CGS, Ng PKL (1996) A revision of the Indo-Pacific genus *Oreophorus* Rüppell, 1830 (Crustacea: Decapoda: Brachyura: Leucosiidae). In: Richer de Forges B (Ed.) Les fonds meubles des lagons de Nouvelle-Calédonie (Sédimentologie, Benthos), Etudes & Thèses Vol. 2. ORSTOM, 1995, 101–205. [+ pls 1–16]

Tan CGS, Richer de Forges B (1993) On the systematics and ecology of two species of mimetic crabs belonging to the family Leucosiidae (Crustacea: Decapoda: Brachyura). Raffles Bulletin of Zoology 41(1): 119–132.

Yokoya Y (1933) On the distribution of decapod crustaceans inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S. S. Sôyô-Maru, during the year [sic] 1923–1930. Journal of the College of Agriculture, Tokyo Imperial University 12(1): 1–226. [figs 1–71]

Zarenkov NA (1994) [= Crabs from seamounts of the Western part of the Indian Ocean]. In: Kuznetsov AP, Mironov AN (Eds) Bottom Fauna of Seamounts. Transactions of the P. P. Shirshov Institute of Oceanology 129: 97–125. [pls 1–14] [in Russian]