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Max Kasparek

Bees in the Genus *Rhodanthidium*

A Review and Identification Guide

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Prof. Maximilian Schwarz Konsulent für Wissenschaft der Oberösterreichischen Landesregierung Eibenweg 6 4052 Ansfelden, Austria E-Mail: maximilian.schwarz@liwest.at

Editorial Board

Fritz Gusenleitner, Biologiezentrum, Oberösterreichisches Landesmuseum, Linz Karin Traxler, Biologiezentrum, Oberösterreichisches Landesmuseum, Linz

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Rhodanthidium aculeatum, female from Konya province, Turkey Biologiezentrum, Oberösterreichisches Landesmuseum, Linz (Austria)

Author's Address

Dr. Max Kasparek Mönchhofstr. 16 69120 Heidelberg, Germany Email: Kasparek@t-online.de



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Introduction

Rhodanthidium is a relatively small genus of anthidiine bees occurring in the Western and East Palaearctic with a distribution extending from the Atlantic coast of Morocco to Central Asia. The genus reaches its northern limit in Central Europe including Switzerland, Austria and the Czech Republic. The range thus extends from approximately 30°N to 50°N and from 10°W to 72°E. From the many taxa described, 13 are accepted here as valid species. While most species are well characterised and have a stable taxonomic status, the taxonomy of two species – *Rhodanthidium septemdentatum* s.l. and *R. caturigense* s.l. – is particular unclear and in urgent need of revision. It may be that these two taxa actually represent complexes of similar species.

There are few morphological features which characterise the genus unambiguously. These include a straight subantennal suture, the presence of arolia, a strongly trifid apical tergum in the male, and a rounded or laterally sharp scutellum not or little overhanging the metanotum. Michener (2007) gives further features. All of these characters need to be applied in combination, and it has to be accepted that there are exceptions so that not all characters are found in all species.

Most members of the genus are robust species, not unlike the members of the genus *Trachusa* which also belong to the tribe Anthidiini. Males of the largest species – *Rhodanthidium superbum* – can reach 31 mm in length, whilst the smallest species is 8 mm long.

Some of the species are known as "snail-shell bees" as females use empty snail shells to deposit their eggs. After the female has deposited its eggs together with pollen and nectar, it closes the shell with a paste of sand and saliva, and buries the entire shell in the undergrowth.

In this first illustrated guide to *Rhodanthidium* material of all species in both sexes is examined. It complements the works already published for two other genera of the Anthidiini, i.e. *Stelis* and *Trachusa* (Kasparek 2015, 2017). One of the foremost aims of the present study is to enable quick and unambiguous identification of the species of *Rhodanthidium*, and to establish a basis onto which further research can build. I hope this work will stimulate further work in this interesting group of bees.

This work would have been impossible without the support of many people and institutions. In first place, Maximilian Schwarz, Ansfelden (Austria) must be mentioned, who placed his entire comprehensive collection of *Rhodanthidium* bees at my disposal, and Esther Ockermüller and Fritz Gusenleitner who loaned me the material deposited in the Oberösterreichisches Landesmuseum, Linz (Austria) and which includes the collection of the late Klaus Warncke. I further wish to thank David Notton (The Natural History Museum London, United Kingdom), Michael Ohl (Museum für Naturkunde, Berlin, Germany), Steffen Pauls (Senckenberg Research Institute and Natural History Museum, Frankfurt a. M., Germany) and Vladimir G. Radchenko (I. I. Schmalhausen Institute of Zoology, Kiev, Ukraine) for the loan of material, Yulia V. Astafurova (Zoological Institute of the Russian Academy of Sciences, Saint Petersburg) for examining on my behalf material deposited in her collection and for taking photographs, Patrick Lhomme (International Center for Agricultural Research in the Dry Areas, Rabat, Morocco) for fruitful discussions, and Claudia Erbar and Peter Leins (Centre for Organismal Studies, University of Heidelberg) for making available their unpublished photographs of the mating and nesting behaviour of *Rhodanthidium siculum*. Andrew Grace (St Leonards, Sussex, United Kingdom) is acknowledged for his comments on a draft of the manuscript and providing linguistic support.

> Heidelberg, January 2019 Max Kasparek

Material and Methods

Terminology and Abbreviations

Terminology used here follows almost exclusively Michener (2007). Attention should be given to the following issues: abdomen: as the first abdominal segment is actually the propodeum, which is incorporated in the thorax, I use the term 'metasoma'. – Axilla: plural: axillae. – Mesepisternum (plural: mesepisterna) = mesopleuron. – Metasoma: see abdomen. – Punctate = punctured. – Puncturation = punctation. – Scutellum: in *Rhodanthidium*, the scutellum is always separated from the axillae by a more or less visible suture. Therefore the term 'scutellum' does not include axillae. – Scutum = mesoscutum = mesonotum = dorsal plate of the middle thoracic segment. – Sternite = sternum (plural: sterna). The term sternite refers here always to metasomal sternites and is abbreviated as S1, S2, S3, … – Tergite = tergum (plural terga). The term tergum refers here always to metasomal tergites and is abbreviated as T1, T2, T3, … – Thorax: including the propodeum, which is actually the first true abdominal segment.

Depositories

Material from the following collections has been used for this study:

NHMUK	The Natural History Museum, London (United Kingdom)
OLL	Oberösterreichisches Landesmuseum, Linz (Austria)
SIZK	I. I. Schmalhausen Institute of Zoology,
	National Academy of Sciences, Kiev (Ukraine)
SMF	Senckenberg Museum, Frankfurt (Germany)
ZMB	Museum für Naturkunde Berlin (Germany)
ZSM	Zoologische Staatssammlung München (Germany)
сМК	collection Max Kasparek, Heidelberg (Germany)
cMS	collection Maximilian Schwarz, Ansfelden (Austria)

Distribution Maps

The baseline map for the distribution maps was designed based on an open source vector world map available at www.simplemappr.net. The maps were modified and adapted for the needs of this publication. The purpose of the distribution maps is to show the overall distribution pattern of the species of *Rhodanthidium*. Although great efforts were made to draw a complete overall picture based on published and unpublished sources (museum material, screening of literature, see reference section), an in-depth survey of local faunistic literature and of more museum collections will surely result in additional records most useful for fine-mapping.

Photographs

The photographs of the author were taken with a Canon MP-E65/2.8 lens mounted on a Canon EOS 6D camera. Multiple photographs were taken of each specimen and then combined to create a picture of a specimen completely in focus. The camera was moved between the shots with a Cognisys StackShot Rail. A Canon Twin Lite MT24EX Macro Flash was used. The camera, the flash and the stackshot rail were operated with Helicon Remote Version 3.9.7 W. The pictures were processed with Helicon Focus (version 6.0.18) software to combine the pictures and to create one completely focused image from several partially focused images (image stacking). Usually 15-25 photographs were taken at different focus distances to give a resulting image with a greater depth of field than any of the individual source images. The resulting images were further processed with Adobe Photoshop CS6 and Adobe Photoshop Elements 15.

The Genus Rhodanthidium: A taxonomic overview

Following the classification of Michener & Griswold (1994) and Michener (1997, 2007), *Rhodanthidium* Isensee, 1927 is regarded here as a genus in the tribe Anthidiini. Some authors such as Isensee (1927) in his original description or Warncke (1980) in his revision of the genus *Anthidium* Fabricius, 1804 have regarded it as a subgenus of *Anthidium*.

The habitus of the members of the genus *Rhodanthidium* is similar to *Anthidium*. Michener (2007) characterises it as follows: A Palaearctic genus of moderate-sized to very large chalicodomiform or euceriform bees with abundant yellow or reddish-yellow markings. Males are larger than females. The metasomal colour bands, when present, are broken medially at least on the anterior terga. Common features are (1) a lack of carinae, except commonly a carina or even a lamella on the pronotal lobe and sometimes a weak upper omaular carina, (2) the straight subantennal sutures, (3) the rounded or laterally sharp scutellum not or only slightly overhanging the metanotum, (4) the presence of arolia, (5) the strongly trifid T7 of the male, (6) the male gonostyli with their apices being simple or having two small teeth and (7) the male sterna, which are not greatly modified, although S4 and S5 sometimes carry median apical combs and S5 has in some species a lateral tooth. The number of segments in the maxillary palpus varies from two to three and perhaps four, but Michener (2007) acknowledges that "it is often difficult to determine the exact number as the segments sometimes seem to be only partly separated, so that one must make arbitrary decisions".

The name *Rhodanthidium* is derived from the Greek 'rhodos' which means 'rose' and refers to the reddish colouration of the type *Rhodanthidium siculum*. This colouration is shared by only two other species, *R. sticticum* and partly *R. superbum*. All other species are black with yellow.

Key to the Genera of the tribe Anthidiini with Arolia present

One of the main and easily recognisable features of the species of the genus *Rhodanthidium* is the presence of arolia. I therefore give here a key to all those species of the tribe Anthidiini which have arolia present. The key is a modified excerpt from the key provided by Michener's (2007) to the genera of the Eastern Hemisphere.

1	Arolia absent Various genera
_	Arolia present
2	Omaulus lamellate, continued onto venter of thorax and there separat- ed from middle coxa by less than width of middle trochanter <i>Anthidiellum</i> (in part)
_	Omaulus lamellate or not, if lamellate then often not continued onto venter of thorax, but if so, then mesepisternum between middle coxa and omaulus (however recognised) as wide as or wider than width of
	middle trochanter

3	Vein cu-v of hind wing usually half as long as second abscissa of M+Cu or longer, oblique; middle tibia as broad as hind tibia or nearly so (T7 of male simple or bilobed)
4	Scopa present in female; front and middle tibiae each with one apical spine or angle (except some <i>Eoanthidium</i> , which have two spines on middle tibia)
	Scopa absent; front and middle tibiae each with two spines, one midapical and one posterior apical
5	Juxtantennal carinae present although sometimes weak; interantennal distance usually less than, rarely equal to, antennocular distance; S6 of female with spine or premarginal ridge, sometimes weak and lateral only, sternal margin thus appearing thick, sometimes elevated to lateral tooth (T7 of male over half as wide as T6)
-	Juxtantennal carinae completely absent; interantennal distance usually greater than antennocular distance; S6 of female unmodified, margin thin
6	Scutoscutellar suture superficially similar to scutoaxillar suture, usual- ly closed, but if smooth shining floor of groove visible, then usually not divided; subantennal suture approximately straight or only slightly arcuate; fovea behind propodeal spiracle absent; body usually over 10
_	mm long
7	Omaular carina absent or extending down only to middle of mesepi- sternum; T7 of male, if trilobed, then with median lobe much longer than lateral lobe or spine: subantennal suture straight (eastern Asia) <i>Bathanthidium</i>
-	Omaular carina strong, sometimes lamellate, and extending onto ven- tral surface of thorax, sometimes across venter; T7 of male, if trilobed, then with median lobe small, either not separated from lateral lobe by emargination or not longer than lateral lobe; subantennal suture usual- ly arcuate outward
8	Tegula of ordinary size and shape, widest medially and longer than wide (scutum wider than long, only moderately so in subgenus <i>Steli-</i> <i>domorrha</i>) Stelis (in part)
_	Tegula enlarged, especially posteriorly, width posteriorly almost as great as length (Yemen)

Subgeneric Classification

Following Michener & Griswold (1994) and Michener (1997, 2007), three subgenera are recognised. Michener (2007) concedes that a forth subgenus may be erected for *Rhodanthidium infuscatum* based on differences with all other members of the subgenus but he refrained from doing so as there is no other species with these characters.

Actually, the subgeneric division is somewhat arbitrary as not all characters hold for all members of the subgenus. Examples are: *R. superbum* clusters with *R. glasunovi* as they are the only species of the genus which have a cushion-like shape of S1, but they are assigned to different subgenera. The presence/absence of median combs on S4 and/or S5 or the presence/absence of a lateral tooth on S5 are strong structural elements, but they do not coincide with the subgeneric classification. *R. superbum* clusters with *R. buteum* as in both species the comb on S5 consists of strong brown hair rather than black bristles as in the other species with ventral combs, but they are placed in different subgenera. A small lateral tooth (denticle) on S5 characterises *Rhodanthidium* s.str., but such a structure is absent in *R. exsectum*, although it is regarded as a member of the subgenetic classification seems not to reflect consistent phylogenetic lines.

Nevertheless, in the absence of alternatives, I here follow Michener (2007), knowing that it contains vague and disputable aspects. It may even be considered appropriate not to assign subgenera although a formal decision on this should be left until further phylogenetic research, including DNA relationships, becomes available.

Rhodanthidium / Subgenus Asianthidium Popov, 1950

- Meganthidium (Asianthidium) Popov, 1950: 315. Type species: Anthidium glasunovi Morawitz, 1894, by original designation.
- Rhodanthidium (Trianthidium) Mavromoustakis, 1958: 435. Type species: Anthidium caturigense Giraud, 1863, by original designation.
- Meganthidium (Oxyanthidium) Mavromoustakis, 1963: 653. Type species: Anthidium aculeatum Klug, 1832, by original designation.
- Axillanthidium Pasteels, 1969a: 39. Type species: Axillanthidium axillare Pasteels, 1969 = Anthidium ducale Morawitz, 1876, by original designation.

Males of this subgenus are characterised by a trifid apex of T7 (median tooth sometimes broad and rounded or truncate) occupying the full width of tergum; both sexes have a pronotal lobe with lamella or carina [weak in *R. (Asianthidium) glasunovi*], and the background colour of the head is black. In *R. (Meganthidium)*, the trifid apex of the male is much narrower than tergum, which has lateral angles and renders the tergum five-toothed; pronotal lobe in *R. (Meganthidium)* without or with very weak carina, and head largely yellow.

Bees of *R. (Asianthidium)* have unusually heavily sclerotized penis valves, each with an apical or preapical spine, lobe, or process. Body length is 11 to 18 mm. The distribution extends from Spain to southwestern Asia and to Central Asia. Three species are assigned to this subgenus, but *R. caturigense* s.l. may actually consist of a group of similar species.

The synonymy indicated above is based on mutual similarity and the small number of species involved (Michener 2007). *Asianthidium* (s.str.), *Axillanthidium*, and *Oxyanthidium* each contain only a single species. *Asianthidium* in the sense of *Rhodanthidium* (*A*.) *glasunovi* (Morawitz) seems the most deserving of separate subgeneric recognition if the subgenus as here understood were to be divided (Michener 2007). The weak rather than strong carina on the pronotal lobe and the elevated median process of T7 of the male (suggesting *Rhodanthidium* s.str.) differentiate it from all other species of the subgenus. *Rhodanthidium* (*A*.) *aculeatum*, the species placed in *Oxyanthidium*, differs from other species in the strongly denticulate and laterally angulate margin of T6 of the female and the translucent preapical lamella above the apex of S6 of the female, the sternum thus having a double margin.

Species (at least three species):

Rhodanthidium aculeatum (Klug, 1832) Rhodanthidium caturigense (Giraud, 1863) s.l. Rhodanthidium glasunovi (Morawitz, 1894)

Rhodanthidium / Subgenus Meganthidium Popov, 1950

Meganthidium Popov, 1950a: 315. Type species: Anthidium christophi Morawitz, 1884 = Anthidium superbum Radoszkowski, 1876, by original designation.

This subgenus is easily recognised by the trifid apex of T7 of male which is much narrower than the tergum and possesses lateral angles rendering the tergum five-toothed; by the pronotal lobe without or with only a very weak carina, and by the head being largely yellow. Aside from the great size (19-22 [31] mm long), characters of the subgenus also include the simple T6 of the male and three teeth arising from a small elevated area on T7. The apex of the male middle tibia appears to have a pair of apical angles as in females, but the angles are preapical and connected by a carina; there is no corresponding pair of angles on the fore tibia, which has a transverse preapical carina. Popov (1950) illustrated the male genitalia and sterna.

Michener (2007) gave as another character of the subgenus the presence of a comb on male S4 but not on S5. This could not be confirmed. All males examined had only a comb on S5 which, however, does not consist of black bristles as in other species but of strong brown hair.

Meganthidium ranges from Turkey to Central Asia. There is only one species.

Species (one species): Rhodanthidium superbum (Radoszkowski, 1876)

Rhodanthidium / Subgenus Rhodanthidium Isensee s. str., 1927

Anthidium (Rhodanthidium) Isensee, 1927: 374. Type species: Anthidium siculum Spinola, 1838, by original designation.

Bellanthidium Pasteels, 1969a: 38. Type species: Anthidium infuscatum Erichson, 1835, by original designation.

As is evident from the key to subgenera, the subgeneric characters of females do not always hold. An additional character for males is the apically notched, thus bidentate, gonostylus; in this respect *Rhodanthidium* s. str. differs from the other subgenera. Length ranges from 8.5 to 19.0 mm. For two species, *R. siculum* and *R. sticticum*, the pale areas are yellowish red, for the other species they are bright yellow.

Rhodanthidium s. str. occurs in the Mediterranean region from Morocco and Portugal to Central Europe, eastward to Iran. There are at least nine species, but *R. septemdentatum* s.l. may actually represent a complex of a few similar species.

Most of the species form a unified group, but *Rhodanthidium infuscatum* is quite distinctive and Pasteels (1969) erected for it the genus name *Bellanthidium*. Since there is only one such species and its relationship to the others is clear, a separate genus or subgenus for it seems unnecessary. Among its distinctive characters is the enormous emargination in T6 of the female. "Thus those who wish to recognise *Bellanthidium* as a monotypic subgenus will have no difficulty in doing so" (Michener 2007).

Ornosa & Ortiz Sánchez (2014) stated that "*Rhodanthidium ducale* is a species belonging to the subgenus *Rhodanthidium*" but this seems to be mis-interpretation of the underlying sources. The species is actually assigned to the subgenus *Asianthidium*.

Species (at least 9 species):

Rhodanthidium acuminatum (Mocsáry, 1884) Rhodanthidium buteum (Warncke, 1980) Rhodanthidium exsectum (Pasteels, 1969) Rhodanthidium rufocinctum (Alfken, 1930) Rhodanthidium infuscatum (Erichson, 1835) Rhodanthidium ordonezi (Dusmet, 1915) Rhodanthidium septemdentatum (Latreille, 1809) s.l. Rhodanthidium siculum (Spinola, 1838) Rhodanthidium sticticum (Fabricius, 1787)

Key to the Subgenera of Rhodanthidium

The key given here is taken from Michener (2007), knowing that not all characters hold for all species, and subgeneric assignment remains challenging (see also above).

2	Trifid apex (median tooth sometimes broad and rounded or truncate) of
	T7 of male occupying full width of tergum; pronotal lobe with lamella
	or carina [weak in R. glasunovi]; head with background colour black
_	Trifid apex of T7 of male much narrower than tergum, which has lateral angles rendering tergum five-toothed; pronotal lobe without or with

very weak carina; head largely yellow R. (Meganthidium)

Morphological Characters

Colouration of mandibles. In males of all species the ground colour of the mandible is yellow with black teeth. In *R. aculeatum, R. acuminatum, R. glasunovi* and *R. infuscatum*, the mandibles have black or dark brown margins. Sometimes, especially in *R. ordonezi* and *R. sticticum*, the yellow colouration is merged with some brown, mainly at the margins.

In females, about half of the species has broad, dark black mandibles. In *R. caturigense* s.l., *R. exsectum*, *R. infuscatum* and *R. ordonezi*, the mandibles are yellow-brown, in *R. sticticum* and *R. superbum*, the mandibles are yellow-red or reddish-brown.

Species	Female	Male
Rhodanthidium aculeatum	Black	Yellow with black margins
Rhodanthidium acuminatum	Black	Yellow with black margins
Rhodanthidium buteum	Yellow	Yellow
Rhodanthidium caturigense s.l.	Yellow-brown	Yellow
Rhodanthidium exsectum	Yellow-brown	Yellow
Rhodanthidium glasunovi	Black	Yellow with black margins
Rhodanthidium infuscatum	Yellow-brown	Yellow with brown margins
Rhodanthidium ordonezi	Yellow-brown	Yellow-brown
Rhodanthidium rufocinctum	Black	Yellow
Rhodanthidium septemdentatum s.l.	Black	yellow
Rhodanthidium siculum	Black	yellow
Rhodanthidium sticticum	Yellow-red	Yellow to red-brown
Rhodanthidium superbum	Reddish brown	yellow

Table 1. Colour pattern of mandibles of Rhodanthidium.

Pronotal lobe. The pronotal lobe is lamellate in most species; however, it is rounded or with only a very weak carina in *R. glasunovi* and *R. superbum* as well as in *R. siculum*. **Scutellum and axillae.** The lateral edges of the scutum form lamellae which extend into the suture between the scutum and the axillae (scutoaxillar suture). The suture between

the scutum and the scutellum (scutoscutellar suture) is much wider than the scutoaxillar suture, although the floor of the groove is mostly not visible. Scutellum and axillae have rich pubescence in many species (see photographs), which covers more or less completely the scutellum and axillae of some of the species.

The inner margin of the scutellum is straight with a small median projection (tooth), which is, however, subject to inter- and intraspecific variation and not always present. Posterior edge of scutellum and axillae rounded or carinate. Axillae rounded, angulate or with tooth-like projection.







Structure of the female sterna. The female in all species has a pale yellow to ochreous scopa. The sterna show some remarkable interspecific differences which can partly be used for distinguishing species:

S1 has an elevation which is

- flat with rounded edges in *R. aculeatum*;
- swollen with rounded edges in *R. superbum*;
- roof-like with a longitudinal carina in *R. acuminatum*, *R. rufocinctum* and *R. septemdentatum* s.l.;
- roof-like with a longitudinal carina and two small dark teeth distally, on each side of the middle in *R. infuscatum*;
- roof-like without a carina in *R. caturigense* s.l., *R. buteum*, *R. exsectum*, *R. glasunovi*, *R. ordonezi*, *R. siculum*, and *R. sticticum*.

The apical margin of S5

- has a median emargination in *R. exsectum*, and
- is straight in all other species.

The shape of S6 is

- flat, semi-circular to triangular, and almost as wide as S5 in *R. acuminatum*, *R. glasunovi*, *R. ordonezi*, *R. rufocinctum*, *R. septemdentatum* s.l., *R. siculum*, *R. sticticum*, and *R. superbum*;
- flat, semi-circular to triangular, but much narrower than S5 in *R. caturigense* s.l., *R. buteum*, and *R. infuscatum*;
- flat, black, triangular-shaped and hairless in *R. aculeatum*;
- has rounded sides and is more or less encapsuled by T7 in *R. exsectum*.

The apical margin of S6 is

- divided into an upper and lower lamella in *R. aculeatum*, and
- has a single lamella in all other species.

Structure of the male sterna. The structure of male sterna show a high degree of variation. The table gives an overview of the various character features.

Important difference is the presence or absence of combs on S4 and S5. Combs are present on both on S4 and S5 in *R. acuminatum*, *R. rufocinctum*, *R. septemdentatum* and *R. siculum*. *Rhodanthidium sticticum* has a comb only on S4, *R. infuscatum* only on S5. *Rhodanthidium superbum* and *R. buteum* have combs on S5 which do, however, not consist of black bristles as in the other species, but of strong brown hair.

A lateral denticle is found in most species of the subgenus *Rhodanthidium* (*Rhodanthidium*) on S5, but is absent in *R. exsectum*.

Table 2. Comparison of the structure of the male sterna and pronotal lobe in the genus Rhodanthidium.

 $\begin{array}{l} \mbox{Racul} = R. \ acuteatum; \ \mbox{Rot} = R. \ buteum; \ \mbox{Rot} = R. \ caturigense \ s.l.; \ \mbox{Rexs} = R. \ exsectum; \ \mbox{Rol} = R. \ glasumovi; \ \mbox{Rinf} = R. \ infuscatum; \ \mbox{Rot} = R. \$

Rsti	٠		•		•					•		
Rsic	•		•		•					•		•
Rsep	•			•	•					•		•
Rruf	٠			•	•					•		•
Rord	•		•		•					•		
Rinf	•					•						•
Rexs	•											
Rbut	•			•		•				•		
Racum	•		•		•		٠	•		•	•	•
Rsup		•										
Rgla		•	•		•							
Rcat	•											
Racul	•		•		•				•		•	
	Roof-like elevation with longitudinal carina	Cushion-like elevation with rounded edges	Elevated area with polished surface	Elevated area, surface not polished	Transversal carina more or less straight	Transversal carina undulated	Longitudinal carina	Longitudinal carina	Transversal carina	Median comb (sometimes divided in the middle)	Apical margin with shallow median emargination	Median comb with black

Rsti			•	•			•		•	•	
Rsic			•	•	•		•		•		•
Rsep			•	•	•				•	•	
Rruf			•	•			•		•	•	
Rord			•	•			•		•	•	
Rinf			•	•		•		•		•	
Rexs									*•	•	
Rbut		•	•	•	•		•	•		•	
Racum			•	•	•				•	•	
Rsup		•	•		•			•			•
Rgla Rsup		•	•		•			•			•
Rcat Rgla Rsup		•	•		•			•	•	•	•
Racul Rcat Rgla Rsup		•	•		•			•	•	•	•
Racul Rcat Rgla Rsup	bristles	Median comb with brown bristles/hair	Apical margin with • • •	Lateral denticle present	Median longitudinal • • • •	Longitudinal elevation	Round translucent spot(s) near apex	Apical margin • • • convexly semi-circular • • • •	Apical margin convex with lateral shoulders	Pronotal lobe with • •	Pronotal lobe rounded • •

*median process tongue-like.

The taxa of Rhodanthidium

The following taxa of Rhodanthidium are recognised here:

Rhodanthidium aculeatum (Klug, 1832) Rhodanthidium acuminatum (Mocsáry, 1884) Rhodanthidium buteum (Warncke, 1980) Rhodanthidium caturigense (Giraud, 1863)

> Subspecies: Rhodanthidium caturigense caturigense (Giraud, 1863) Rhodanthidium caturigense ducale (Morawitz, 1876) Rhodanthidium caturigense jerusalemicum (Mavromoustakis, 1938)

Rhodanthidium exsectum (Pasteels, 1969) Rhodanthidium glasunovi (Morawitz, 1893) Rhodanthidium infuscatum (Erichson, 1835) Rhodanthidium ordonezi (Dusmet, 1915) Rhodanthidium rufocinctum (Alfken, 1930) Rhodanthidium septemdentatum (Latreille, 1809)

> Subspecies: Rhodanthidium septemdentatum septemdentatum (Latreille, 1809) Rhodanthidium septemdentatum faciale (Friese, 1917)

Rhodanthidium siculum (Spinola, 1838) Rhodanthidium sticticum (Fabricius, 1787) Rhodanthidium superbum (Radoszkowski, 1876)

As the taxonomic rank of the subspecies of *R. caturigense* and *R. septemdentatum* need clarification and may deserve elevation to species rank, they are listed here as '*R. caturigense* s.l.' and '*R. septemdentatum* s.l.'.

Among the many synonyms available (see species accounts), the following names used in some recent works are not recognised here as valid taxa:

Anthidium glasunovi hissarense (Mavromoustakis, 1939) Rhodanthidium hissarense (Mavromoustakis, 1939) Rhodanthidium infuscatum bellicosum (Lepeletier, 1841) Rhodanthidium pyrenaeum (Alfken, 1927)

Key to the species of Rhodanthidium

The key has been designed to avoid reliance on characters related to the ventral side of the metasoma, which is often difficult to assess in collection material. Thus, the key is completely different from that provided by Warncke (1980).

Females

1	T1 and T2 with red colouration2T1 and T2 with yellow colouration or entirely black4
T1 a	nd T2 with red colouration
2	Reddish-brown colouration on terga confined to T1–T2, other terga with yellow lateral bands; lower carina of T6 with a semi-circular projection on each side
3	Clypeus reddish with black apical margin (rarely some dark brown or black darkening at base of clypeus); mandible reddish-brown with black teeth
Terg	a almost entirely black (at most with some irregular yellow maculation)
4	Metasomal terga with some irregular yellow maculation (sometimes entirely black or maculation only visible as slightly translucent brighten- ing); head and mesosoma black with red maculation on head; legs red glasunovi Metasomal terga black with yellow lateral bands
5	Mandibles yellow with black teeth
Man	dibles yellow (with black teeth and black margins)
6 	T6 with wide apical emargination



Rhodanthidium ordonezi, R. sticticum

Rhodanthidium exsectum

- 7 T6 with reverse heart-shaped emargination and small protruding wings *R. exsectum*

- form the distal point; inner carina without median incision *R. infuscatum*



Mandibles black (at most with some reddish-brown lightening)

T6 slightly protruding <i>R. caturigense</i> s.1. T6 strongly convex, trapezoid to semi-circular 10
T6 with strong lateral projection whose apex is directed towards the
rear; outer side of the projection with smooth margin
confined to the apex
Bulge next to the small median incision of T6 absent, area covered with
short hair; large species >16 mm R. acuminatum
Area next to the small median incision of T6 with two small, longish
polished bulges; small to medium-sizes species (mostly 8-13 mm) 12
Marginal zone of terga brown and slightly translucent; clypeus black;
small species (<10 mm) R. rufocinctum
Marginal zone of terga black and opaque; colouration of clypeus varia-
ble from entirely yellow to entirely black; medium-sized species (mostly
10–13 mm) <i>R. septemdentatum</i> s.1

Males

1	T1 and T2 with red colouration	2
_	T1 and T2 with yellow colouration or entirely black	4
T1 a	nd T2 with red colouration	
2	Reddish-brown colouration on terga confined to T1–T2, remaining terga with yellow lateral bands; T7 with five teeth	т
	T7 with three teeth	3
3	Lateral teeth of T7 slender and obtuse apically; apical margin of T6 translucent reddish-brown	т



Terga almost entirely black (at most with some irregular yellow maculation)

0	
4	Metasomal terga black with irregular yellow maculation (either entirely black or with a slightly brightening translucent maculation; head and mesosoma black with red maculation on head; legs red
Terg	a with yellow bands
5	T6 with a rectangular or trapezoid, truncated median projection at least as broad as the median projection of T7
6	T6 with an acute lateral tooth
7	Median projection of T6 flat, overhanging T7
8	Median projection of T7 black, lateral projections brown to ochreous; median projection of T6 black, truncated; T6 with large lateral teeth; antennae black; large species (>20 mm)
	species (<15 mm) R. ordonezi



Apical terga of Rhodanthidium acuminatum (left) and R. ordonezi and R. sticticum (right).

- 9 Marginal zone of terga brown and slightly translucent; clypeus black; small species (<10 mm) *R. rufocinctum*
- Marginal zone of terga black and opaque; colouration of clypeus variable from entirely yellow to entirely black; medium-sized species (mostly 10–13 mm)

- Truncate part of apical margin of T6 about as broad as T7 R. infuscatum



Rhodanthidium buteum

Rhodanthidium infuscatum

- Apical margin of T6 tapering towards the middle; lateral projections of T7 with shallow emarginations (rendering T7 five-toothed) R. exsectum
- 12 T7 strongly protruding; T7 with a long and strong, tapering median spine and a strong lateral wing; third coxa with a large yellow expansion



Rhodanthidium aculeatum

Rhodanthidium caturigense s.l.

Biology and Ecology

Nest-building and reproduction

The nests of *Rhodanthidium septemdentatum* s.l., *R. siculum*, and *R. sticticum* are constructed in empty snail shells (Xambeu 1896; Ferton 1911; Gandi 1934; Peisl 1999; Fabre 1923; Grandi 1934, 1961). *Rhodanthidium rufocinctum*, the close relative of *R. septemdentatum*, surely also nests in empty snail shells, although there is no record available. *Rhodanthidium infuscatum* has also been listed as species using empty snail shells (Pasteels 1977, Ortiz y Sanchez 1990), but no further information is available.

Erbar & Leins (2017) describe in detail the behaviour of *R. sticticum* during reproduction: Before the female undertakes her first foraging flight she is approached by several males to copulate. Severe struggles among several males may take place. Males compete aggressively for access to the newly emerged females, clashing aerially and aggressively attacking one another with open mandibles. The adopted snail shell and its immediate surroundings become the territory of one of the males during the period of nest provision undertaken by the female. When the female is on foraging flights or is inside the snail shell, the male may perch on the snail shell. The returning female is intercepted and copulation takes place, often at a high frequency. Copulation can occur repeatedly within 10-20 seconds (Erbar & Leins 2017).

When sealing the completed nest, the female forms a ring of sand on the inner surface of the snail shell near the opening, using the sand lying between the opening and the apex of the shell the sand appearing to be mixed with saliva. The final closure of the shell by the female may take several hours. The female uses mainly her mandibles and head, but also the forelegs. If the procedure is interrupted by bad weather, it will be continued the following day (Erbar & Leins 2017).

The nest architecture of these snail shell nesting species is similar: one or two cells are provisioned deep in the whorls of the snail shell (Fabre 1923; Grandi 1961; Pasteels 1977). Although partitions between cells are built of resin, the inner walls of the snail shell are left unlined. Following the description of Litman (2012), a layer of sand grains, small pebbles and vegetable debris follows the final provisioned cell; the material in this layer is simply piled up and not cemented together. The entire nest is sealed with a plug of resin; the plug is often not flush with the opening of the shell but is rather further within the shell, so that the final whorl of the shell is left empty (Fabre 1923). In smaller shells, the final whorl may be left empty and the final plug of resin omitted (Fabre 1923). The final nest closure may consist of a plug of shell fragments cemented together with resin (Grandi 1961, Erbar & Leins 2017), or of pebbles cemented together with resin (Fabre 1923).

The sealed shell with the completed nest within is then buried under stones or in the sand (Fabre 1923, Pasteels 1977) and is moved for this purpose to an appropriate site. This last labour of the female may last hours or even days (Erbar & Leins 2017). The difficult transport happens centimetre for centimetre, and may happen uphill and downhill across the uneven surface of the soil or sand using the hind legs, whereby the bee rests the front of her head on the sand to obtain leverage and direction. Erbar & Leins (2017) noted the







Mating and nesting behaviour of the snail-shell bee *Rhodanthidium siculum*. – A. A male 'guarding' an empty snail shell in the absence of the female. – B. Female preparing the snail shell for egg disposition, while the male guards the shell. – C–F. Male and female copulating next to the snail shell. – G–I. The female closes the entrance after egg deposition with a large fragment of shell and saliva. – J. Sealed snail shell (with pollen, nectar and the bee eggs inside). – K–L. Transportation of the snail shell to a suitable location. – M. Female burying the snail shell in the sand.

Photographs taken 2014 in Sicily by Claudia Erbar and Peter Leins. Further photographs and detailed descriptions of the mating and nesting behaviour are available in Erbar & Leins (2017).

longest distance of such a journey to be as much as ten metres. However, in areas where burial is difficult such as in rocky soil, the nest may simply be left where it was built (Bischoff 1927).

The nests of *Rhodanthidium caturigense* are unique among anthidiines, for having the nest cells constructed both of plant resin and plant fibers. *Rhodanthidium caturigense* excavates its nest in the soil and nests are often found in large aggregations (Micheli 1935, Maneval 1936, Pasteels 1977, Müller et al. 1997). 130 to 150 females can be found close together in such an aggregation (Micheli 1935, Maneval 1936). Between three and six nest cells are located at the end of a short burrow; cells are often oriented haphazardly to accommodate the presence of stones and roots in the soil. Each individual brood cell consists of two distinct layers. The outer layer is built of plant hairs, according to Pasteels (1977) from *Verbascum thapsus*. The inner layer is built of resin. The nest entrance is sealed with a plug of resin coated with plant hairs (Pasteels 1977).

Nothing is known about the reproduction biology of the remaining species.

Mimicry

All species of *Rhodanthidium* have a black-and-yellow colouration, resembling black and yellow marked species of wasps such as *Vespa* and *Vespula*, with the exception of *R*. *glasunovi*, which has a predominantly back colouration, and *R*. *sticticum* and *R*. *siculum*, in which the yellow is replaced by a reddish colour.

A remarkable mimicry is represented by *R. superbum*: With reddish-brown colouration of the first two terga and black-and-yellow markings on the other abdominal terga, this species shows a stunning mimic of hornets (*Vespa crabro / Vespa orientalis*). The size of these bees almost equals that of the hornet worker. Appearance is also very similar to the similar-sized Hornet Mimic Hoverfly (*Volucella zonaria*) and also some parasitic fly in the Conopidae (e.g. *Conops flavicaudus*) shares this colour pattern. Such mimicry helps to protect *R. superbum* from predators while it searches for nectar.



Mimicry in the genus *Rhodanthidium*: Left the Oriental Hornet, *Vespa orientalis*, right *Rhodanthidium superbum*. Note that T1 and T2 are reddish-brown, the remaining terga with yellow bands.



Examples for similarities between the host and its cleptoparasite. *Rhodanthidium septemdentatum* (host; Left) and *Stelis ruficornis*, its cleptoparasite (right). From: Kasparek (2015).

While *Rhodanthidium* imitates other hymenopterans, they themselves are also imitated by cleptoparasites. A good example is *Stelis ruficornis* a cleptoparasite of *R*. *septemdentatum*. Both species have a similar habitus and colouration, but are differ in size.

Frequency

There are no quantitative field assessments of *Rhodanthidium* available. Judging from the relative frequency of specimens in museum collections and my own field observations, the species in the genus can be classified into three frequency status groups: abundant, medium and rare.

The most abundant species seems to be *Rhodanthidium septemdentatum* and its close relative *R. rufocinctum*, which is endemic to Crete. The two reddish *Rhodanthidium* species, *R. siculum* and *R. sticticum* are relatively abundant in the central and western Mediterranean. In central and southern Morocco, *R. ordonezi* is found relatively abundantly, and there replaces *R. sticticum*.

At the other end of the frequency scale are *R. buteum*, *R. exsectum*, and *R. infuscatum* – species from which hardly more than a handful of records each are available. *Rhodanthidium aculeatum*, *R. acuminatum*, *R. caturigense*, and *R. glasunovi* fall between these extremes of frequency.

Distribution and Endemism

The distribution of *Rhodanthidium* extends from the Atlantic coast of Morocco to the high mountains of Central Asia. In a South-North direction, the distribution extends roughly from 30° to 50° North, and reaches the northern limit in the Prague area of the Czech Republic.

Table 3. Assessment of the frequency and the level of endemism of the members of the genus Rhodanthidium. – Frequency: $\bullet \bullet \bullet =$ abundant; $\bullet \bullet =$ frequent; $\bullet =$ rare. The range size given here is approximate.

	Frequency	Distribution type	Rough estimation of the size of the distribution area
Rhodanthidium aculeatum	••	East Mediterranean, Iranian	c. 400,000 km ²
Rhodanthidium acuminatum	••	Trans-Mediterranean	c. 4,000 km in east-west direction
Rhodanthidium buteum	•	East Anatolian	c. 10,000 km ²
Rhodanthidium caturigense (s.l.)	••	Trans- Mediterranean, Iranian	c. 5,000 km in east-west direction
Rhodanthidium exsectum	•	Turco-Iranian, Levantine	c. 1 million km ² c. 2000 km in east-west direction
Rhodanthidium glasunovi	••	Central Asian	c. 250,000 km ² c. 750 km in east-west direction
Rhodanthidium infuscatum	••	West Mediterranean	c. 2,000 km in east-west direction
Rhodanthidium ordonezi	•••	Restricted to Moroc- co at the western end of the Palaearctic region	<150,000 km ²
Rhodanthidium rufocinctum	•••	endemic	c. 250 km <10,000 km²
Rhodanthidium septemdentatum (s.l.)	•••	Trans-Mediterranean and Caucasian	c. 5,000 km
Rhodanthidium siculum	•••	North African and southern Mediterra- nean	c. 3,500 km in east-west direction
Rhodanthidium sticticum	•••	West Mediterranean	c. 2,100 km
Rhodanthidium superbum	••	Turco-Iranian in- cluding Caucasus	c. 400,000 km ² c. 2,500 km in east-west direction

Species of the genus *Rhodanthidium* are known to occur in 41 countries (Table 4). The distribution of most species, especially of the rare ones, is insufficiently known. At the country level large gaps in our knowledge exist, especially in the Balkans where records are absent or rare for most countries. Relatively high numbers of species have been

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cul = R. aculeatum; Racum = R. acuminatum; Rbut = R. but	rd = R. ordonezi; Rruf = R. rufocinctum; Rsep = R. septemde
acul = R. aculeatum; $Racum = R$. acuminatum; $Rbut = R$. but	cord = R. $ordonezi$; $Rruf = R$. $rufocinctum$; $Rsep = R$. $septemde$

	Racul	Racum	Rbut	Rcat	Rexs	Rgla	Rinf	Rord	Rruf	Rsep	Rsic	Rsti	Rsup	No.
Albania				•						•				2
Algeria							•			ċ	•	•		3-4
Andorra							•							1
Armenia													•	1
Austria										•				1
Azerbaijan										•				1
Belarus										۰.				¢.
Bulgaria				•						•				2
Croatia							•			•		ċ		2-3
Czech Republic										•				1
Cyprus										•				1
Egypt											•			1
France				•			•			•	ż	•		4-5
Georgia				•									•	2
Greece		•		•					•	•		÷		4-5
Hungary										•				1
Iran	•			•	•					•			•	5
Israel				•	•					•				3
Italy		•		•						•	•	•		2

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Rord									•													
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Rgla		•	•															•				•
Rexs				•												•				•		
Rcat	•			•											•		•			•		
Rbut																				•		
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	Jordan	Kazakhstan	Kyrgyzstan	Lebanon	Libya	Macedonia (FYR)	Malta	Montenegro	Morocco	Portugal	Romania	Serbia	Slovakia	Slovenia	Spain	Syria	Switzerland	Tajikistan	Tunisia	Turkey	Turkmenistan	Uzbekistan

recorded in France, Greece, Iran, Italy, Morocco, Spain and Turkey. This does not come as a surprise as most of these countries are among the largest in the West Palaearctic. Most of them are also relatively well-studied. With seven species, more species are known from Turkey than from any other country.

The definition of endemism has proven difficult. Range size is often used to define the degree of endemism. BirdLife International uses for birds and other vertebrates an extent of occurrence (EOO) of 50,000 km², while for invertebrates a threshold of 10,000 km² has been suggested. Although the distribution ranges of some species of *Rhodanthidium* are poorly known at present, these figures have been taken as guidance for classifying endemism.

The species with the smallest distribution range are *R. ordonezi*, which is confined to Morocco, and *R. rufocinctum*, which occurs only in Crete and possibly Malta. *Rhodanthidium buteum* is known from only a very small area, but being a rare species, the actual distribution area may be much larger. According to the strict definition of endemism above, only *R. rufocinctum* (Crete) and *R. buteum* (eastern Turkey) would qualify as endemic species.
Species Accounts

Rhodanthidium aculeatum (Klug, 1832)

Anthidium aculeatum Klug, 1832. – Lebanon (non Syria).

Anthidium uncatum Mocsáry, Termész. Füzet., 11, 1887: 28. – Put into synonymy by Friese (1898).

Meganthidium (Oxyanthidium) aculeatum (Klug, 1832). – Mavromoustakis (1962).

Oxyanthidium aculeatum (Klug, 1832). - Elevated to genus status by Pasteels (1969).

A medium-sized to large *Rhodanthidium* species; males somewhat larger than females. Both sexes have characteristic apical terga which distinguishes the species from its congeners easily. Maxillary palpus three-segmented with an oval basal segment, an elongate middle segment and a short and thinner apical segment.

Female. The female is characterised by the shape of T6: it has on each side a broad lobe with smooth outer sides. The remaining apical margin of T6 is irregularly crenulate to obtusely denticulate and has a small incision in the middle (width less than an antennal diameter). Lateral lobes and apical margin black, large yellow area in the middle of T6. – Head: Clypeus yellow with black apical margin. Broad black longitudinal macula in the middle of the clypeus, sometimes reduced to a few small brownish maculae. Mandible with large apical tooth, followed by two smaller subapical teeth and a further small tooth separated by a wide, shallow emargination. Head black with yellow paraocular area, almost extending to top of eye. Yellow band extending from vertex onto mid-genae on both sides, sometimes broken in the middle of vertex. - Mesosoma: Yellow maculation of mesosoma strongly variable; scutum with rectangular vellow maculation anterolaterally, but sometimes strongly reduced or completely absent. Scutellum with two yellow maculae, sometimes absent; two yellow maculae also on axillae but these are also sometimes absent. Axillae angulate. Omaulus angular. - Metasoma: The yellow bands on the terga are interrupted on T1-T4; their distal margins – especially of the anterior yellow bands - often irregular and rugged. T5 yellow with a small black median V-shaped notch, sometimes entirely divided in two lateral bands as in T1-T4. S6 triangular with black smooth surface and the apex protruding over T6; S6 has a sandwich-like structure with an outer margin consisting of two lamellae. - Wings: Brown infuscation throughout.



Apical terga of female (left) and male (right) of Rhodanthidium aculeatum.



Rhodanthidium aculeatum. Habitus. Left female, right male.

Male. Apical tergum with a lateral lobe on each side and a strong median spine. The lobes are angular and have broad, smooth and glossy outer margins. The relatively long spine is somewhat more than one antennal diameter wide; apex rounded and curved inward. - Head: Mandible yellow with a black, strong apical tooth and two black subapical teeth; clypeus slightly convex and yellow with black, truncate apical margin; paraocular area and band on vertex extending to the mid-genae yellow (similar to female); the band sometimes reduced to two lateral spots. - Mesosoma: Scutum with a yellow, narrow anterolateral band, which is sometimes reduced or absent. Two yellow spots on axillae, sometimes absent. -Legs: Hind coxa with a large, obtuse tooth, often yellow and then contrasting with the dark remainder of the coxa. - Metasoma: Terga with broad vellow lateral bands not reaching the middle; bands on T1 normally widely separated from each other, bands on T2-T3/T4 subcontiguous; distal margin of the bands often rugged, without a clear black-yellow pattern. S2 smooth, with a median smooth carina and a small tooth in the middle; S5 widely emarginate; S6 a produced semi-circle, with black sides and shining, brownish translucent apex; shallow furrow between the dark lateral sides.

Biology. Found in eastern Turkey between June and August (Özbek & Zanden 1996; material in OLL and cMS). According to Mavromoustakis (1962) found in Lebanon visiting the large flowers of *Salvia microstegia* Boiss. (Lamiaceae). *Nepeta* is another one of the flower genera visited (Grace 2010). Mavromoustakis (1962) also observed that it is a resin-user, as two females had their mandibles covered with resin very probably from the Lebanon Cedar, *Cedrus libani* (= *C. linanoticus*).



Rhodanthidium aculeatum. Head of two different females from Turkey. Note the broad black bar in the middle of the clypeus (specimen from Konya-Ereğli in Inner Anatolia above), which is reduced to a few remnants of brownish maculae in a specimen from Hakkâri (eastern Turkey, below).



Rhodanthidium aculeatum. Head of male.



Rhodanthidium aculeatum. Habitus female (Konya-Ereğli, Turkey).



Rhodanthidium aculeatum. Female from Turkey. Note the sandwich-like double carina of S6.



Rhodanthidium aculeatum. Ventral side of male metasoma.



Rhodanthidium aculeatum. Apical terga. Above left: female; above right and below: male.

According to Müller (1996), *R. aculeatum* is an oligolege of Labiatae and can be regarded as a sister species of the other *Rhodanthidium*, the *Anthidiellum*, and the *Eoanthidium* species.

Distribution. The species has an Eastern Mediterranean and Middle Eastern distribution and is found in Turkey, Iran (Warncke 1982), and Lebanon (Mavromoustakis 1936). In Turkey and Iran present up to approximately 2000 m (Özbek & Zanden 1996, Warncke 1982).

The type specimen was collected by F. W. Hemprich and C. G. Ehrenberg and described by Klug (1832). As Hemprich and Ehrenberg did not visit what is Syria-today (for their travel itinerary see e.g. Bradley 1968), but only the area between Beirut to Baalbek



Rhodanthidium aculeatum. Apical sternum S6 of female from ventral.



Female (left) and male (right) mandible of Rhodanthidium aculeatum.

which belonged to the Ottoman Empire and was called "Syria", but which is today Lebanese territory, the type locality is corrected herewith.



Distribution of *Rhodanthidium aculeatum*.

Rhodanthidium acuminatum (Mocsáry, 1884)

Anthidium acuminatum Mocsáry, 1884. – Termész. Füzet. 8: 257-258 (male and female; Turkey: Bursa).

Rhodanthidium acuminatum (Mocsáry, 1884). - Combined by Mavromoustakis (1968).

Medium to large-sized *Rhodanthidium*. Both sexes are unambiguously characterised by the shape of their apical terga. Closely related especially to *R. buteum* from which it can be separated by several characters of colour and structure (see under *R. buteum*). One of the distinguishing features is the shape of the mandibles: the condylar ridge is in both sexes of *R. acuminatum* conspicuously bulged subapically, while it is widely rounded in *R. buteum*.

Female. 13-14 mm. A very characteristic feature is the smooth, lamellate apical margin of T6 which has a very narrow, deep incision in the centre (much narrower than an antennal diameter). Above this, there is a second layer with an irregular, ragged margin and with markedly convex sides. - Head: Dark brown to black; transverse reddish-brown band attenuated and interrupted in middle (or reduced to a lateral macula on each side of the vertex). Clypeus moderately shining, somewhat strongly rugosely punctured, protruding with an emargination at apex; apical margin roughly crenulate with relatively large granules especially on both sides of the centre. Mandible with a large blunt apical tooth, followed by a smaller subapical tooth and an edentate tooth ridge. The subapical tooth sometimes merged with the tooth ridge and then not recognisable as a distinct feature. Reddish-brown pubescence on face, vertex and genae. - Mesosoma: Dark with rich reddish-brown pubescence dorsally and laterally. Scutum strongly rugosely punctured; apical margin of scutellum subemarginate in the middle. - Legs: Femora blackishbrown, apices ochreous; tibiae and tarsi ochreous. - Wings: Strongly infuscated brown. -Metasoma: Lateral yellow bands on T1–T5, with the inner distance between the bands becoming smaller posteriorly. Pale-white depressed pubescence on terga, very short and sparse, and hardly visible; pubescence on T6 denser and pale fulvous; ventral scopa fulvous.

Male. 15-16 (-22) mm. Colouration similar to the female. *Head*: Clypeus and paraocular area to antennal sockets yellow; vertex with a reddish-brown stripe on each side; mandibles tridentate with a broad shallow emargination between the two subapical teeth; mandible yellow, teeth dark black-brown. Clypeus covered by thin, long whitish hair. – *Mesosoma*: Yellow markings absent; pubescence on scutellum, axillae and mesepisternum dense. – *Legs*: As in the female, but with more hair; inner side of hind basitarsi densely covered with bright fulvous hair. – *Metasoma*: T6 with a broad light yellow macula on each side; broad projection with acute tooth at each side; in the middle a broad, trapezoid projection, much broader than the adjacent central spine of T7; apical margin of the median projection truncate and shining; T7 black, with three large spines: median longer and stronger than lateral ones; median spine black with brownish apex, lateral spines light yellowish-red. S4 and S5 broadly emarginate with a median comb at apical margin: two small patches of black bristles on S4, one batch on S5. S5 with a lateral denticle on each side.

Biology. Collected in Sicily in April (van der Zanden 1996). All records from Greece and Turkey from May and June (OLL, cMS, Warncke 1980). In a study on pollen loads,



Rhodanthidium acuminatum. Left female, right male.



Rhodanthidium acuminatum. Left: head of female, right: head of male.

Müller (1996) characterises *R. acuminatum* as a polylectic species with a strong preference for a single plant family. In pollen grain counts, he found 73.6% of the pollen belonging to Leguminosae (mainly members of the Hedysareae) and 25.5% to Compositae (Cardueae). Males recorded at *Ononis natrix* (Grace 2010).

Distribution. Widely distributed in the Mediterranean from Morocco and southern Italy (Sicily) to Greece and Turkey. Countries: Turkey (Warncke 1980, OLL), Greece (Mavromoustakis 1968, OLL, cMS), Italy (van der Zanden 1996), and Morocco (van der Zanden 1996). The species is likely to have a more dense distribution than that suggested by the few records..



Rhodanthidium acuminatum. Above: T5+T6 of female, below T6+T7 of male.



Rhodanthidium acuminatum, mandible of female (left) and male (right).



Rhodanthidium acuminatum. Apical terga. Left female, right male.



Rhodanthidium acuminatum. Apical terga of female. Note the smooth apical edge (with a median incision) of T6 and the ragged carina above.



Rhodanthidium acuminatum. Dorsal view of male metasoma.



Distribution of Rhodanthidium acuminatum.

Rhodanthidium buteum (Warncke, 1980)

Anthidium (Rhodanthidium) buteum Warncke, 1980. Entomofauna, 1: 136-139, 156-157 (male, Turkey).

Rhodanthidium buteum resembles most closely the slightly larger *R. acuminatum*. Females can be distinguished by for example the colouration of the mandibles (yellow to brownish in *R. buteum*, dark brown to black in *R. acuminatum*). In male *R. buteum*, the paraocular area is yellow to the top of the eye (only up to antennal sockets in *R. acuminatum*), a bright yellow band is present on vertex (only lateral reddish-yellow maculae in *R. acuminatum*), and *R. buteum* has an anterior yellow band on scutum (absent in *R. acuminatum*). The condylar ridge of the mandible is widely rounded in *R. buteum* and not bulged subapically as in *R. acuminatum*.

Warncke (1980) focused in his description of this species on the length of the third antennal segment and the number of black bristles on S4 and S5. However, these character features do not unambiguously separate the species from *R. acuminatum*. Colour features and the shape of the mandible (not mentioned by Warncke) are, however, much more useful to distinguish between them. The description of the female given here (Warncke had described only the male) is based on two females in OLL.

Female. 12 mm. Can be distinguished from its congeners by the colour pattern of the metasomal terga and the shape of the apical tergum. – *Head*: Clypeus yellow with black apical margin; mandible yellow with black teeth. Apical tooth and approximately three subapical teeth, which are, however, coalesced and not clearly distinguishable as individual teeth (tooth bar). Paraocular area yellow up to the top of the eye; yellow maculation between ocelli and antennal sockets, and yellow band next to the occipital ridge. – *Mesosoma*: Anterolateral yellow band; scutum and axillae almost entirely yellow; scutellum with an outer translucent lamella and a shallow emargination in the middle.



Rhodanthidium buteum. Left female, right male. Note the bicoloured brown-yellow mandibles of the female.

Erect ochreous pubescence on scutum; mesepisternum with whitish-grey longer pubescence. Two yellow spots on mesepisternum. – *Legs*: Proximal side of femora dark, apical side yellow; tibiae and tarsi yellow (with the exception of some darkening on the inner side of tibiae). – *Wings*: Brown infuscated. – *Metasoma*: T1 and T2 with lateral yellow bands widely separated from each other; bands on T3 and T4 subcontiguous; bands on



Rhodanthidium buteum. Apical terga of female (above) and male (below).



Rhodanthidium buteum. Female (left) and male (right) mandibles.

T4 continuous. T6 consists of two lamellate layers: the lower layer is impunctate and shining, with a median incision. The upper layer has two lateral lobes and a small shallow emargination in the middle; its surface is rough and partly covered by yellow hair. S6 triangular.

Male. 15 mm. *Head*: Clypeus yellow with dark, crenulate apical margin; mandible yellow, tridentate (subapical teeth widely separated by shallow emargination); condylar ridge widely rounded (bulging subapically in *R. acuminatum*); paraocular area yellow to top of eye (only to antennal socket in *R. acuminatum*); yellow band on vertex to midgenae (lateral yellow stripes on each side in *R. acuminatum*). – *Mesosoma*: Scutum with anterior broad yellow band, interrupted in the middle at one third of its length; pronotal lobes yellow, lamellate; scutellum with translucent lamella at outer margin; narrow yellow band along distal margin, broken in the middle and not extending to axillae



Rhodanthidium buteum. Above female, below male (both from Mardin, Turkey).

(mesosoma entirely dark in *acuminatum*). – *Legs*: Bright yellow with black longitudinal stripes on femora and inner side of tibiae (reddish yellow in *R. acuminatum*). – *Metasoma*: Terga with broad yellow lateral maculations, the distance between the yellow bands

decreasing from T1 to T5 (contiguous in T6); S4 and S5 with a few (3-5) median black bristles at their apical margin.

Genitalia with narrowly forked gonostyli and heavily sclerotized dark teeth on each volsella.

Biology. Collected in Turkey in June (Warncke 1980, material in OLL).

Distribution. Only known from Siirt and Mardin provinces in south-eastern Turkey (Warncke 1980, OLL).



Rhodanthidium buteum: Apical terga of female (left) and male (right).



Rhodanthidium buteum. Male genitalia from dorsal and ventral view.



Distribution of *Rhodanthidium buteum*.

Taxonomic status of Rhodanthidium caturigense s.l.

Rhodanthidium caturigense s.l. comprises several taxa which have been placed by some authors even in different genera, whilst other authors have combined all of them under one name. Mavromoustakis (1958) recognised one species with four subspecies, while Pasteels (1969) distinguished five species and put them into three genera, of which he generated two for this purpose and which do not contain other species. Warncke (1980) combined these taxa with *caturigense* at species level with four subspecies and assigned it to the genus *Anthidium*.

I am aware that the evolutionary history of *R. caturigense* s.l. is still not understood, and it may well be that a few species are concealed within this name. The taxonomy of *R. caturigense* s.l. is challenging and it is still not clear whether it consists of a complex of closely allied species or if the geographic variation in colouration and structure can be explained by the existence of a set of allopatric subspecies. I take a conservative approach and recognise differences at the subspecies level until a full revision with material from all parts of the distribution area including biochemical analysis has been carried out.

In the case of material from the Pyrenees including the type material of *Anthidium caturigense* var. *pyrenaeum* Alfken, 1927 deposited in SMF, there are slight differences from *R. caturigense caturigense* from the Alps, but there is also broad overlap in these characters. These differences refer to colouration as well as to the size and form of the abdominal yellow maculation. The yellow spot on the genae which is present on the type material of *Anthidium caturigense* var. *pyrenaeum* is absent in other material from the Pyrenees. I therefore regard Alfken's (1927) *pyrenaeum* as synonymous with nominate *R. caturigense*. The status of a full species given by Fauna Europeae, DiscoverLife, ITIS List of Valid Bee Species, etc. is not justified. This conclusion is further supported by

	Mavromoustakis (1958)	Pasteels (1969)	Warncke (1980)	This study
	One species with four subspecies in the genus <i>Rhodanthidium</i>	Five species, in two genera (<i>Trianthidium</i> , <i>Axillanthidium</i>)	One species with four subspecies in the genus Anthidium	One species with three subspecies in the genus <i>Rhodanthidium</i>
Genus	Genus <i>Rhodanthidium,</i> subgenus <i>Trianthidium</i>	Genera Trianthidium and Axillanthidium	Genus Anthidium	Genus Rhodanthidium
Anthidium caturigense Giraud, 1863	Rhodanthidium caturigense caturigense (Giraud)	<i>Trianthidium</i> <i>caturigense</i> (Giraud)	Anthidium caturigense caturigense Giraud	Rhodanthidium caturigense caturigense (Giraud) (including Anthid- ium caturigense pyrenaeum Alfken)
Anthidium caturigense var. pyrenae- um Alfken, 1927	Rhodanthidium caturigense pyrenaeum (Alf- ken)	<i>Trianthidium</i> pyrenaeum (Alfken)	Anthidium caturigense pyrenaeum Alfken	No valid taxon. (= <i>Rhodanthidium</i> <i>caturigense</i> <i>caturigense</i> (Giraud))
<i>Anthidium moreënse</i> Friese, 1917	Rhodanthidium caturigense (Giraud) moreense (Friese)	Trianthidium moreense (Friese)	Anthidium caturigense ducale Morawitz = Anthidium moreense Friese	Rhodanthidium caturigense ducale (Morawitz) = Anthidium moreense Friese = Axillanthidium axillare Pasteels
Anthidium moreënse subsp. jerusalemicum Mavro- moustakis, 1938	Rhodanthidium caturigense (Giraud) jerusalemicum (Mavro- moustakis)	Trianthidium jerusalemicum (Mavro- moustakis)	Anthidium caturigense jerusalemicum Mavro- moustakis	Anthidium caturigense jerusalemicum Mavromoustakis
Axillanthidi- um axillare Pasteels, 1969		Axillanthidium axillare Pasteels	Anthidium caturigense ducale Morawitz = Axillanthidi- um axillare (Pasteels)	

Table 5. Taxonomic treatments of Rhodanthidium caturigense s.l.



Rhodanthidium caturigense s.l. Holotype of '*Anthidium caturigense* var. *pyrenaeum* Alfken, 1927' from the Pyrenees (SMF). It is regarded here as a synonym to *Rhodanthidium caturigense*.

Schmid et al. (2015), who found that the genetic barcode (DOI sequence) of a specimen from the Balearic Islands was very similar to the sequences of specimens from Provence-Alpes-Côte d'Azur.

The segments of maxillary palpi are more or less fused in *R. caturigense*, so that the number of segments can often only be speculated. Pasteels' (1969) attempt to put individuals with two-segmented maxillary palpi into a newly established genus – *Axillanthidium* – was therefore not successful. Also the form of angulate axillae did not prove to be a character which allowed the taxon to be unambiguously defined. *Axillanthidium axillare* is therefore, in line with Warncke (1980), not accepted as a valid taxon.

A comparison of the type material of *ducale* from Borshomi in Georgia (deposited in Saint Petersburg) shows that it is close to *moreense* from Greece. The dorsal surface of the median quadrangle of T7 and its blunt apex are black (not bicoloured black and brown or yellow) and the yellow pattern on head and mesosoma are identical with *moreense*. In line with Warncke (1980), *moreense* is therefore regarded as a junior synonym



Rhodanthidium caturigense aff. caturigense. Left female, right male. Both specimens from Switzerland.

of *ducale*. On the other hand, material from Turkey shows marked differences from the material both from Greece and Georgia.

Warncke (1980) assigned his material from Turkey to *ducale*. Re-examination of this material showed that some characters are closer to *jerusalemicum* than to *ducale*. However, a final decision on the taxonomic rank can only be taken after a thorough revision of *R. caturigense* s.l.

Rhodanthidium caturigense (Giraud, 1863)

Anthidium caturigense Giraud, 1863. Ver. zool.-bot. Ges. Wien 13 p. 36-38 (Piémont, North Italy).

Trianthidium caturigense (Giraud, 1863). – (Pasteels 1969).

Anthidium ducale Morawitz, 1876. Hor. Soc. ent. Ross. 12: 50-52 (Bordschomi [Borshom], Georgia). Male and female.

Anthidium moreënse Friese, 1917 (Male; Peloponnese, Greece).

Axillanthidium axillare Pasteels, 1969 (Female, Peloponnese, Greece). - Warncke (1980).

Anthidium caturigense ducale (Morawitz, 1876). – Warncke (1980).

Rhodanthidium (Asianthidium) caturigense ducale (Morawitz, 1876).

Anthidium moreense Friese, 1917 (Male; Peloponnese, Greece). - Warncke (1980).



Rhodanthidium caturigense. Head of the female. Above left: female from Switzerland (*R. caturigense*); above right: female from Greece (*R. caturigense* aff. *moreense*); below: female from Jordan (*C. caturigense* aff. *jerusalemicum*). Note the colouration of clypeus and mandibles and the presence/absence of a yellow spot below the anterior ocellus.

Anthidium caturigense var. pyrenaeum Alfken, 1927.
Anthidium moreense ssp. jerusalemicum Mavromoustakis, 1938. Ann. Mag. Nat. History, 11. Ser., 2: 17-18.
Anthidium caturigense ssp. jerusalemicum Mavromoustakis, 1938. – Warncke (1980).
Rhodanthidium (Trianthidium) caturigense (Gir.) jerusalemicum (Mavromoustakis, 1938). – Mavromoustakis (1962).



Rhodanthidium caturigense aff. caturigense. Above female, below male. Both specimens from Switzerland.

Anthidium moreense jerusalemicum Mavromoustakis, Ann. Mag. Nat. Hist. (12), 1955 viii, p. 331.

Rhodanthidium caturigense (Gir.) subsp. jerusalemicum G. A. Mavromoustakis, Ann. Mag. Nat. History. (13), 1958, vol. 1, p. 438. – Assigned by Warneke (1980).

Trianthidium pyrenaeum (Alfken, 1927)). - Pasteels (1969).

Rhodanthidium pyrenaeum (Alfken, 1927). – Used in ITIS database, DiscoverLife, Fauna Europaea, etc.



Rhodanthidium caturigense s.l. Apical terga of female (above) and male (below).

Trianthidium moreënse (Friese, 1917). – Pasteels (1969).
Trianthidium jerusalemicum (Mavromoustakis, 1938). – Pasteels (1969).
Rhodanthidium jerusalemicum Mavromoustakis, 1938. – Used in ITIS database, Discover-Life, Fauna Europaea, etc.

Males are easily identifiable by their characteristic apical terga: T7 is relatively broad and little protruding as in most other species, and has a lateral hook-like tooth, directed inwards. There is some similarity with *R. exsectum*, but that species has an emargination between the median and lateral projection of T7 (which *R. caturigense* does not have) and the lateral integument of T6 of *T. exsectum* is deformed (undulated structure with smooth edges), while *R. caturigense* has an overhanging lateral bulge. Females of *R. caturigense* s.l. have a small apical incision of T6, while females of *R. exsectum* have a wide characteristic opening.

As a general feature, specimens from northern populations are larger and darker. However, this cannot always be clearly attributed to a subspecies. As in other *Rhodanthidium*, males are much larger than females.

A thorough revision of material from all parts of the distribution area is necessary in order to clarify the taxonomic status. Three subspecies are recognised here (see taxonomic account).

• *R. caturigense caturigense* (Morawitz, 1876): From the Pyrenees (France, Spain) to the Southern Alps (Switzerland, North Italy). – Relatively dark and large subspecies. Clypeus black-brown or at least with a broad median longitudinal black-brown band. Apical margin of clypeus with relatively deep emargination; mesonotum almost entirely dark.



Rhodanthidium caturigense aff. caturigense. Apical terga of the male. Specimen from Switzerland.



Rhodanthidium caturigense aff. *caturigense*. Apical sterna and terga of the male from ventral. Note apices of gonosyli and the semicircular shape of S7. Specimen from Switzerland.

- *R. caturigense ducale* (Morawitz, 1876): Balkan countries including Albania, Bulgaria, Greece, but also Georgia. In typical specimens clypeus not or only little emarginate, almost entirely yellow. Lateral bands on the anterior terga subcontiguous or interconnected.
- *R. caturigense jerusalemicum* (Mavromoustakis, 1938): Turkey, Israel, and Jordan. Characterised by rich yellow colouration; in typical specimens, tergal bands continuous.



Rhodanthidium caturigense, head of male. Above male from Italy, *R. caturigense* aff. *caturigense*, below male from Greece (*R. caturigense* aff. *ducale*).



Rhodanthidium caturigense, ventral side of metasoma.

The subspecific characters are not always unambiguous and overlap. In particular the situation in Turkey is not clear, and it seems that intermediate forms between *ducale* and *jerusalemicum* occur there. Specimens with acute or angulate axillae (see Pasteel's '*Axillanthidium axillare'*) can be found both in Spain and on the Balkan.

NHMUK houses a specimen which has been labelled by J. J. Pasteels "*Rhodanthidium anatolicum* Pasteels, MS" (type specimen). This taxon has never been published.

Female. 8-10 mm. *Head*: Black with a broad yellow maculation in the lower paraocular area, which becomes narrow in the upper paraocular area; the extend of the yellow colouration varies, and particular southern populations are richer in yellow. For example the yellow maculation in the upper paraocular area is wider in the south (*R. c. aff. jerusalemicum*) than in the Balkan and West European populations (*R. c. aff. caturigense* and *R. c. aff. ducale*). A yellow band in front of the occipital ridge often extends down to the mandibular area in the south, but is in more northern populations usually confined to the vertex; sometimes it is broken in the middle. Also a yellow spot below the frontal ocellus is small or even absent in the north but large in the south. Clypeus slightly convex, apical margin crenulated with relatively large black tubercles; mandibles black with four teeth. There is great variation in the colouration of the clypeus and the mandible: The clypeus may be entirely black (mostly in northern populations), or may have some dark maculations or otherwise may be entirely yellow with only a black apical margin (predominantly in southern populations). Mandibles normally black with some reddish-brown lightening especially next to the teeth. Females with partly or entirely yellow mandibles



Rhodanthidium caturigense aff. jerusalemicum. Apical and terga of the female.



Rhodanthidium caturigense aff. jerusalemicum, apical terga of male. Material from Konya, Turkey.

(leaving only the teeth and margins black) have been observed in the south. The differences between populations are also visible in the colouration of the mesosoma: entirely black mainly in the north, but an L-shaped anterolateral yellow band and a large yellow maculation on mesepisternum mainly in the south. Intermediate forms exist. Pronotal lobe with anterior lamella; the pronotal lobes are black, yellow, or black with a yellow area confined to the outer half. Lateral margin of scutum with sharp carina which is also present between scutum and axilla. Scutellum with a relatively sharp outer margin; axilla angulate. – *Metasoma*: Lateral yellow bands, widely separated on T1, but becoming gradually closer to each other towards T5 (where the bands are subcontiguous, contiguous or form a continuous band); some ill-defined black maculation mostly present within the yellow bands; T6 black or black with yellow maculation, and with a small median incision. S6 semi-circular with lateral shoulders.



Rhodanthidium caturigense aff. jerusalemicum. Male from Turkey.

Male. 10–14 mm. Head black with yellow or whitish-yellow paraocular area which is broad below the antennal sockets and narrowing above. In northern populations the area above antennal socket often forms a thin line, but is broad in more southern populations. Yellow or whitish-yellow band along preoccipital ridge, often broken or confined to one spot on each side of head; in southern populations also reaching the mandibular area. A



Rhodanthidium caturigense s.l.: Female lectotype of 'Anthidium ducale Morawitz, 1876' from Bordschomi, Georgia (Zoological Museum Saint Petersburg). – Photograph: Y. Astafurova.



Rhodanthidium caturigense s.l.: Male Allolectotype of '*Anthidium ducale* Morawitz, 1876' from Bordschomi, Georgia (Zoological Museum Saint Petersburg). – Photograph: Y. Astafurova.

broad longitudinal yellow mark below median ocellus, mainly in east Mediterranean populations. Clypeus yellowish with a broad black or brown median band, greatly variable in size and shape (mostly broad at anterior side, becoming narrower towards the apex), and sometimes entirely absent so that the clypeus is entirely yellow; apical margin of clypeus more or less emarginate, coarsely crenulate; clypeus with long whitish pubescence often covering apical margin; mandible yellow with black margins; transition from yellow to black often with brownish gradient zone; mandible tridentate. - Mesosoma: Colour pattern of scutum variable. Entirely black forms or forms with only a short and narrow anterior band are found predominantly in the north and west, while forms with a broad yellow L-shaped or boomerang-shaped anterolateral band are found mainly in the eastern Mediterranean. The lower branch of the lateral stripe sometimes reaches axillae; scutellum and axillae black or with yellow band/spot; axilla angulate or produced to a small lateral tooth; small yellow spot on mesepisternum sometimes present; pronotal lobe with strong anterior lamella; its colouration varying from black to yellow. - Metasoma: Terga with yellow bands, usually not reaching the middle, but sometimes contiguous bands or a continuous, unbroken band; the yellow bands are often incomplete or speckled with brown maculation, especially on T2 and T3. T7 trifid with an acute lateral spine on each side, the apex curved inwards; median prolongation broad, emerging from an area elevated and expanded above the tergal margin. The median prolongation and the adjoining surface mostly dark black; lateral spines brown sometimes with yellowish apices; S7 with broad, shining semicircular apex, apices of gonostyli visible laterally.

Biology. The species is found in dry and warm areas including dry grassland and rocky steppes (Scheuchl & Willner 2016) and prefers open areas in mountain pine forests and alpine meadows. It is described as an orophilous species, i.e. thriving in sub-alpine or mountainous regions. This characterises the populations in Western Europe, but not those in the eastern Mediterranean where it is also found close to sea level.

Flight season extends from May to August (e.g. Güler 2011, Ornosa et al. 2008, Özbek & Zanden 1993, Pasteels 1969). The flight season of the female appears to be longer than that of the male (Amiet et al. 2004).

Nests are constructed in the ground, with a short burrow leading to a terminal cell. The outer walls of the cell consists of plant hairs, the inner walls of resin. The cell is closed with loose particles (Amiet et al. 2004). According to Litman (2012), the nests of *R. caturigense* are remarkable among anthidiines in that cells are built of both plant resin and plant fibers. *Rhodanthidium caturigense* excavates its own nests in the soil and nests are often built in large aggregations (Micheli 1935; Maneval 1936; Pasteels 1977; Müller et al. 1997). Between three and six cells are located at the end of the short burrow; cells are often oriented haphazardly to accommodate the position of stones and roots in the soil. Each individual brood cell consists of two distinct layers: an outer layer woven of plant fibers and an inner layer built of resin. Pasteels (1977) found that the source of these plant fibers is *Verbascum thapsus*. The nest entrance is sealed with a plug of resin coated with plant hairs (Pasteels 1977).

Although most female members of the genus *Rhodanthidium* do not include plant fibres in their nests and exhibit extremely reduced mandibular teeth consistent with those of other resin-nesting anthidiines, Litman (2012) noted that *R. caturigense* has four clearly defined mandibular teeth and suggests that this may be an adaptation for scraping fibres



Distribution of *Rhodanthidium caturigense* with its three subspecies recognised here. Note that the borders between the subspecies are not clear, particularly in Turkey where *ducale* and *jerusalemicum* meet.

from plant surfaces, while mandibles with less-defined teeth are adapted to the manipulation of plant resin.

Müller (1996) and Amiet et al. (2004) stated that *R. caturigense* is polylectic, in that it prefers foraging upon a wide range of flowering plants in the families Boraginaceae, Cariofilaceae, Cruciferae and Lamiaceae but with a strong preference for Papilionoideae (Fabaceae = Leguminosae) species. Morawitz (1876) collected the species in the Caucasus (Georgia) at 'yellow flowering thistles' (Asteraceae). In Lebanon observed visiting flowers of *Ononis natrix* L. (Mavromoustakis 1962), in Iran visiting *Centaurea* sp. (Nadimi et al. 2014). Müller (1996) reports that *R. caturigense* removes the pollen from the tip of the keel using the hind legs before depositing it into the metasomal scopa. The middle legs are used to press the floral wings or the keel down in order to cause the anthers or the pollen grains to protrude.

Chrysis analis, C. emarginatula and *C. simplonica* are cuckoo wasps (= emerald wasps) known as parasites of *R. caturigense* (Giraud 1863, Scheuchl & Willner 2016).

Distribution. A predominantly Mediterranean species (or species complex) with a distribution extending from Spain in the west to Iran in the east. The nominate subspecies occurs in northern and north-eastern Spain, France, Switzerland and Italy. The species reaches the northern limit of its distribution in southern Switzerland (Canton of Valais) (e.g. Schwarz et al. 1996, Amiet et al. 2004), Piemont and Trentino in Italy (e.g. Scheuchl & Willner 2016) and France (e.g. Rasmont et al. 1995). It is, however, apparently not known from Austria (despite the statement by Nadimi et al. 2014). The subspecies *ducale* is found in Albania, Bulgaria and Greece; populations in Western Turkey may also be assigned to this subspecies, but confirmation is needed. The distribution of the subspecies *jerusalemicum*, originally described from Israel, extends from the Levant northwards to Turkey. While specimens from Eastern Turkey match the characters of *jerusalemicum*, the status of material from West Turkey is not clear.

In Switzerland, a rare species up to 1600 m (Amiet et al. 2004), in Turkey up to 1900 m (Özbek & Zanden 1993). In the Elburz Mountains, Iran, found at 2305 m (Nadimi et al. 2014).

Remarks: The name *caturigense* refers to the 'caturiges', a Gallic tribe in the ancient Roman province of Alpes Maritimae, from where the species has been described. The name 'moreënse' refers to 'Morea' which was the name of the Peloponnese Peninsula in southern Greece during the Middle Ages and early modern period.

Warncke (1980) assigns material which had been determined by Mavromoustakis as *Anthidium moreense* ssp. *jerusalemicum* Mavr. to *Anthidium exsectum* (Pasteels). It is not clear to what material (unpublished museum material?) Warncke refers to.

Rhodanthidium exsectum (Pasteels, 1969)

Bellanthidium exsectum Pasteels, 1969. Israel Journal of Entomology 4: 409-434 (Turkey). *Anthidium exsectum* (Pasteels, 1969). – Warncke (1980). *Rhodanthidium exsectum* (Pasteels, 1969).

A small *Rhodanthidium*. Females are distinguished from other similar small congeners by the alate emargination of T6. Males can easily be identified by the two deep emargination on each side of T7.

Female. 8-10 mm. Head: Clypeus yellow with crenulate, black apical margin and a broad black longitudinal middle line which varies in shape and width and is sometimes reduced to a narrow black line; mandibles yellow with black teeth (brownish in the areas close to the teeth); the four teeth decreasing in size from distal to proximal; paraocular area yellow to top of eyes; yellow oval spot on the frons under the front ocellus; preoccipital stripe extending along the entire vertex and gena usually leaving a narrow black margin between the stripe and the occipital ridge. Inner margin of eyes slightly converging ventrally. - Mesosoma: Scutum dark, with boomerang-shaped anterolateral yellow band; scutellum widely rounded and slightly emarginate in the middle; axillae with small lateral tooth; distal side of scutum and axillae yellow, and with a narrow translucent margin. Pronotal lobe yellow with sharp lamella. Large yellow maculation on omaulus (mesepisternum); in most cases a second small yellow spot present behind. – *Metasoma*: Lateral yellow bands on T1 to T5. Distance between these bands decreasing from proximal to distal, so that bands on T4 become subcontiguous and band on T5 often continuous. T6 yellow with lateral black maculation; heart-shaped emargination in the middle of apical margin, with sides forming wing-shaped lamellae. At the base of the emargination, a triangular black field with a small spine; the triangular apex of S6 can be seen inside the emargination. T6 is widely folded so that part of the tergum faces ventral side. Scopa ochreous.

Male. 10-12 mm. *Head*: Clypeus and paraocular area yellow, narrower above antennal sockets than below; oval yellow spot below anterior ocellus usually present; yellow band along preoccipital ridge extending to malar area; clypeus sometimes with an ill-defined darkening on each side; apical margin of the clypeus crenulate, dark or black, and



Rhodanthidium exsectum. Female in lateral view.



Rhodanthidium exsectum. Male in lateral view.



Rhodanthidium exsectum. Male (left) and female (right).

slightly widely emarginated; long, dense white hair on frons and clypeus, scattered hair on vertex; mandible tridentate with wide and deep emargination between the two inner teeth and a deep narrow incision between the two outer teeth. – *Mesosoma*: Yellow boomerang-shaped yellow anterolateral band; mesepisternum with large bright yellow maculation greatly varying in size and sometimes divided into an upper and a lower maculation; the yellow may extend onto ventral surface of thorax close to centre, i.e. to the suture between the two mesepisternal sclerites. Pronotal lobe yellow with sharp lamella. – *Legs*: Coxa, trochanter, femora, tibiae and tarsi yellow, with some black longitudinal stripes on femora and sometimes also on inner side of tibiae and metatarsi. – *Metasoma*: T1–T4 with lateral bands reaching almost to middle of the terga (contiguous or subcontiguous); T5 with continuous yellow band, T6 yellow with a median wedgeshaped incision; sides with brownish maculation; the tergum surface laterally is irregularly undulate with a translucent rounded projection at each side; T7 with a median projection which has a rounded apex, and emerges from an area with two bulges; apical



Rhodanthidium exsectum. Head of the female (above) and the male (below).



Rhodanthidium exsectum. Apical terga of the female (above) and the male (below).


Rhodanthidium exsectum. Apical terga. Female (above) and male (below).



Rhodanthidium exsectum. Mandible of female (left) and male (right).

margin of T7 with two semicircular emarginations on each side, the outer projection forming an acute, inward-curving tooth. – S6 with tongue-shaped projection; gonostyli are visible on each side.

Biology. In Iran found in July (Warncke 1982, OLL), in Turkey from June to August (Pasteels 1969, Güler et al. 2014, OLL). In a pollen load examined by Müller (1996), 96% of all pollen belonged to Leguminosae. Güler et al. (2014) recorded the species in Turkey on the wing at *Centaurea iberica*.

Distribution. Turkey, Iran and Lebanon (Warncke 1982). DiscoverLife mentions also Israel without giving more information, perhaps a confusion with Lebanon which is not mentioned. Found in eastern Turkey at 1624 m and between 2600 and 3000 m altitude, in Iran at 2800 m and in Lebanon at 1400 m (Güler et al. 2014, Warncke 1982).

Remark. As the drawing of the female apical terga of the type specimen by Pasteels (1969) is not unambiguous, the type material deposited in NHMUK was examined. It completely corresponds with the description and the material presented here.



Rhodanthidium exsectum. Male. Left ventral side of metasoma, right male genitalia.



Distribution of Rhodanthidium exsectum.

Rhodanthidium glasunovi (Morawitz, 1893)

Anthidium Glasunovi (Morawitz, 1893). Horae Societatis Entomologicae Rossicae 28: 1-87. Anthidium glasunovi (Morawitz, 1893).

Anthidium glasunovii (Morawitz, 1893). - Mis-spelled in many publications.

Anthidium tridentatum [= Anthidium 3-dentatum] (Friese, 1931) (Taşkent, Uzbekistan).

- Meganthidium (Asianthidium) glasunovi (Morawitz, 1893). Assigned to this genus and subgenus by Popov (1950).
- Anthidium tridentata (Friese, 1931). Put into synonymy with Meganthidium (Asianthidium) glasunovi (Morawitz, 1893) by Popov (1950).
- Anthidium glasunovi hissarense (Mavromoustakis, 1939). Valid subspecies according to DiscoverLife database. Syn. n.
- Rhodanthidium hissarense (Mavromoustakis, 1939). ITIS database and many internet sources (e.g. GBIF). Syn. n.

Easily distinguished from other *Rhodanthidium* species, the overall impression being of a large and dark *Rhodanthidium* with reddish tibiae and tarsi. Light, sometimes yellow markings mostly present on T5 and T6 in both sexes, but highly variable in colouration and extent; mandibles of the male are also yellow; some inconspicuous reddish-brown markings on head and abdomen.

Female. 14-20 mm. *Head*: Black with a narrow, reddish-brown macula on paraocular area reaching up to almost top of eye; reddish-brown maculation also on both sides of vertex; punctation fine and dense; in supraclypeal area punctures coarser and more scattered, and with an impunctate polished central line; clypeus flat, apical margin produced into a blunt triangular tubercle in the middle; mandibles black with a strong apical and three smaller subapical teeth, separated from one another by wide, rounded



Rhodanthidium glasunovi. Apical terga of female (left) and male (right).



Rhodanthidium glasunovi. Habitus lateral. Female above, male below.

emarginations (almost semi-circular between the two inner teeth); outer ridge and condylar ridge of mandible very strong and significantly elevated. – *Mesosoma*: Dark, with brownish hair; pronotal lobes small and inconspicuous, with angulate to slightly lamellate anterior margin. – *Legs*: Femora black with reddish-yellow apex; tibiae and tarsi entirely reddish-yellow. – *Metasoma*: Black, but sometimes some small irregularlyshaped reddish-brown lighter areas on T5 and T6. These may also be entirely yellow. Terga with fine punctation and an impunctate apical margin; T6 laterally expanded, with a narrow incision in the centre; scattered, fine hair on disc and longer, dark brown hair laterally; scopa brown.

Male. 18-25 mm (on average larger than females). – *Head:* Clypeus and paraocular area to top of eyes yellow; large rusty spots on both sides of vertex. Clypeus convex, expanded on each side; coarsely punctured; two dark spots at base, but sometimes reduced to inconspicuous darkening. Mandible yellow with black teeth; the apical tooth strong, two subapical teeth widely separated by shallow emargination (inner tooth short). Eyes



Rhodanthidium glasunovi. Metasomal terga (left female, right male). Note the yellow maculation on T4 and the lateral reddish-brown patterning on T3 and T4 in the male.



Rhodanthidium glasunovi. Head. Female left, male right.

subparallel, inner margins slightly convergent below. Face with long, ochreous pubescence especially on clypeus and on paraocular area; pubescence on vertex less dense and reddish-brown. – *Mesosoma*: Dark brown to black, with fine punctation; pronotal lobe rounded with angulate or slightly carinate anterior margin; pubescence on dorsal side brown, on ventral side whitish; outer margin of scutellum and axillae V-shaped with rounded edges. – *Legs*: Femora black with reddish apices and longitudinal stripes; tibiae and tarsi reddish. – *Metasoma*: Terga black with dense punctation, the punctures reaching their outer margin; inconspicuous reddish-brown maculae apparent on both sides of



Rhodanthidium glasunovi. Apical terga of female (above) and male (below).

all terga. These irregularly shaped maculae sometimes yellow on T5 and T6. T6 truncate and shining in the middle and swollen on both sides; T7 with a strong, bilobed middle spine and a somewhat short, flattened, obtuse lateral spine on each side. Brown hair especially on sides.



Rhodanthidium glasunovi. Mandible of female (left) and male (right).



Rhodanthidium glasunovi. Mandible of the male (Tashkent, Uzbekistan).

Mavromoustakis (1939) described 'Anthidium glasunovi subsp. hissarense' from Kvak in Varzob valley in Tadjikistan on the basis of rich yellow colouration of the metasomal terga and slight differences in the colouration of the hair. Examination of a series of 6 females and 4 males from Taşkent (approximately 300 km far from Kvak Valley) showed that the principal pattern of yellow maculation is found in all specimens, often as an inconspicuous reddish-brown colour apparent from a deeper layer of the integument. These inconspicuous lighter areas are sometimes yellow especially in the apical terga (T5-T6). As there seems to be a continuous gradient from entirely black individuals through those with some translucent patches to those with yellow maculations, hissarense is not accepted as a subspecies or species.

Biology. Found on the wing at Fabaceae and Rosaceae (Murao et al. 2015). Murao et al. (2015) give June for Kyrgyzstan and Kazakhstan, Friese (1931) August for Uzbekistan.



Rhodanthidium glasunovi. Metasomal sterna.

Distribution. Endemic to Central Asia. Type locality (Takfon at Jaghnob [Jagnob] River) is situated in the north of Tajikistan. Other records from Tajikistan as well as Kazakhstan, Kyrgyzstan and Uzbekistan (OLL, cMS; Friese 1931, Murao et al. 2015). Occurs at high altitudes. Friese (1931) gives 2800 m, Murao et al. (2015) 670-950 m for Kazakhstan and 1710-1989 m for Kyrgyzstan.



Distribution of Rhodanthidium glasunovi.

Rhodanthidium infuscatum (Erichson, 1835)

Anthidium infuscatum Erichson, 1835. In: Waltl, Reise d. Tirol, Oberitalien etc., 2, p. 108 (Spain).
Anthidium bellicosum Lepeletier, 1841. Hist. Nat. Ins. Hym., 2: 385 (Algeria).
Anthidium bellicosum Lepeletier, 1841. – Put into synonymy by Warncke (1980).
Stelis nemorosa Gistel, 1857. – Put into synonymy by Warncke (1992). Regarded as "nomen dubium" by Baker (1997)
Bellanthidium infuscatum (Erichson, 1835). – Genus erected by Pasteels (1969).
Rhodanthidium (Rhodanthidium) infuscatum bellicosum (Lepeletier, 1841). – Regarded as subspecies of *R. infuscatum* by Rasmont et al. (1995), Ornosa et al. (2008) and others. – Subspecies status not confirmed (this study).
Females can easily be identified by the large, nearly semicircular indentation of the apical margin of T6, males by the trifid T7 in combination with a median projection of T6 which is about as broad as T7.
Female. 9-10 mm. Head: Clypeus yellow with crenulate, black apical margin. Two

Female. 9-10 mm. *Head*: Clypeus yellow with crenulate, black apical margin. Two small ill-defined darkenings at base often present; mandible yellow with four black teeth; shallow emargination between the two middle teeth, deep emargination between the inner the middle tooth; inner orbits slightly converging below; paraocular area yellow to top of eye; small yellow oval spot on frons beyond the front ocellus; yellow preoccipital stripe along the entire vertex and genal area (up to the occipital ridge, not leaving a black gap as in *R. exsectum*); ventral surface of antennae light ochreous, dorsal surface with a greyish tint. – *Mesosoma*: Boomerang-shaped yellow anterolateral maculation; pronotal lobe yellow with sharp lamella; scutum slightly emarginate in the middle; axillae angular; scutum and axillae entirely yellow with the exception of the anterior margin of scutum; upper part of omaulus slightly lamellate. – *Legs*: Yellow with sometimes some darkening at femora. – *Metasoma*: Lateral bands on T1 and T2 not joining at the centre,



Rhodanthidium infuscatum. Female head. Left: female from Morocco, right: female from France.



Rhodanthidium infuscatum. Female (left) and male (right) from Morocco.

a wide space between them; bands on T3–T5 almost reaching the middle, subcontiguous; ground colouration of terga black or brown, apical margin translucent-brown; apical tergum with a large median semicircular to semioval emargination; one tooth each present distally; a small translucent-brown lamella beneath the emargination, visible at the inner side of the indentation.

Male. 10-11 mm. *Head*: Paraocular area yellow, reaching to top of eye; yellow band along the preoccipital ridge, often becoming broader on the genae and reaching the mandibles; sometimes broken in the lower genae; longitudinal stripe below ocellus sometimes present; clypeus yellow, apical margin with mostly dark crenulation; truncate to slightly emarginate; clypeus with long white pubescence; mandible yellow (brownish at margins) and teeth black; tridentate with proximal tooth almost as strong as apical tooth; deep and wide emargination between median and proximal tooth, incision between apical and median tooth. – *Mesosoma*: Scutum with yellow boomerang-shaped anterolateral band, sometimes reduced to a narrow stripe next to the anterior margin; scutellum and axillae with narrow translucent apical margin; scutellum with median emargination, axillae with angle or tooth on outer side; outer two thirds of scutellum and axillae yelow. – *Metasoma*: T1 with continuous yellow band, the central areas often blurred



Rhodanthidium infuscatum. Female and male apical terga.

brownish or reddish-brown shading; T2–T4 with yellow bands mostly broken in the middle; T5 with contiguous lateral bands; T6 with a trapezoid projection in the middle which has a slightly bilobed apex; a laterally overhanging bulge; T7 with median spine (apex rounded) and two lateral projections slightly curved inward. Black median comb on the ventral surface of S5.

Note. Within the Subgenus *Rhodanthidium (Rhodanthidium), R. infuscatum* is quite distinctive and has been given the genus name *Bellanthidium*. Among its distinctive characters are the strong shoulders rather than spines at the sides of T6 of the male, a marginal comb on S5 but not on S4 of the male (in other species there is a comb on S4 and sometimes also S5), and especially the enormous emargination in T6 of the female.

Subspecies. Anthidium infuscatum was described in 1835 from Andalusia, Anthidium bellicosum 1841 from Algeria. Friese (1898, 1911) assumed synonymy and Pasteels (1969), Warncke (1980), Aguib et al. (2010) and others put bellicosum into synonymy with infuscatum. Other authors such as Rasmont et al. (1995) and Ornosa et al. (2008) regard them as two subspecies. Although Friese (1898) listed material of bellicosum from Spain, Ornosa et al. (2008) regard infuscatum as the subspecies occurring in Spain, and bellicosum as the North African subspecies. Ortiz-Sánchez (2011) lists both subspecies for Spain. The material examined by the author both from North Africa and Spain shows some slight differences in colouration which, however, does not justify taxonomic differences. Bellicosum is therefore not regarded as a valid subspecies.



Rhodanthidium infuscatum. Male from France.



Rhodanthidium infuscatum. Scutellum of a male from Morocco. Note the emarginated apical margin, the toothed axillae and the translucent outer margin.



Rhodanthidium infuscatum. Apical terga of female (left) and male (right) of specimens from France.



Rhodanthidium infuscatum. Ventral surface of metasoma of male.

Biology. Found on the wing between May and August in western Europe and North Africa; a record from Croatia from as early as March (OLL). The species uses according to Pasteels (1977) and Ortiz y Sanchez (1990) empty snail shells for nesting, but there is no detailed information available.

Distribution. A predominantly west Mediterranean species which is widely distributed from Morocco, Algeria and Tunisia in North Africa to the Iberian Peninsula (Spain, Portugal), Andorra and France. There is a single isolated record from Croatia (Island of Korčula in Dalmatia; material in OLL examined).







Distribution of Rhodanthidium infuscatum.

Rhodanthidium ordonezi (Dusmet, 1915)

Anthidium Ordoñezi Dusmet, 1915 (Morocco).

Anthidium sticticum F., var. Amismiziana nov. Dusmet, 1915 (Morocco).

- Rhodanthidium sticticum ordonezi (Dusmet, 1915). Asssigned to Rhodanthidium and given subspecies status by Pasteels (1969).
- Anthidium sticticum ssp. ordonezi Dusmet, 1915. Subspecies status accepted by Warncke (1980), but not generic classification.
- Rhodanthidium (Rhodanthidium) sticticum (Fabricius, 1787) (partim). Subgeneric classification established by Michener & Griswold (1994). See also Michener (2007).
- Rhodanthidium ordonezi (Dusmet, 1915). Status revised by Kasparek & Lhomme (2019).



Rhodanthidium ordonezi. Left female, right male.



Rhodanthidium ordonezi. Apical terga; left female, right male.

Rhodanthidium ordonezi has often been regarded as a subspecies of *R. sticticum* despite the striking differences in colouration. While both species are structurally similar, they differ in the colouration of tergal bands and the maculation on vertex (red or rufous in *T. sticticum*, yellow in *R. ordonezi*) and also the colour of the marginal areas of terga (rufous and translucent in *R. sticticum*, black in *R. ordonezi*).



Rhodanthidium ordonezi. Head of male.

Rhodanthidium ordonezi belongs to the *R. septemdentatum* species group. Males can easily be distinguished from the other members of the group by the shape of T7: *R. septemdentatum* s.l. has a strong and broad median projection with parallel sides, while the median projection has a tapered apex in *R. ordonezi*. T6 in *R. septemdentatum* is superimposed over T7 and its sides are bent down. By contrast, T6 in *R. ordonezi* has a more or less flat median projection.

Females of *R. ordonezi* are distinguished from *R. septemdentatum* s.l. by the fine structure of the surface of T6 (small, shining elevations on each side of the small median V-shaped incision, which are absent in *R. ordonezi*) and the colouration of the mandibles (entirely black in *R. septemdentatum* as against yellow and ochreous with black margins and teeth in *R. ordonezi*).

Female. 12-14 mm. *Head*: Dark brown to black with ochreous paraocular area (broad at lower face, narrow above antennal sockets) and an ochreous spot on each side of vertex. The vertex maculation sometimes meeting centrally and merging to form a band along the preoccipital ridge. Inner orbits of eyes converging below; clypeus with strong black crenulation at apical margin, but shallower in the middle of clypeus; mandible yellow centrally and fulvous in the remainder; margins and teeth black; one apical and three shallow inner teeth; pubescence of face fulvous, greyish-white on genae. – *Mesosoma*: Black; pubescence rufous dorsally and greyish-white laterally and ventrally. – *Metasoma*: Lateral yellow bands not reaching the middle on all terga; marginal area and margin of terga opaque black and shining. T6 with a small median incision and a lateral lamella on each side.

Male. 13-15 mm. *Head*: Dark brown to black; maculation pattern of paraocular area and vertex as in the female. However, paraocular area bright yellow rather than ochreous, while colour of vertex maculation ochreous in both sexes. Clypeus bright yellow with



Rhodanthidium ordonezi. Left female, right male.



Rhodanthidium ordonezi. Ventral side of metasoma.

black apical margin; mandible with strong apical tooth and two inner teeth separated by a wide and deep emargination. Pubescence on vertex rufous, silver on frons and genae. – *Mesosoma*: Dark brown to black with rufous pubescence on scutum and scutellum and



Rhodanthidium ordonezi. Male genitalia.

silvery pubescence laterally and ventrally. – *Metasoma*: Lateral yellow bands not reaching the middle on T1–T5. T6 with median projection, slightly emarginate at the horn-coloured or black apex. Obtuse tooth on each side. T7 trifid with a strong median tooth and two smaller lateral teeth. S4 with a median comb of black bristles, divided in the middle (approximately 10 bristles on each side). S6 black or at least darker than the other sterna with a small, round shining area in the middle; S7 expanded with a circular area apically which consists of a thin, transparent piece of integument. Volsellae very large and heavily sclerotized (dark brown).

Biology. Collected on the wing from *Lavandula stoechas* (H.-J. Flügel, cMS). Flight period extends from late March to mid-May.

Distribution. Endemic to central and southern Morocco. In the Fès region in the Middle Atlas Mountains the distribution areas *of R. ordonezi* and *R. sticticum* adjoin each other with no evidence for the existence of a transition zone. The two taxa are thus in allopatry throughout most of their respective ranges but probably co-occur in the Middle Atlas mountain. Distribution map see under *R. sticticum*.

Rhodanthidium rufocinctum (Alfken, 1930)

Anthidium rufocinctum Alfken, 1930 (\bigcirc , Greece: Crete).

- Anthidium septemdentatum ssp. rufocinctum Alfken, 1930. Accepted as subspecies by Warncke (1980) and in the following also by Scheuchl (2006) and others. Taxon not listed by Rasmont et al. (1995).
- Rhodanthidium (Rhodanthidium) septemdentatum (Alfken, 1930) (partim). Subgeneric classification established by Michener & Griswold (1994) and transferred to Rhodanthidium subgen. Rhodanthidium. See also Michener (2007).

Rhodanthidium rufocinctum (Alfken, 1930). - Name used in Fauna Europaea.

A species closely related to *Rhodanthidium septemdentatum*. Endemic to the islands of Crete and probably Malta.



Rhodanthidium rufocinctum. Habitus of male.



Rhodanthidium rufocinctum. Left: female terga, right dorsal view of male.

Rhodanthidium rufocinctum is on average smaller than *R. septemdentatum* s.l. As there is overlap between large individuals of *R. rufocinctum* and small individuals of the other species (especially with individuals of the Levantine population), this character is not sufficient for identifying the species unambiguously.

Rhodanthidium rufocinctum can be distinguished from *R. septemdentatum* s.l. by the following characters:

- The marginal zone of all metasomal terga is in both sexes brown and slightly translucent. It is black and opaque in *R. septemdentatum* s.l.
- The paraocular area is yellow in both *R. rufocinctum* and *R. septemdentatum* s.l., but the marking above the antennal sockets is narrower in *R. rufocinctum*.
- The female has always an entirely black clypeus; the population of *R. septemdentatum* on the nearby Levantine coast has always a yellow clypeus. Females of *R. septemdentatum* with a black clypeus are also found in the Western Mediterranean (France, Spain, Portugal) and rarely also in Turkey (mostly yellow with some black maculation).
- In the male, T6 is yellow with black on the sides, a longitudinal spine-like dark brown or black maculation in the middle, and a black apical margin. The median projection of T7 is brown or black; in populations of *R. septemdentatum* s.l. of the nearby Levantine coast, the dark median maculation on T6 is absent or very small, and T7 is mostly much lighter brown.

These features characterise *R. rufocinctum* as a good species.

A single female available from Malta (cMS, M. Kafka leg. 25.06.2014) is close to *R. rufocinctum*, but shows some differences in colouration with the black areas shining, not dull; the marginal zones of terga less translucent and the lateral preoccipital bands reaching up to the lateral ocelli. It is provisionally assigned to *R. rufocinctum* until more material becomes available.



Rhodanthidium rufocinctum. Male genitalia.



Rhodanthidium rufocinctum. Apical terga. Left female, right male. Note the brown marginal zone of the apical terga. In the male, the yellow maculation of T6 is divided in the middle by a dark, spine-like bar.



Rhodanthidium rufocinctum. Head. Left female. Note the black clypeus and the reddish-brown mandibles. Right male. Note the yellow mandibles with black teeth and the longer pubescence.

Biology. Found on the wing in Crete between April and early June, in Malta (*R*. aff. *rufocinctum*) in late June. It can be expected that it uses snail shells for nest building as does its close cogener *R*. *septemdentatum*.

Distribution. Endemic to the Greek island of Crete and probably to Malta.



Rhodanthidium rufocinctum. Ventral side of metasoma.

Rhodanthidium septemdentatum (Latreille, 1809)

Anthidium septemdentatum Latreille, 1809. Annals Mus. Hist. Nat. 13: 41, 210 (France).

- Megachile florentina Spinola, 1806. Insect. Liguriae 1: 137 (non Fabricius, 1775). Put into synonymy by Giraud (1863).
- Anthidium rufiventre Brullé, 1832 (nec. Latreille, 1809). Exped. scient. Moree 3: 339 (Southern Greece).

Anthidium quadridentatum Lepeletier, 1841. Hist. nat. Insect. Hymen. 2: 402 (France).

Anthidium fuscipenne Lepeletier, 1841. Hist. nat. Insect. Hymen. 2: 369 (Southern France).

Anthidium binominatum Smith, 1854. Catal. Hymen. Brit. Mus. 2: 265. – nom. nov. für A. rvfiventre Brullé, 1832.

Anthidium quadridentatum Giraud, 1857. Verh. zool.-bot. Ges. Wien. 7: 180 (non Lepeletier, 1841) (Austria, Region of Vienna). – Listed as synonym by Friese (1898).

Anthidium sexlineatum Chevrier, 1872. Mittheil. Schweiz. ent. Ges. 3: 499 (Switzerland).

Anthidium nigrosetosum Stanek, 1968. Bull. Rech. agron. Gembloux, N. S., 3: 362 (Dardanelles, European Turkey).

Anthidium septemdentatum faciale Friese, 1917.

Rhodanthidium septemdentatum (Latreille, 1809). – Mavromoustakis (1958).

Rhodanthidium (Rhodanthidium) septemdentatum faciale (Friese, 1917).

Rhodanthidium septemdentatum is probably the most abundant species of the genus throughout its distribution range and rich material can be found in scientific collections. It appears to be a very variable species but our knowledge is not sufficient to decide whether this is due to intraspecific variation or if the taxon is actually a complex of similar species. Warncke (1980) distinguishes three subspecies: the nominate subspecies in Western and Central Europe as well as in Western Turkey, the subspecies *faciale* (Friese,



Rhodanthidium septemdentatum s.l. Left female from SW Turkey, right male from France.

1917) in the Levantine countries including Cyprus and Rhodes, and the subspecies *ru*focinctum (Alfken, 1930) in Crete. The latter is given species rank here (see separate species account above). There seem to be clearly distinct populations but also transition zones containing specimens that exhibit overlapping characters, and it is therefore not advisable to give or to re-use names for these populations before a comprehensive revision has been carried out. I therefore use here the term "*R. septemdentatum* s.l.".

Female. 10-12 mm. Black with yellow markings. – *Head*: Clypeus black, yellow with black apical margin, or yellow with more or less irregular black markings. Apical margin irregularly crenulate with a small shallow emargination without crenulation. Mandible black with a more or less straight tooth bar usually without distinctive teeth. Paraocular area yellow, broad beneath the antennal sockets and narrow above. Yellow maculations on both sides of the vertex, sometimes meeting to form a narrow band along the preoccipital ridge. Sparse greyish-yellow pubescence mainly around the antennal sockets. – *Mesosoma*: Scutum black, scutellum sometimes with yellow maculation. Scutellum with small emargination in the middle, outer margin sharp-edged; pronotal lobe with carina, outer side yellow, inner side black. – *Legs*: Femora (except for black base), tibiae and tarsi fulvous.– *Metasoma*: T1-T5 with yellow lateral bands not reaching the middle; they take sometimes an oval shape; the distance between the bands decreases from proximal to distal segments. T6 with a large yellow maculation which is often divided into two



Rhodanthidium septemdentatum. Left female, right male. - From: Scheuchl (2006).

spots by a black central line. Apical margin of T6 a sharp carina with a small median incision. Above the carina, an overhanging protrusion on each side. Above the median incision, a small, elongate elevation on each side with shining surface. Ventral scopa fulvous.

Male. 12-15 mm. Similar to the female, paraocular area, clypeus and mandibles always yellow. Mandibles tridentate with a large apical tooth and two inner teeth which are separated by a deep emargination; pubescence longer and denser than in the female, whitish-yellow. – *Mesosoma*: As in female. – *Metasoma*: T1–T5 with lateral yellow bands not reaching the middle; distance between the bands decreases from proximal to distal segments. T6 with truncate median projection which is saddle-like superimposed over the projection of T7. T6 with a wide, acute lateral projection on each side. T7 with a truncated median projection (rectangular in dorsal view) and a spine whose apex is curved inwards on each side. The colouration of the median projection of T7 is variable with significant differences between populations, ranging from black to yellow. The base of the lateral spine of T7 dark, its apex light. There is a small median black comb at apical margin of S4 (consisting of approximately 6–15 bristles); S5 deeply emarginate with a larger comb in the middle (consisting of approximately 25–35 bristles); S6 with a median furrow.

Biology. A relatively abundant species. Preferring dry and warm habitats such as arid grassland and rocky steppes. Unlike most other Anthidiini, females emerge in spring prior to the males (proterogyny) (Amiet & Krebs 2012). Flight season starts quite early in April and ends in July (Banaszak & Romasenko 1998). In Attica appears from May (Grace 2010). Amiet et al. (2004) give early May to mid-September for Switzerland. Many records throughout the species' range fall within this period. This is an unusual long flight season, and Pasteels (1977) therefore believes that it is possible that



Rhodanthidium septemdentatum s.l. Comparison of the head of a female from France (left) and from Jordan (right). Note the differences in the colouration of the clypeus (black in the specimen from France, yellow in the specimen from Jordan). They may belong to different species; a comprehensive revision of the species complex is necessary.



Rhodanthidium septemdentatum s.l. Above: Female (left) and male (right) from France. – Below: Female (left) from Jordan and male (right) from Syria.



Rhodanthidium septemdentatum. Apical terga of female (above) and male (below).

R. septemdentatum is a polyvoltine species. Pasteels (1977) also reported that specimens emerged in the laboratory from snail shells sometimes after not less than two years. From snail shells collected in May in Lebanon, adult *R. septemdentatum* emerged in November (Kasparek, unpubl.).

A polylectic species, which collects pollen from a variety of plant families, mainly Fabaceae and Lamiaceae. Müller(1996) in an analysis of the scopal pollen loads of anthidiine bees identified as many as 17 different plant families.

This species has been recorded in Turkey feeding on Monk's Pepper Vitex agnus-castus and Yellow star-thistle Centaurea solstitialis (Astercaceae) (Özbek & Zanden 1993), in Lebanon on Goldleaf Jerusalem Sage Phlomis chrysophylla (Lamiaceae) (Kasparek, unpubl.), Calycotome (Fabaceae) and French Lavender Lavandula stoechas (Mavromoustakis 1955) and Cirsium syriacum (Grace 2010). Was noted flying to Marrubium and Stachys italica in Attica, and to Teucrium divaricatum, Ballota integrifolia, B. undulata, Echium sericeum, Onosma fruticosum and Centaurea solstitialis in Cyprus (Grace 2010). Gogola (1991) gives for Slovenia Lathyrus and Sempervivum tectorum. J. Devalez (in DiscoverLife) recorded it in Thasos (Greece) at Clinopodium suaveolens (Sm.) Kuntze and in Lesvos (Greece) at Origanum onites L. Maharramov et al. (2014) collected it in Nakhchivan Autonomous Republic (Azerbaijan) at Salvia viridis L. Friese (1911) mentioned Lotus corniculatus, Anchusa officinalis and Centaurea paniculata. Gabiot (2017) noted that the female prefers the flowers of thymes, rosemary and Grey-leaved Cistus (Cistus albidus).

Mavromoustakis noted that females collect resin from the trunks of the evergreen pine tree *Pinus halepensis*. They nest close to these stands in the forest, making their brood



Rhodanthidium septemdentatum s.l. Habitus of a female (above) and male from Jordan in lateral view.



Rhodanthidium septemdentatum s.l. (aff. ssp. faciale). Male from Lebanon.



Rhodanthidium septemdentatum s.l. Ventral side of metasoma of male.

cells in empty shells of land snails such as *Cepaea, Eobania vermiculata* (= *Helix vermiculata*), *Levantina bellardi, L. cypria, Theba pisana* (= *Helix pisana*), and *Cornu aspersum* (= *Helix aspersa*) (Armburster 1913, Friese 1911, Gogola 1991, Grace 2010, Xambeau 1896). Brood cells consist of resin and small stones (Scheuchl & Willner 2016). Armburster (1913) found that females develop in the inner whorls of the snail



Development of a larva of Rhodanthidium septemdentatum in a snail shell. - From: Grandi (1934).

shell, while the larger males develop in the outer whorls. He also found that the amount of diet (the inner brood cells have less space for storing diet) has no impact on the determination of the sex.

Nachtigall (1998) studied the flight behaviour of *R. septemdentatum* in southern France. He distinguishes several types of flight behaviour, including circling, penetrating partly into thick vegetation (bushes), hovering phases, continuously circling or circling after sucking nectar form the basic outlines. Other insects either entering the territory or sitting on flowers within the territory are attacked and driven away and hereby occasionally hurt. *Rhodanthidium septemdentatum* always reacts extraordinarily fast, is very flexible in its repertoire of flight styles and has instant control over its manoeuvrability.

For copulation, Nachtigall (1998) observed the male approaching the smaller female while it was sucking nectar on flowers by flying very fast and nearly or truly ramming it. This is the same behaviour males show against intruders. Males grasp the females with their widespread legs. The territories examined by Nachtigall (1998) were 2-3 m² large.

Mazzucco & Mazzucco (2007) noted that *R. septemdentatum* is in the morning the first *Anthidium* bee that visits the flowers of *Vitex agnus-castus*, and is then mainly active in the outer, sunny branches. During the hot noon hours, it retreats to the inner, semi-shady parts of the bush, while species such as *Anthidium florentinum* are now found in the outer parts.

The anthidiini cuckoo bee *Stelis ruficornis* Morawitz, 1872 is a cleptoparasite of *R. septemdentatum* (Kasparek 2015). The habitus and colour pattern of the two species is very similar, with the parasite being smaller in size. Also the cuckoo wasps *Chrysura refulgens* (Spinola, 1806) is a known parasite of *R. septemdentatum* (Xambeau 1896, Friese 1911).

Distribution. *Rhodanthidium septemdentatum* s.l. has a predominantly Mediterranean distribution. Westernmost distribution records are from Portugal; apparently rare in



Larva of *Rhodanthidium septemdentatum*. A. Head in dorsal view. B. Antenna. C. Part of the cuticula of the abdominal segments. D. Upper labrum. E. Part of the cuticula from the thorax segment. – From: Grandi (1934).

Spain; the sparse data from the Spanish Mediterranean region cannot be fully explained by a lack of collectors as there are many records of e.g. *R. sticticum* available from the region. Absent from Northern Africa, a record from Algeria needs confirmation. The species is found on the Balearic islands, on Sardinia, Sicily and Cyprus. In Crete and apparently also Malta it is replaced by *R. rufocinctum*.

In the Swiss Alps, recent records are only from Valais (Wallis) and Ticino (Tessin), and historical records from the areas of Geneva, Waadt, Bern and Grosons (Graubünden) (Amiet et al. 2004, Scheuchl & Willner 2016). For Austria, *Anthidium quadridentatum*, today regarded as synonym of *R. septemdentatum*, was described in 1857 from the region of Vienna. An occurrence in Austria was regarded doubtful by Schwarz et al. (1996) but meanwhile it has become known that the distribution extends from Tyrol, Carinthia and Styria to Lower Austria, Burgenland and Vienna (e.g. Schwarz & Gusenleitner 1999, Stöckl 2000). The species is also present in Bohemia and Moravia in the Czech Republic where it reaches, at approximately 50° North, its northern distribution limit (Warncke 1986, Straka et al. 2007), but the occurrence there is insufficiently documented.

Widely distributed in Italy, the Balkan countries and in Greece, with an apparent concentration in warmer coastal regions. In Greece, present on several islands such as Rhodes, Karpathos, Ios, Paros, Kos, Ikaria, Kea, Chios, Lesvos, Limnos, and Thasos (records mainly by J. Devalez in DiscoverLife). Distributed throughout Turkey, although the species appears to prefer the warmer western parts of the country. Rare in the east Anatolian highlands, and extending from there to East Azerbaijan Province of Iran (Khaghaninia et al. 2010) and Nakhichevan Autonomous Republic of Azerbaijan (Maharramov et al. 2014).

In the region of Melk, Lower Austria, a relatively large and increasing population was recently found, where it inhabits mainly railway embankments (Schweighofer 2015). By contrast, it is regarded as extinct in the Transdanubian Mountains in Hungary (Józan 2011).

Schulthess (1929) reports the species from Moulay Idriss in Meknès province northern Morocco. As he describes the female as having a yellow clypeus, and reddish (except the end) antennae and mandibles, his species identification cannot be correct (female *R. septemdentatum* have at least black mandibles and black antennae). Schulthess' specimen most probably belongs to *R. ordonezi*.

Louadi et al. (2008) lists the species from Algeria. This record seems to be based on a damaged specimen identified in 1997 by G. van der Zanden in the Collection of the Laboratoire Biosystématique et Écologie des Arthropodes of the University Mentouri Constantine, Algeria, and which stems from north-east Algeria (Aguib et al. 2010). Confirmation of the occurrence of this species in north Africa is needed. An occurrence in Belarus listed in Fauna Europaea (https://fauna-eu.org) has no known basis.

The species occurs from sea level up to the mountainous regions. The species seems to be more common in warm and dry Mediterranean lowlands than in higher altitudes. In Switzerland described as rare, occurring up to 1400 m (Amiet et al. 2004). In Turkey found up to 1450 m (Özbek & Zanden 1993). Comba & Comba (2010) give for Italy 15–650 m.



Distribution of *Rhodanthidium septemdentatum* s.l. and *R. rufocinctum*.

Rhodanthidium siculum (Spinola, 1838)

Anthidium siculum Spinola, 1838. Ann. Soc. ent. France 7: 525-526 (Italy: Sicily; non Egypt). Anthidium fontanesii Lepeletier, 1841 (Algeria). Anthidium andrei Mocsáry, 1884 (Algeria). Anthidium (Rhodanthidium) siculum Spinola, 1838. Rhodanthidium (Rhodanthidium) siculum (Spinola, 1838).

One of the two red *Rhodanthidium* species and therefore relatively easy to identify. Females are distinguished from the other reddish species, *R. sticticum*, by its black clypeus and mandibles (reddish-yellow with black margins in *R. sticticum*), males by a black



Rhodanthidium siculum. Female from Libya.



Rhodanthidium siculum. Female from Italy (Sicily).



Rhodanthidium siculum. Male from Tunisia.

median process of T7 (red with at most a dark apex in *R. sticticum*), in lateral view broad lateral teeth of T7 (thin with acute apex in *R. sticticum*), and the presence of black ventral combs on both S4 and S5 (only on S4 in *R. sticticum*).

Males apparently consist of two size classes, one is on average 17–19 mm long, the other 23–25 mm. According to Erbar & Leins (2017), the smaller males are subordinate and non-territorial, while the larger ones maintain active territories. While the differences exist in size, no morphological differences were found. The smaller males yet remain larger than the females.

Female. 13.5–16 mm. *Head*: Large reddish to orange maculation in the paraocular area; broad below antennal sockets, narrow above and almost reaching top of eye; broad reddish/orange band on vertex and upper malar area; clypeus black, projecting semicircularly, apical margin crenulate with strong tubercles; relationship length between hind ocellus and preoccipital ridge / inner distance between hind ocelli 1.2–1.3. Face with long red hair, dense especially around antennal sockets; antennal segments Sg1–Sg5 and underside of Sg6 (including scape and pedicel) bright reddish-yellow (orange). – *Mesosoma*: Black with ginger hair; outer margin of scutum and axillae widely rounded; pronotal lobe also black, with small anterior lamella. – *Legs*: Reddish/orange, femora with black base. – *Metasoma*: T1–T5 with reddish/orange lateral bands not reaching the middle, and not reaching the outer side; T6 with apical lamella which has a small median incision; T6 with lateral projection on each side.



The males of *Rhodanthidium siculum* show large differences in size.

Male. 17–25 mm. Head black with yellow paraocular area and clypeus. One red lateral maculation on each side of vertex. Mandible yellow with black margins and black teeth; three teeth, the inner two separated by a wide emargination; rich ochreous pubescence on lower face including clypeus; pubescence on vertex and malar area shorter; the first four segments of the antennae red, the fifth segment only on dorsal surface; remaining segments black. – *Mesosma*: Dark with rich ochreous pubescence. – *Metosoma*: Lateral reddish to red bands on T2–T4 interrupted in middle; bands on T1 and T5 mostly reach the middle (contiguous bands or continuous band); T6 with a large median projection, often slightly bilobed; reddish to red with a small V-shaped black incision at base and a broad black band at apical margin; at each side a broad black, blunt tooth; T7 with a strong median tooth and two smaller lateral teeth; median tooth black and obtuse; lateral teeth broad with acute apex directed inward; at least apex light brown. S2 with a broad, black, shining plate covering most of the surface; S4 and S5 each with a median comb of black bristles (bristles on S4 about half as long as on S5).

Biology. A spring species. Found on the wing in Sicily during April (Erbar & Leins 2017) and in Spain in May (Ortiz 1990). Aguib et al. (2010) give for Algeria April and May.

The sex and breeding behaviour has been studied in detail by Erbar & Leins (2017) in sand dunes in Sicily. The female searches for an empty snail shell (mostly of *Theba pisana*) and examines its suitability. Once a suitable shell is found they deposit a mixture



Rhodanthidium siculum. T6 of female (above) and T6+T7 of male (below).

of sand and saliva in the navel. A severe struggle between several males occurs. At every opportunity, the males try to copulate with the females. Large males occupy the snail shell that is being used by the female which has begun a nest by transporting loads of pollen and nectar (preferably from *Galactites tomentosus, Centaurea sphaerocephala, Glebionis coronaria* and *Lotus creticus*). The procedure of harvesting can last several hours. During this period, the female is visited for copulation every 2 min (initially even more frequently), usually by a large male, but small males occasionally mate as well. After laying one or two eggs, the female seals the shell with pieces of seashell or snail shell, mixed with sand and saliva. The female transports the closed snail shell to a safe site. Depending on weather conditions, this may take several days. The maximum distance of movement observed was about 10 m. Finally, the completed snail shell nest is buried, most often beneath a plant. The burial follows a certain pattern of movement (Erbar & Leins 2017).

Erbar & Leins (2017) also noted in their study in Sicily that males visit flowers only for their own energy demands. Both the variety and the frequency of flow visits are high. Males were frequently encountered searching for nectar on flowers of *Centaurea* sphaerocephala, Galactites tomentosus and Lotus creticus, and less frequently on Borago officinalis, Lathyrus clymenum, Medicago marina, Orobanche litorea and Prasium majus. Males were observed switching between flowers of Borago, Lathyrus



Rhodanthidium siculum. Above: Male from Libya. Below: Female from Libya (left) and male from Algeria (right).

and *Medicago*. One male alternated repeatedly between *Orobanche* and *Lotus*. Other males visited successively different flower heads of *Centaurea*. Females were found visiting the flowers of *Centaurea sphaerocephala*, *Galactites tomentosus* and *Lotus creticus*, where they collected nectar as well as pollen. In one case, the load in the scopa (which could rarely be observed) could be determined as pollen of *Glebionis coronata* (Asteraceae), judged from the pollen colour and abundant pollenkitt. Erbar & Leins (2017) never observed female *R. siculum* visiting the inflorescences of *Glebionis*, although there were large populations in their study areas. Females ensure higher pollination efficiency than the males due to their higher flower constancy (Erbar & Leins 2017).


Rhodanthidium siculum. Male from Libya.



Rhodanthidium siculum. Clypeus and mandible. Left female from Libya, right male from Tunisia.

Aguib et al. (2010) and Aguib (2014) listed the following flowers visited by *R. siculum*: *Heydsarium coronarium* L. (Fabaceae), *Malva sylvestris* L. (Malvaceae), *Rosmarinus officinalis* L. (Lamiaceae), and *Sinapis arvensis* L. (Brassicaceae).

Distribution. North African and Western Mediterranean. Occurs from Morocco across Algeria and Tunisia to Libya. In Europe, found in Portugal, Spain, Italy (Sicily) and Malta. Egypt is mentioned by Isensee (1927). This may be a confusion as Spinola (1838)



Rhodanthidium siculum. Female from Tunisia.



Rhodanthidium siculum. Apical terga of male.

described the species on the basis of material from Sicily but within an article on hymenopterans from Egypt. Smith (1854) in his catalogue of hymenopterous insects in the collection of the British Museum subsequently attributed it to Egypt. Ornosa et al. (2008) characterised *R. siculum* as a species of the Mediterranean "and Asia Minor", and this was followed by Aguib (2014) and Aguib et al. (2010). However, no evidence for an



Rhodanthidium siculum. Left: Apical terga of male from Libya. Right: Male genitalia (from: Isensee 1927).





Rhodanthidium siculum. Male ventral metasoma.

occurrence in Turkey was found. Ornosa et al. (2008) and Discover Life shows an occurrence in France but the source is not available. So far, the northernmost confirmed record is from Tarragona in Spain (specimen in OLL).



Distribution of *Rhodanthidium siculum*. The triangles show a country record from France whose precise location is not known and which need confirmation.

Rhodanthidium sticticum (Fabricius, 1787)

Apis stictica Fabricius, 1787. Mant. Insect. 1: 302 (Algeria).

Anthidium sticticum (Fabricius, 1787). - Synonymy established by Fabricus (1804).

Trachusa stictica (Fabricius, 1787). - Transferred to Trachusa by Jurrine (1807).

- Dianthidium sticticum (Fabricius, 1787). Cockerell (1904) ("I find that it belongs to Dianthidium").
- Rhodanthidium sticticum (Fabricius, 1787). "probably should be included in Rhodanthidium" Isensee (1927).
- Rhodanthidium sticticum (Fabricius, 1787). Asssigned to Rhodanthidium by Pasteels (1969).

Anthidium sticticum (Fabricius, 1787). – Warncke (1980).

Rhodanthidium (Rhodanthidium) sticticum (Fabricius, 1787). – Subgeneric classification established by Michener & Griswold (1994). See also Michener (2007).

One of the two red *Rhodanthidium* species. The most striking differences from *R. siculum*, the other red species, include: The clypeus and mandibles are in the female red with black margins (entirely black in *R. siculum*), and in the male, the median projection of T7 is red with a dark apex (entirely black in *R. siculum*).

Rhodanthidium ordonezi, previously regarded as subspecies of *R. sticticum*, is structurally very similar but can easily distinguished by the colour of the maculation on head and



Rhodanthidium sticticum. Lateral habitus. Above female, below male. Both from Morocco.



Rhodanthidium sticticum. Apical terga of female (above) and male(below).

terga which is red in *R. sticticum* and yellow in *R. ordonezi*. Additionally the marginal zone of terga is black in *R. ordonezi*, while it is brownish-red translucent in *R. sticticum*.

Female. 13-16 mm. *Head*: Dark brown to black with reddish paraocular area (broad at lower face, narrow above antennal sockets) and a reddish spot on each side of vertex. The vertex maculation sometimes forms a subcontiguous band along the preoccipital ridge. Inner orbits of eyes converging below; clypeus with strong black crenulation at apical margin, crenulation shallower in the middle of clypeus where there is a shallow emargination; mandible reddish in the middle and fulvous in outer parts; margins and teeth black; one apical and three shallow inner teeth; pubescence of face fulvous, grey-ish-white on genae. – *Mesosoma*: Black; pubescence rufous dorsally and greyish-white laterally and ventrally. – *Metasoma*: Lateral yellow bands on terga not reaching the middle; marginal zone and margin of terga translucent brown. T6 with a small median incision and a somewhat inconspicuous lateral lamella on each side.

Male. 11-15 mm. *Head*: Dark brown to black; maculation of paraocular area and vertex as in the female. However, colouration of paraocular area bright yellow rather than ochreous; band on vertex ochreous. Clypeus yellow with black apical margin; mandible with strong, bent apical tooth and two inner teeth separated by a wide and deep emargination. Pubescence on vertex rufous, silver in face and on genae. Inner segments of antennae reddish, outer segments at least on ventral surface. – *Mesosoma*: Dark brown to



Rhodanthidium sticticum. Head. Above female, below male.



Rhodanthidium sticticum. Apical terga of male.



Rhodanthidium sticticum. Ventral side of male metasoma.



Distribution of *Rhodanthidium ordonezi* (red dots) and *R. sticticum* (green dots) in the Mediterranean basin and the northeast Atlantic coastal area. Records of *R. sticticum* beyond the known distribution which need confirmation are indicated by black triangles (Δ). – Source: Kasparek & Lhomme (2019) with supplementary records.

black with rufous pubescence on scutum and scutellum and silvery pubescence laterally and ventrally. – *Metasoma*: Lateral yellow bands on T1-T5 not reaching the middle. T6 with median projection, slightly emarginate at the horn coloured or black apex. Obtuse lamellate projection on each side. T7 trifid with a strong median tooth and a small lateral tooth on each side. Median projection truncate at apex; S2 with a broad, shining elevated plate; S4 with a median comb of black bristles, divided in the middle (approximately 10 bristles on each side). S6 with a small, round shining area in the middle; S7 bulged with a circular area apically which consists of a thin, transparent piece of integument.

Biology. An early spring and late autumn species with possibly two generations per year: The species was found in Spain from March to May (exceptionally from February and in to June), and again in October/November. Greca (2010) found it around Mount Etna (Sicily) from March to May. A single record from August (Ortiz 1990). A flight period of April to June is given by Aguib et al. (2010). *Rhodanthidium sticticum* may thus be a polyvoltine species.

Polylectic species. Agulló et al. (2015) provide some quantitative observations on flower-visiting of *R. sticticum* to Cat's Head Rockrose *Helianthemum caput-felis* (Cistaceae), a perennial subshrub, in coastal dunes of Alicante province, southern Spain. Fernández-Mazuecos et al. (2013) in a study on Bifid Toadflaxes (*Linaria*) in Spain found that *R. sticticum* visited the flowers of *Linaria clementi, L. salzmannii* and *L. viscosa*. Aguib et al. (2010) listed the following flowers visited by *R. sticticum*: Fabaceae: *Hedysarium coronarium* L., *Hedysarium* sp., *Cytisus linifolius* L.; Asteraceae: *Carduus* sp., *Centaurea nichaeensis* All., *Crepis vesicaria* L.; Malvaceae: *Malva sylvestris* L. According to Torres et al. (2001) and Torres et al. (2003), *R. sticticum* was in his study area in Central Spain the main pollinator of *Antirrhinum microphyllum*, an endemic dragon flower. It was only active on sunny days. Its activity began at 9 a. m. and ended at 4 p. m. with a peak between 11 a. m. and 1 p. m. Usually *R. sticticum* landed on the lower lip of *A. microphyllum* flowers and opened the corolla with the legs. As the nectar is at the bottom of the corolla the bee is obliged to crawl towards the flower base and in coming into contact with stigma and stamens. This way the pollen grains are attached onto the vertex of the head and onto the thorax.

Torres et al. (2003) observed that males of *R. sticticum* are territorial and they occupy and patrol territories of a few square metres to defend them from other males and insects while females collect pollen. The movements of the females are mainly between plants less than 10 m apart.

Aguib et al. (2010) also mentioned that the species is often collected close to snail shells, where they are looking for nesting places.

Schremmer (1960) produced a film in which he shows that *R. sticticum* competes with *R. septemdentatum* for snail shells: *R. sticticum* fought successfully with *R. septemdentatum* over a snail shell, removed the other species' egg from it, laid its own egg next to the accumulated pollen and resealed the entrance. This is the only evidence for this form of cleptoparasitism in this species.

The chalcid wasp *Monodontomerus anthidiorum* (Lucas) has been reared from *R. sticticum* (Zerova & Seryogina 2002). The species of *Monodontomerus* are parasitoids of cocoons and larvae of Lepidoptera, Hymenoptera and puparia of parasitic Diptera.

Distribution. Western Mediterranean. In Northern Africa from Morocco across Tunisia and Algeria to Libya. In Europe, from Portugal over Spain to southern France. In Italy confined to Sicily. Also found in the Balearic Islands and Corsica. Records from Northern Spain, Central France, Croatia, and Greece doubtful (Kasparek & Lhomme 2019).

Rhodanthidium superbum (Radoszkowski, 1876)

Anthidium superbum Radoszkowski, 1876. Hor. Soc. ent. Ross. 12: 91 (Female from Amasya in Turkey).

Anthidium Christophi Morawitz, 1884 (Male and female from "Achal-Tekke bei Nuchus unweit Artschman" = Aşgabat area in Turkmenistan). – Synonymised by Warneke (1980).

Anthidium christophii Morawitz, 1884. - Mis-spelled by Friese (1898).

Anthidium grande Friese, 1897 (Male, Amasya, Turkey). - Synonymised by Warncke (1980).

Meganthidium christophi (Morawitz, 1884). - Assigned to Meganthidium by Popov (1950).

Rhodanthidium (Meganthidium) superbum (Radoszkowski, 1876). – Meganthidium assigned as subgenus of Rhodanthidium by Michener & Griswold (1994).

A very large species (19–31 mm), the largest Palaearctic member of the Anthidiini, with a stunning mimicry of hornets (*Vespa crabro / Vespa orientalis*). Like hornets, *R*.



Rhodanthidium superbum. Head. Above female, below male, both from Turkey.



Rhodanthidium superbum. Habitus dorsal. Left female, right male.

superbum has a reddish-brown colouration of integument and pubescence. The first two terga are also reddish-brown, the others have bright yellow bands. The last tergum of the male is characterised by five teeth. Friese (1898) described it as 'the largest and most beautiful species' among the Anthidiini.

Female. Head with a characteristic black area including supraclypeal area, antennal sockets and ocelli; within this area, a small yellow spot in the supraclypeal area (sometimes absent) and below the lower ocellus. Paraocular area and vertex bright yellow, lower half of genae black. Clypeus widely rounded with black apical margin; mandibles reddish-brown with four black teeth; reddish-brown pubescence. – *Mesosoma*: Dense reddish-brown pubescence on dorsal and lateral surfaces; scutellum and axillae merged, apical margin widely rounded. – *Legs*: Femora dark brown with light brown apices and longitudinal stripes; tibiae and tarsi light brown. – *Metasoma*: The first two terga with reddish-brown complete bands, the remaining terga with yellow maculation: T3 with subcontiguous lateral bands, T4 with contiguous lateral bands, T5 also contiguous bands or continuously yellow; T6 yellow with black darkenings laterally, sides swollen and slightly overhanging; a rounded projection on each side of the apical margin.

Male. Highly variable in size. 20-28 [-31] mm. Appearance similar to female. – *Head*: Colouration pattern as in female; small yellow spot below front ocellus sometimes absent as in female; mandible yellow with three teeth; maxillary palpus three-segmented. – *Mesosoma*: Pronotal lobe dark with anterior carina. – *Metasoma*: Apical tergum (T7) with five teeth: two small lateral teeth, slightly curved inward, and three teeth which



Rhodanthidium superbum. Apical terga. Above female, below male, both from Turkey.



Rhodanthidium superbum. Apical terga of female (above) and male (below).



Rhodanthidium superbum. Mandible of female (left) and male (right).



Rhodanthidium superbum. Male genitalia (left) and apical sterna (right). - From: Popov (1950).



Rhodanthidium superbum. Female mandible (Armenia).



Rhodanthidium superbum. Ventral side of metasoma. Note the comb of strong, brown hair on S5 (not black bristles as in other species).

arise from a small, elevated area on T7; the strong middle projection with rounded apex and beside it, two smaller teeth, one on each side. S5 has an apical row of strong brown hair in the middle. These hairs are much weaker than the black bristles forming a comb found in certain other species. This row of hair is, contrary to the observation of Michener (2007) and used by him for characterising the subgenus *Rhodanthidium*



Rhodanthidium superbum. Head of female in dorsal view.

(*Meganthidium*), present only on S5 and not on S4. S6 with a lateral lobe on each side. – *Genitalia*: See figure from Popov (1950).

Biology. Found on the wing in Turkey between May and July (Özbek & Zanden 1993). According to Müller (1996), *Rhodanthidium superbum* can be classified as oligolectic and collects pollen exclusively on Leguminosae. He regards *R. superbum* as the oligolectic sister of the polylectic species of the subgenus *Rhodanthidium* (*Rhodanthidium*).

Distribution. Mountainous areas from Turkey to Iran and Turkmenistan. Also recorded in Armenia (Aliev 1985) and Georgia (Kirkitadze & Japoshvili 2015). In Turkey found up to 2270 m (Özbek & Zanden 1993).



Distribution of Rhodanthidium superbum.

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A Review and Identification Guide

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The genus *Rhodanthidium* is small group of pollinator bees which are found from the Moroccan Atlantic coast to the high mountainous areas of Central Asia. They include both small inconspicuous species, large species with an appearance much like a hornet, and vivid species with rich red colouration. Some of them use empty snail shells for nesting with a fascinating mating and nesting behaviour. This publication gives for the first time a complete overview of the genus, with an identification key, the first in the English language. All species are fully illustrated in both sexes with 178 photographs and 60 line drawings. Information is given on flowers visited, taxonomy, and seasonal occurrence; distribution maps are including for all species. This publication summarises our knowledge of this group of bees and aims at stimulating further research.