

Taxonomy, distribution and bionomics of *Celonites tauricus* Kostylev, 1935, stat. n. (Hymenoptera, Vespidae, Masarinae)

Volker Mauss¹, Alexander V. Fateryga^{2*}, Rainer Prosi³

1 Staatliches Museum für Naturkunde, Abt. Entomologie, Rosenstein 1, D-70191 Stuttgart, Germany **2** Karadag Nature Reserve, Nauki Str. 24, Kurortnoye, 298188 Feodosiya, Russia **3** Lerchenstraße 81, D-74564 Crailsheim, Germany

Corresponding author: Volker Mauss (volker.mauss@gmx.de)

Academic editor: M. Ohl | Received 18 October 2015 | Accepted 30 December 2015 | Published 1 March 2016

<http://zoobank.org/388B0CD9-070B-4409-AAEC-B0E5C8ACDFBD>

Citation: Mauss V, Fateryga AV, Prosi R (2016) Taxonomy, distribution and bionomics of *Celonites tauricus* Kostylev, 1935, stat. n. (Hymenoptera, Vespidae, Masarinae). Journal of Hymenoptera Research 48: 33–66. doi: 10.3897/JHR.48.6884

Abstract

Male and female of *Celonites abbreviatus tauricus* Kostylev, 1935 are redescribed and a neotype is designated. Based on morphological characters *Celonites a. tauricus* is synonymized with *Celonites spinosus* Gusenleitner, 1966 and *Celonites abbreviatus invitus* Gusenleitner, 1973. The taxon is hypothesized to be reproductively isolated from *Celonites abbreviatus* Villers, 1789 by differences in the male genitalia and in the colour pattern of the male antennae and is therefore regarded as a separate biospecies named *Celonites tauricus*. *Celonites tauricus* is allopatrically distributed with regard to *C. abbreviatus* and has been recorded from the Crimea, Kos, Asia Minor and Cyprus. Within this range six intraspecific taxa can be separated by morphological characters and colour patterns. Habitat, flower association, flower visiting behaviour, mate seeking behaviour and nesting of *C. tauricus* are almost similar to *C. abbreviatus*.

Keywords

Hymenoptera, Vespidae, Masarinae, *Celonites*, taxonomy, bionomics, Palearctic, Crimea, Asia Minor, Cyprus, flower association, Lamiaceae, female brood care

* **Disclaimer:** Author(s) from Crimea of articles appearing in the Journal of Hymenoptera Research is/are solely responsible for the proper indication of his/her/their actual postal address and affiliation. The Journal of Hymenoptera Research is a scientific journal and cannot be held responsible for political tensions or disputes between governments or persons.

Introduction

Nearly 100 years ago the first specimen of a species of the pollen wasp genus *Celonites* Latreille, 1802 was recorded from the Crimea. It was a single female collected by V.N. Wuczeticz on 13 June 1916 on the southern slope of Karagach in the Karadag (Kostylev 1928; original spelling “Karagatsh”) which is a small mountain massive on the south-eastern coast of the Crimea. Kostylev (1928) identified the specimen as *Celonites abbreviatus* (Villers, 1789). Seven years later he formally described the *Celonites* taxon from the Crimea as a new subspecies of *C. abbreviatus* named *Celonites abbreviatus tauricus* Kostylev, 1935. He noted that specimens from the Crimea differed from specimens from the Caucasus by finely serrate margins of the second and subsequent terga and concluded that they possibly belong to a different subspecies (Kostylev 1935). Kostylev did not designate any type specimens of the subspecies either in his original description or in any further publication. Moreover, it is unknown how many specimens were available to him, when he described the taxon. In his world checklist of masarine wasps Carpenter (2001) recognized *C. a. tauricus* as a valid taxon. He speculated that the holotype of *C. a. tauricus* might be in the collection of the Zoological Institute of the Russian Academy of Sciences in Saint Petersburg (Russia), but we could not find it there, though carefully searching for it. The holotypes of all other wasp species described by Kostylev are deposited in the Zoological Museum of the Lomonosov Moscow State University in Moscow (Russia). These types are stored in a separate box apart from the main collection. There is no specimen of *Celonites* from the Crimea in the “type box” or in the main collection, whereas all other wasps from the Karadag listed by Kostylev (1928) are there. It can be assumed, that Kostylev (1935) based his description on the female collected by Wuczeticz. Therefore, the type locality was probably situated in the Karadag Mountains (as reported by Kostylev 1928). Evidently Wuczeticz’s specimen and any further material (if it had ever existed) have been lost.

In 1966 Gusenleitner described a new species belonging to the *Celonites abbreviatus*-complex from western Turkey, named *Celonites spinosus*. He argued that this taxon could not be identical with *C. a. tauricus* Kostylev, based on the incorrect translation or interpretation of Kostylev’s description, that antennal article A3 should not be longer than A4+A5 in *C. a. tauricus*. In fact, Kostylev attributed this character state explicitly to a specimen from Spain and stated that A3 is longer than A4+A5 in *C. a. tauricus*, which is similar to *C. spinosus*. Moreover, in both taxa the posterior margins of the metasomal terga II–V were described as “serrated” or “spine-like crenulated” respectively (Kostylev 1935, Gusenleitner 1966), indicating further similarity between them.

Another subspecies of *Celonites abbreviatus* named *invitus* was described by Gusenleitner in 1973 from central Turkey and Armenia. He separated this taxon from *C. abbreviatus* by the very shiny cuticula of vertex and mesosoma and the incomplete colour banding on the metasomal terga III–V. As a result of the investigation of further material, Gusenleitner in 1985 recognized *C. a. invitus* as an eastern form of *C. spinosus* and synonymized both taxa formally.

A specimen of *Celonites abbreviatus tauricus* was first collected from the Crimea in 1916, but none were recorded in the following 86 years. Then in 2002 two specimens were collected in the Karadag Nature Reserve (Fateryga and Ivanov 2009). Following this find intensive field research led to the discovery of nine localities of *C. a. tauricus* on the Crimean peninsula (Fateryga and Ivanov 2010). In addition, it was discovered that a previously unnoticed specimen of *C. a. tauricus* had been collected in the Crimea in 1963 (Ivanov and Fateryga 2009), indicating the continuous existence of an endemic *C. a. tauricus* population in the area. Further field observations provided some bionomical data concerning flower associations and nesting (Ivanov and Fateryga 2009, Fateryga 2010, Fateryga and Ivanov 2010). However, until now the taxonomic identity and status of *C. a. tauricus* with regard to *C. abbreviatus* and *C. spinosus* had not been studied and remained uncertain.

The purpose of the study presented below was to revise the taxonomic status of *Celonites abbreviatus tauricus*, to designate a neotype, to describe both sexes and to summarize and discuss what is known of the distribution, geographical variation and bionomical characters of the taxon.

Material and methods

The specimens of *Celonites* studied belong to the public collections of the Taurida Academy of the Vernadskiy Crimean Federal University (Simferopol, Russia) (VTNU), the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia) (ZIN), the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine (Kiev, Ukraine) (IZAN), the Kharkov Entomological Society (Kharkov, Ukraine) (KHEO), and the Upper Austrian State Museum (Linz, Austria) (OLML), as well as to the private collections of A.V. Amolin (Donetsk, Ukraine) (AA), J. Guseinleitner (Linz, Austria) (JG), V. Mauss (Michelfeld, Germany) (VM), S.A. Mosyakin (Simferopol, Russia) (SM), D.V. Puzanov (Yevpatoriya, Russia) (DP), C. Saure (Berlin, Germany) (CS), C. Schmid-Egger (Berlin, Germany) (CSE) and E. Yildirim (Erzurum, Turkey) (EY). Without success we searched for material of the taxa under consideration in the collections of the Zoological Museum of the Lomonosov Moscow State University (Moscow, Russia), the Bavarian State Collection of Zoology (Munich, Germany) and the Stuttgart State Museum of Natural History (Stuttgart, Germany).

The specimens were investigated under a WILD M3 stereo microscope (maximum magnification 80 times). Measurements of the exoskeleton were made using an ocular micrometer (highest resolution 0.011 mm). The genitalia of all males were extracted after re-softening the specimens and were then studied in 80% ethanol. Drawings were made with a drawing tube (WILD Type 308700). Micro-photos were taken with a Leica IC 80 HD camera mounted on a Leica MS 5 stereomicroscope. Multifocus-pictures were generated with Leica Application Suite (LAS) software. The scapus of the antenna is referred to as antennal article A1 and the pedicellus as A2, the flagellum consists of the articles A3–A12.

Systematic bionomical observations were made on the Crimea population by A. Fateryga at Cape Aya in 2004, in the vicinity of Veseloye near Sudak in 2004, and in Lisy Bay from 2005 until 2014 (for details see material studied), and documented using a Canon Powershot A570 IS.

The Kos population was studied by V. Mauss from 25 May to 4 June 2015 (for details see material studied). Observations were made with a close-up binocular (Pentax Papilio 8.5×21) and documented with a Canon EOS 70D with a 180 mm macro-lens (scale up to 1:1, resolution 20 mega pixel) and macro flash-lights. Time intervals were measured using a digital stop-watch. Specimens of flowering plants were collected and preserved dried. The material was placed in the herbarium of the Stuttgart State Museum of Natural History (Herbarium STU). The plant taxa were identified following Pils (2006) and Tutin et al. (1964–1980). Flower preferences of imagines were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the area at six localities (total investigation time 11.30 h). Flower visiting behaviour of the imagines at *Satureja thymbra* and *Thymus capitata* was investigated at various patches of these plants at six localities for 19.45 h in total. From three localities pooled pollen samples from the crops of up to three females previously fixed in Duboscq-Brasil solution (Romeis 1989) were prepared using the method outlined by Westrich and Schmidt (1986). The different pollen types were ascertained under a light microscope at magnifications of 400× or 1000× and determined to generic level with the aid of a reference collection consisting of pollen samples of 500 mainly Mediterranean plant species.

Systematics

Celonites tauricus Kostylev, 1935, stat. n.

Celonites abbreviatus tauricus Kostylev, 1935, Arch. Mus. Zool. Univ. Moscou 2: 108 [Since the original type material is lost, we hereby designate a new specimen as a Neotype: 1♀ (dbM 4305), Crimea, Vicinity of Feodosiya: Lisy Bay, 44°54'N 35°09'E, leg. A. Fateryga 16.06.2010, coll. OLML, figs 1a, 2, 5]

Celonites spinosus Gusenleitner, 1966, Polskie Pismo Entomol. 36: 359–362, figs 2a, b, c [Holotype: 1♀ (dbM 4665), Turkey, Kusadasi, leg. J. Gusenleitner 11.06.1964, coll. JG]

Celonites abbreviatus invitus Gusenleitner, 1973, Boll. Mus. Civ. Stor. Nat. Venezia 24: 58, fig. 2b [Holotype: 1♀ (dbM 4662), Turkey, Gürün, 44°54'N, 35°09'E, leg. J. Gusenleitner 05.06.1970, coll. JG]

Celonites abbreviatus (Vill.) *invitis* Gusenl.; Schmidt 1984, Steir. Entomologenrunde 18: 89, misspelling

Material studied. Taxon 1 (Crimea, “*tauricus*”)

Russia: *Crimea:* Alushta, 44.66667°N, 34.41667°E, 06.07.1963, 1♀ IZAN; Simferopol, Marino, 44.91667°N, 34.11667°E, 31.07.2007 1♀ leg. A. Fateryga VTNU;

Vicinity of Feodosiya: Karadag Nature Reserve, 44.91667°N, 35.21667°E, 07.07.2002 1♂ (dbM No. 4704) 1♀ (dbM No. 4702) leg. S. Ivanov VM; Vicinity of Feodosiya: Lisy Bay, 44.90000°N, 35.15000°E, 22.06.2003 1♀ (dbM No. 4306) leg. S. Ivanov VM 1♀ leg. S. Ivanov VTNU 1♀ leg. S. Ivanov IZAN, 06.07.2005 1♀ leg. A. Fateryga VTNU 1♀ leg. A. Fateryga IZAN, 13.06.2007 2♀♀ leg. A. Fateryga VTNU, 25.06.2009 1♀ leg. S. Ivanov VTNU 1♀ leg. S. Ivanov ZIN, 27.06.2009 1♀ (dbM No. 4701) leg. A. Fateryga VM 1♀ leg. A. Fateryga VTNU, 12.06.2010 1♂ (dbM No. 4308) leg. A. Fateryga VM, 16.06.2010 1♀ (dbM No. 4305) leg. A. Fateryga VM, 09.07.2012 1♀ (dbM No. 4304) leg. A. Fateryga VM; Vicinity of Opolznevoye in the Yalta Mountain Forest Reserve, 44.40000°N, 33.93333°E, 04.07.2006 1♀ leg. S. Ivanov VTNU; Vicinity of Sevastopol: Cape Aya, 44.41667°N, 33.65000°E, 05.07.2004 1♂ (dbM No. 4705) leg. A. Fateryga VM 1♂ leg. A. Fateryga VTNU 1♂ leg. A. Fateryga IZAN 1♂ A. Fateryga KHEO 1♂ leg. A. Fateryga AA 1♀ S. Ivanov VTNU, 07.07.2004 1♀ leg. S. Naumenko DP, 08.07.2004 1♂ (dbM No. 4703) leg. A. Fateryga VM 1♂ leg. A. Fateryga ZIN 1♂ leg. A. Fateryga DP 1♀ leg. A. Fateryga VTNU, 07.2004 1♂ leg. L. Svolynskaya SM 1♀ V. Gromenko AA 1♀ V. Gromenko KHEO; Vicinity of Veseloye near Sudak, 44.86667°N, 34.88333°E, 02.07.2004 1♀ leg. D. Puzanov VTNU; Yalta, Sovetskoye, 44.51667°N, 34.18333°E, 05.06.2010 1♂ (dbM No. 4307) leg. S. Ivanov VM.

Taxon 2 (Kos)

Greece: *Dodekanes, Island Kos:* SE Mastichari, 36.83333°N, 27.08333°E, 31.05.–01.06.2003 2♀♀ (dbM No. 3607, 3608) leg. J. Tiefenthaler OLML; 1 km SE Mastichari, Hang mit Phrygana Fragment unterhalb Kapelle, 36.841317°N, 27.085367°E, 50 m, 26.05.2015 2♀♀ (dbM No. 4776, 4777) leg. V. Mauss VM; 2 km N Kefalos, Phrygana E des Berges Korakies, 36.765583°N, 26.960067°E, 110 m, 27.05.2015 2♀♀ (dbM No. 4778, 4797) leg. V. Mauss VM; 4 km SW Kefalos, Phrygana W Agia Anastasia, 36.719300°N, 26.924533°E, 40 m, 31.05.2015 2♀♀ (dbM No. 4783, 4795) leg. V. Mauss VM; 4 km SW Kefalos, Phrygana W Agia Anastasia, 36.719983°N, 26.930767°E, 90 m, 31.05.2015 1♀ (dbM No. 4782) V. Mauss VM, 02.06.2015 2♀♀ (dbM No. 4792, 4793) leg. V. Mauss VM, 04.06.2015 2♂♂ (dbM No. 4789, 4790) 3♀♀ (dbM No. 4788, 4794, 4798) leg. V. Mauss VM; 4 km SW Kefalos, Phrygana in sandigem Trockenflusstal N Cape Kata, 36.727733°N, 26.922833°E, 20 m, 31.05.2015 1♂ (dbM No. 4785) 1♀ (dbM No. 4784) leg. V. Mauss VM, 03.06.2015 1♀ (dbM No. 4796) leg. V. Mauss VM; 4 km W Andimachia, Phrygana Fragment nahe "Hippokrates Garden", 36.813783°N, 27.051233°E, 60 m, 28.05.2015 1♂ (dbM No. 4780) 1♀ (dbM No. 4779) leg. V. Mauss VM, 31.05.2015 1♂ (dbM No. 4781) 1♀ (dbM No. 4791) leg. V. Mauss VM, 04.06.2015 1♂ (dbM No. 4787) 1♀ (dbM No. 4786) leg. V. Mauss VM.

Taxon 3 (Western Asia Minor, "spinosus")

Turkey: *Ankara:* 15 km S Ankara, Beynam, 39.685958°N, 32.895143°E, 23.07.1987 1♀ (dbM No. 4682) leg. Kl. Reinhold JG; Kizilcahamam N of Ankara, 40.470123°N, 32.648873°E, 09.07.2000 3♂♂ (dbM No. 3597, 3598, 3599) leg. M. Halada OLML. – *Antalya:* 100 km E Antalya: S von Taskesigi, 36.753821°N,

31.633813°E, 1998 3♂♂ (dbM No. 3586, 4511, 4512) leg. M. Halada OLML; 50 km NE Antalya, 37.183333°N, 31.183333°E, 550 m, 17.06.2001 1♀ (dbM No. 3585) leg. J. Straka OLML; Alanya, 36.558341°N, 31.997983°E, 20–24.05.1993 1♂ (dbM No. 3431) leg. A. Kudrna OLML; Arapsuyu, 36.874761°N, 30.653459°E, 5 m, 30.06.2002 1♀ (dbM No. 4526) leg. H. Özbek EY. – *Aydin*: Kusadasi, 37.857802°N, 27.257981°E, 11.06.1964 3♂♂ (dbM No. 4693, 4694, 4695) 1♀ (dbM No. 4665) leg. J. Gusenleitner JG. – *Bilecik*: wn. Osmanieli, 40.356692°N, 30.001768°E, 14.06.1997 1♀ (dbM No. 3429) leg. M. Halada OLML. – *Burdur*: 28 km SEE Burdur, 37.666667°N, 30.466667°E, 1350 m, 08.07.2006 1♀ (dbM No. 3591) leg. M. Halada OLML. – *Denizli*: Çardak, 37.826119°N, 29.672490°E, 07.06.1964 1♂ (dbM No. 4697) leg. J. Gusenleitner JG; Pamukkale, 37.921213°N, 29.114931°E, 31.05.1966 1♀ (dbM No. 4674) leg. K. Kusdas JG. – *Izmir*: 10 km NE Ödemiş, 38.333333°N, 28.066667°E, 1200 m, 03.07.2006 1♂ (dbM 3596) 1♀ (dbM No. 3592) leg. M. Halada OLML; Izmir, 38.417154°N, 27.129925°E, 12.06.1964 1♀ (dbM No. 4666) J. Gusenleitner JG 1♂ (dbM No. 4696) 2♀♀ (dbM No. 4670, 4681) leg. H.H.F. Hamann JG; Tar.Ars.Enst. Menemen, 38.613484°N, 27.077789°E, 02.07.1992 12♀♀ (dbM No. 4530, 4531, 4532, 4533, 4534, 4535, 4536, 4537, 4538, 4539, 4540, 4541) leg. H. Özbek EY. – *Kayseri*: 25 km S Kayseri, 38.540470°N, 35.490265°E, 23.07.2003 1♀ (dbM No. 3593) leg. J. Straka OLML. – *Konya*: 30 km S of Akşehir, 38.188770°N, 31.495138°E, 24.06.1998 2♂♂ (dbM No. 3587, 4510) 1♀ (dbM No. 3428) leg. J. Halada OLML; Alti-Napa-Baraji, 37.880339°N, 32.303139°E, 12.06.1978 1♀ (dbM No. 4675) leg. J. Schmidt JG; Silile bei Konya, 37.929344°N, 32.420692°E, 09–17.06.1975 1♀ (dbM No. 4667) leg. J. Schmidt JG, 08.06.1978 1♀ (dbM No. 4676) leg. J. Schmidt JG, 12.06.1978 2♀♀ (dbM No. 4677, 4678) leg. J. Schmidt JG; W Seydisehir, 37.423314°N, 31.824113°E, 1800 m, 04.08.1991 1♀ (dbM No. 3632) leg. K. Warncke JG. – *Nevesehir*: Göreme, 38.642663°N, 34.830003°E, 1000 m, 20.07.1986 1♀ (dbM No. 4684) leg. Blank JG. – *Uşak*: 7 km NW Sivasli, 38.58333°N, 29.58333°E, 21.05.1983 3♀♀ (dbM No. 4687, 4688, 4689) leg. Aspöck, Rausch, Ressel JG; Between Uşak and Sivasli (= 27 km SE Usak), 38.61667°N, 29.58333°E, 830 m, 21.05.1983, 1♀ (dbM No. 4686), leg. E. Hüttinger JG. – *Region unknown*: Versilokgy oberhalb, 31.05.2007 1♀ (dbM No. 4725) CSE.

Intermediate between Taxon 3 and 4

Turkey: *Agri*: 40 km N Muradye, 39.246612°N, 43.67878°E, 2200 m, 05.07.2000 1♀ (dbM No. 3602) leg. M. Halada OLML. – *Artvin*: Yusufeli Taskiran, 40.803573°N, 41.551595°E, 1350 m, 06.07.2003, 1♂ (dbM No. 4545) leg. I. Aslan EY; Yusufeli, Morkaya, 40.729267°N, 41.602720°E, 700 m, 15.06.2010 1♀ (dbM No. 4528) leg. E. Yildirim EY. – *Erzincan*: W Refahiye, 39.900486°N, 38.759372°E, 2200 m, 23.08.1991 2♀♀ (dbM No. 3682, 3683) leg. Halada OLML. – *Erzurum*: Aribahçe, 40.073708°N, 41.167181°E, 2400 m, 20.07.2001 1♂ (dbM No. 4529) leg. E. Yildirim EY; Asagikatikli, Tortum, 40.392175°N, 41.474995°E, 26.07.1980 1♀ (dbM No. 4523) leg. E. Yildirim EY; Caliyazi-Pasinlei, 40.124501°N, 41.669960°E, 2400 m, 10.07.1997 1♀ (dbM No. 4543) leg. E. Yildirim EY; Çamlibel, Oltu,

40.488294°N, 41.762214°E, 1700 m, 14.07.1996 1♀ (dbM No. 4521) leg. E. Yildirim EY; Dikyar / Uzundere, 40.532510°N, 41.547963°E, 08.09.1996 1♀ (dbM No. 4522) leg. I. Aslan EY; Pazaryolu, Kumaskaya, 40.531839°N, 40.751973°E, 1800 m, 20.07.2011 1♀ (dbM No. 4527) leg. S. Çoruh EY; Umudum Yayl., 40.027957°N, 41.246457°E, 2100 m, 08.08.1991 1♀ (dbM No. 4525) leg. H. Özbek EY. – *Icel*: Sertavul-Ort, 36.885202°N, 33.277297°E, 1300 m, 11.06.1977 1♀ (dbM No. 4685) leg. J. Schmidt JG. – *Kayseri*: 10 km S Kayseri, 38.616667°N, 35.516667°E, 1660 m, 20.07.2003 1♀ (dbM No. 3594) leg. J. Straka OLML. – *Nigde*: NO Çamardi, 37.832838°N, 34.986299°E, 2100 m, 10.08.1991 1♀ (dbM No. 4683) leg. Warncke JG. – *Sivas*: Gürün, 38.720560°N, 37.278278°E, 05.05.1970 1♀ (dbM No. 4662) leg. J. Gusenleitner JG, 07.06.1970 1♂ (dbM No. 4663) leg. K. Kusdas JG; 20 km E Gürün: Mezikiran Gecidi, 38.747021°N, 37.151695°E, 10.07.1997 1♀ (dbM No. 3601) leg. Ma. Halada OLML. – *Tokat*: Tokat, 40.324460°N, 36.553842°E, 900 m, 19.08.1992 1♀ (dbM No. 4542) leg. E. Yildirim EY.

Taxon 4 (Eastern Asia Minor, “invitus”)

Iran: *Elburs*: 50 km S (90 km Straße) Chalus, 36.326699°N, 51.360601°E, 2800 m, 26.07.1977 1♂ (dbM No. 3656) 7♀♀ (dbM No. 3649, 3650, 3651, 3652, 3653, 3654, 3655) leg. J. Gusenleitner JG; 75 km S Chalus, 36.142606°N, 51.446689°E, 2400 m, 13.07.1977 2♀♀ (dbM No. 3648, 4664) leg. J. Gusenleitner JG.

Turkey: *Adiyaman*: Karadut, Nemrut Dag, 37.980373°N, 38.747183°E, 09.06.1998 1♂ (dbM No. 3430) leg. M. Halada OLML. – *Bayburt*: Bayrampasa, Demirözü, 40.1729804°N, 39.8201781°E, 31.07.1992 1♀ (dbM No. 4524) leg. H. Bastan EY. – *Bitlis*: Nemrut Dag, 38.650366°N, 42.218203°E, 2300 m, 15.08.1991 1♂ (dbM No. 3630) 1♀ (dbM No. 3629) leg. K. Warncke JG 1♀ (dbM No. 3681) leg. M. Halada OLML. – *Erzurum*: Palandöken Dagi südwestlich Erzurum: Dutçu, Komyolu, 39.84492°N, 41.25075°E, 2190 m, 28.07.2003 1♀ (dbM No. 2795) leg. V. Mauss & E. Yildirim VM; Palandöken, 39.84492°N, 41.25075°E, 16.08.1987 1♀ (dbM No. 4519) leg. H. Özbek EY, 17.07.1990 1♀ (dbM No. 4520) leg. E. Yildirim EY; Pehlivanli, Tortum, 40.513101°N, 41.484767°E, 29.06.1990 1♀ (dbM No. 4518) leg. E. Yildirim EY. – *Hakkari*: Tal S Gevria-Pass, 37.499257°N, 43.958866°E, 3000 m, 04.08.1986 1♀ (dbM No. 3634) leg. K. Warncke JG. – *Icel*: Mut, Passhöhe, 36.630138°N, 33.466345°E, 1520 m, 09.06.1966 1♀ (dbM No. 3578) leg. K. Kusdas JG. – *Kars*: 50 km S Kars: Pasli, 40.287056°N, 42.964613°E, 01.07.1997 1♂ (dbM No. 3595) leg. Ma. Halada OLML. – *Tunceli*: Esil, 39.5667°N, 40.1883°E, 12.06.1983 1♀ (dbM 3631) leg. J. Schmidt JG.

Intermediate between Taxon 4 and 5

Turkey: *Bitlis*: Nemrut Dag, 38.650366°N, 42.218203°E, 2850 m, 08.08.1986 1♀ (dbM No. 3627) leg. K. Warncke JG, 2300 m, 15.08.1991 1♀ (dbM No. 3628) leg. K. Warncke JG; Nemrut Dagi, 38.650366°N, 42.218203°E, 2800 m, 07.08.1986 1♀ (dbM No. 3626) leg. Blank JG; Tatvan, Nemrut Mt. 38.644449°N, 42.214363°E, 2000 m, 23.07.2003 1♀ (dbM No. 4544) leg. H. Özbek EY. – *Hakkari*: S Vargös / Mt. Sat, 37.3333°N, 44.25°E, 1700 m, 04.08.1982 1♀ (dbM No. 3633) leg. K. Warncke JG.

Taxon 5 (South-east of Taurus range)

Syria: *North Syria:* Marbij [Manbij], 36.528792°N, 37.935693°E, 09.05.1996 1♀ (dbM No. 3690) leg. M. Halada OLML.

Turkey: *Icel:* Mut, 36.6464°N, 33.4375°E, 13.06.1965 1♀ (dbM No. 4668) leg. M. Schwarz JG, 27–30.05.1967 1♀ (dbM No. 4672) leg. J. Schmidt JG, 28.05.1967 1♂ (dbM No. 4690) 1♀ (dbM No. 4673) leg. J. Gusenleitner JG, 06.06.1968 1♀ (dbM No. 4679) leg. J. Gusenleitner JG 1♀ (dbM No. 4680) leg. J. Schmidt JG, 19.05.1970 1♂ (dbM No. 4691) leg. J. Gusenleitner JG. – *Şanlıurfa:* Birecik / Urfa, 37.066514°N, 38.104280°E, 22.05.1983 1♂ (dbM No. 3635) leg. K. Warncke JG; Urfa, 37.165902°N, 38.795883°E, 31.05.1968 1♀ (dbM No. 4669) leg. J. Gusenleitner JG; Urfa: Urfa Umgebung, 37.165902°N, 38.795883°E, 30.05.1978 1♂ (dbM 4692) 1♀ (dbM No. 4671) leg. M. Schwarz JG.

Taxon 6 (Cyprus)

Cyprus: *Troodos:* Mt. Olympos, 34.93°N, 32.86°E, 1900 m, 19.06.2013 7♀♀ (dbM No. 4875, 4876, 4877, 4878, 4879, 4880, 4881) leg. C. Saure CS, 20.06.2013 6♂♂ (dbM No. 4719, 4720, 4721, 4722, 4723, 4724) 4♀♀ (dbM No. 4715, 4716, 4717, 4718) leg. C. Schmid-Egger CSE.

Field observations, records from literature. Armenia: Erevan, Monti desertici, Aighpat 40 km SE, 23.07.1963 1♂ 1♀ leg. Giordani Soika coll. Giordani Soika det. J. Gusenleitner, GUSENLEITNER 1973 [intermediate between Taxon 4 and 5].

Russia: *Crimea:* Echkidag, 44.89667°N, 35.12167°E, 07.06.2014 field obs. A. Fateryga; Vicinity of Feodosiya: Lisya Bay, 44.90200°N, 35.15805°E, 02.07.2011 nest record A. Fateryga, 27.06.2013 28.06.2013 11.07.2013 10.06.2014 all field obs. A. Fateryga; Vicinity of Sevastopol: Cape Aya, 44.42367°N, 33.66133°E, 05.07.2004 field obs. A. Fateryga; Vicinity of Veseloye near Sudak, 44.86667°N, 34.88333°E, 02.07.2004 nest record D. Puzanov det. A. Fateryga [all Taxon 1].

Diagnosis. Axilla of mesoscutellum with short blunt lateral projection that only slightly projects over adjacent posterior part of tegula. Frons and clypeus covered with pale, stiff pollen collecting setae, about as long as diameter of median ocellus. In females most of these setae with tiny spherical enlargement at tip (“knob”), in males setae with distal enlargement only present in centre of frons. Cuticula of frons and clypeus dull and densely shagreened. Males with only two oval-shaped tyloids situated ventral on articles A9 and A10 of club-shaped antennae and small spine anterior at distal end of midcoxa. Posterior margin of metasomal tergum VII divided into four lobes.

Separated from *Celonites abbreviatus* by distinctly different colouration of club of antenna: Club has a dark tip, that is, at least distal end of A12 is blackish markedly contrasting on ventral side to adjacent light reddish brown area of antennal club. On dorsal side blackish marking extends usually over distal parts of A11 fading gradually towards proximal end. In *C. abbreviatus* club of individuals from Balkan populations completely orange, in some dark coloured individuals from western populations club becomes darker dorsally, while immediate tip and especially ventral side of A12 remain lighter. Male genital broader than in *C. abbreviatus*, in dorsal view transverse width

of each stipes larger than distance between dorso-medial margins of stipites. Medial process of volsella larger than in *C. abbreviatus*.

Description. *Female.* Colour: Black. The following are weakly yellowish white (Fig. 1a): two spots on frons; small narrow streak on occiput along occipital carina at dorso-lateral corner of head (absent in two specimens); large spot on antero-dorsal angle of pronotum (humeral spot); stripe along dorso-medial (inner) margin of pronotum, slightly enlarged anteriorly, interrupted in the middle by zone of reddish-brown colour; large spot on dorsal mesopleura; median spot on scutellum of moderate size; dorsal and ventral side of propodeal lamella; continuous posterior band on tergum I extending over lateral margin on ventral part of tergum; posterior bands interrupted on each side of middle into median and two lateral markings on terga II–V (in two specimens not completely interrupted on tergum II). Reddish-brown are: distal two third of mandible; labrum; zone in the middle of whitish stripe along dorso-medial margin of pronotum; tegula except small blackish marking at antero-medial margin; distal part of femora, tibiae and tarsi; sternum I; sternum II, becoming slightly darker posteriorly. Dark to blackish brown are: strongly sclerotized parts of labio-maxillary complex; propleura; coxae, trochanters and proximal part of femora; sterna III–V. Antenna with A1–2 black, distal margin of A2 dark brown, A3 proximally dark brown distally reddish brown, A4–11 reddish brown. A12 at least with distal tip black, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, dorsally extending over distal part of A11 (except in one specimen) fading gradually towards proximal end. Wings translucent blackish-brown.

Structure: Head in front view slightly longer than broad. Clypeus a little broader than long; dull with somewhat sparsely weak macropunctuation; densely shagreened; covered with pale, stiff setae arising from weak macropunctures; setae about as long as diameter of median ocellus, with tiny spherical enlargement at tip (“knob”) (Fig. 2), few somewhat shorter; some setae on ventro-lateral corners with distal ends curved towards median axis of clypeus; dorso-lateral vertical parts of clypeus more shiny not shagreened with moderately spaced micropunctures. Frons with very weak moderately spaced macropunctuation; cuticula dull, densely and strongly shagreened; covered with pale outstanding knobbed setae arising from macropunctures; frontal line weak or absent, not raised to form medial carina. Vertex with close macropunctuation becoming more distinct and closely reticulate behind ocelli (Fig. 3), where longitudinal interstices are more strongly raised forming lines; cuticula of interstices shiny, weakly longitudinally striated anterior to ocelli, completely smooth behind them; covered with short setae arising from macropunctures. Compound eye sparsely covered with small setae (Fig. 2). Gena narrow, preoccipital carina sharp. Antennal articles A8–12 forming ventrally flattened club (Fig. 2) slightly more than 2 times as long as broad (viewed dorsally).

Anterior margin of pronotum raised to carina distinctly present along anterior margin of pronotum, especially sharp medially (erroneously termed anterior pronotal carina by Mauss 2013). Short anterior pronotal carina (sensu Carpenter 1988) distinctly present at antero-ventral angle of pronotum running parallel to anterior margin, preceding crenate groove; distance between anterior pronotal carina and anterior

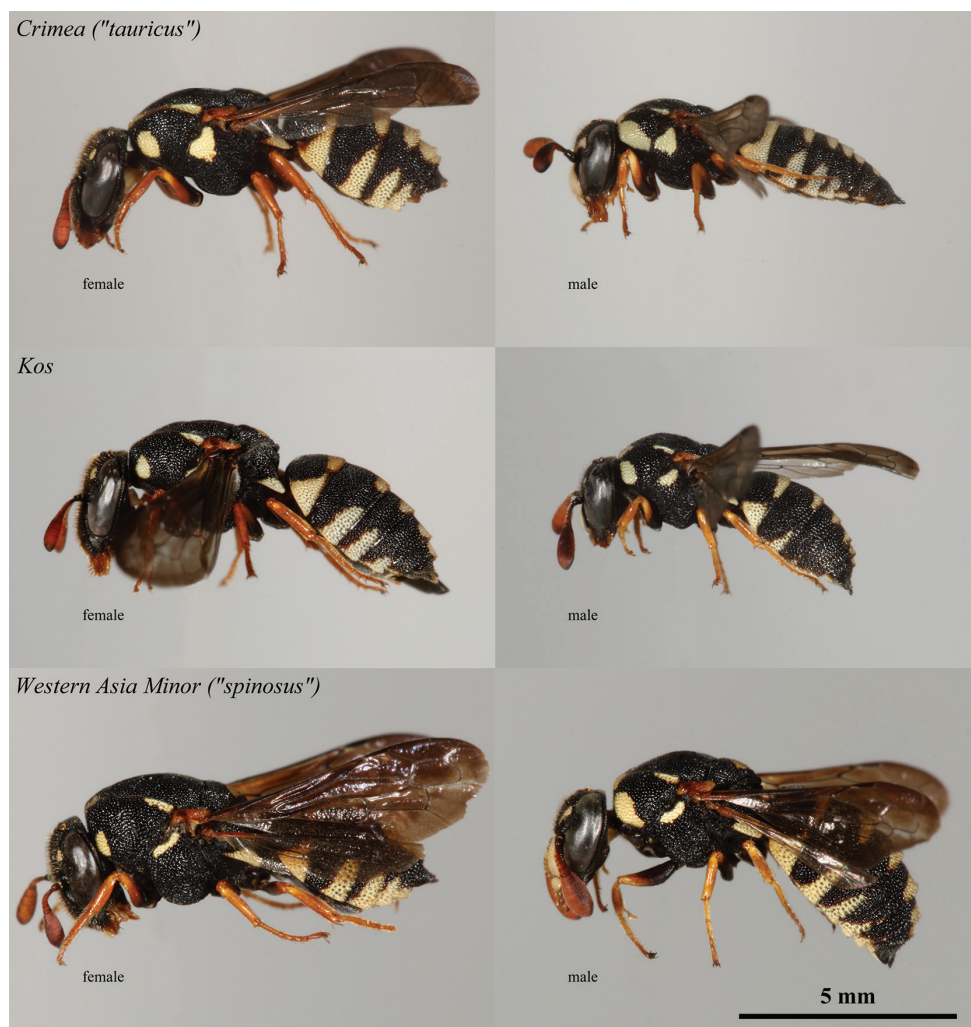


Figure 1a. Specimens of *Celonites tauricus* from populations from different geographical regions in lateral view (insect pins and in a few specimens also protruded proboscis were retouched with photo software to improve comparability of the pictures), Crimea female dbM No. 4305 male dbM No. 4307, Kos female dbM No. 4776 male dbM No. 4790, Western Asia Minor female dbM No. 3585 male dbM No. 3586.

margin of pronotum about width of fore metatarsus. Posterior pronotal carina forms low narrow translucent sinuate crest on humeral angle of pronotum. Pronotum with anterior side nearly vertical; dorso-medially slopes down towards mesoscutum, resulting in slight depression along the dorso-medial margin; posterior margin raised to short carina dorsally in front of upper half of tegula; cuticula shiny, with close, reticulate macropunctuation, interstices smooth, rounded, without micropunctures; horizontally striated due to more strongly raised longitudinal interstices, becoming more coarsely punctured postero-ventrally with interstices raised to knife-like edges. Cutic-



Figure 1b. Specimens of *Celonites tauricus* from populations from different geographical regions in lateral view (insect pins and in a few specimens also protruded proboscis were retouched with photo software to improve comparability of the pictures), Eastern Asia Minor female dbM No. 3629 male dbM No. 3430, South-east of Taurus range female dbM No. 4671 male dbM No. 4690, Cyprus female dbM No. 4717 male dbM No. 4720.

ula of mesoscutum shiny, reticulate with close deep macropunctuation and narrow, distinctly raised interstices. Postero-medial cuticula of mesoscutum and mesoscutellum with longitudinal interstices more strongly raised leading to striated appearance; finely longitudinally wrinkled, postero-medially with, in addition, moderately spaced micropunctures especially along posterior margin. Mesoscutellum laterally with distinct carina along posterior margin, carina medially increasingly reduced so that cuticula of medial lobe continues evenly into the margin. Carina along posterior margin of



Figure 2. *Celonites tauricus* female (dbM No. 4305) head in lateral view, clypeus and frons covered with “knobbed setae”.

metanotum medially with small tooth-like projections. Axilla with short blunt lateral projection only slightly projecting over adjacent posterior end of tegula. Tegula shiny, closely covered by macropunctures except completely smooth central convex area.

Mesepisternum with pronounced epicnemial carina deflexed backwards to run transversely in front of mid coxa; cuticula shiny, with close macropunctuation; horizontally striated by raised interstices; area ventral to scrobal groove coarsely punctured with some interstices strongly raised to knife-like edges forming coarse honeycomb-like sculpture. Process at mesepisternal scrobal groove of moderate size, cuticula on posterior side faintly shiny, finely but densely shagreened with irregularly moderately spaced micropunctuation. Basal horizontal propodeal triangle laterally delimited by a perpendicular declivity, somewhat laterally produced at postero-lateral edge, posteriorly bordered by serrated carina; cuticula shiny, coarsely punctured, interstices almost



Figures 3–6. *Celonites tauricus* **3–4** head in dorsal view **3** female (dbM No. 4304) **4** male (dbM No. 4307) **5–6** metasoma in dorsal view **5** female (dbM No. 4305) **6** male (dbM No. 4307).

knife-like. Posterior surface of propodeum striated by strong vertical cuticula-folds; cuticula shiny, weakly coriaceous and covered with fine pale setae. Cuticula of sides of propodeum and metepisternum shiny, densely horizontally wrinkled. Lateral lamella broad, somewhat convex; lateral margin almost straight; posterior margin straight, not crenate; medially where lamella joins central part of propodeum with a rounded emargination, ventro-medial edge of which produced to a small blunt protrusion; dorsal cuticula of lamella shiny, with moderately spaced macropunctuation, interstices weakly wrinkled. Claws ventral with small tooth.

Metasomal terga with posterior two-fifth separated from anterior part by slight declivity especially laterally (Fig. 5); postero-lateral corners slightly produced; posterior margin of tergum I weakly crenulated, crenulation not produced into spines and not projecting over smooth translucent lower posterior margin of tergum; posterior

margin of terga II–V strongly crenulated (Fig. 5), crenulation produced into distinct spines raised at an angle of approximately 30° projecting distinctly over the translucent lower posterior margin of terga (Fig. 5); cuticula with silken sheen, densely covered with coarse macropunctuation, with about nine micropunctures along median axis of tergum III; single thin seta arises from bottom of each macropuncture, only slightly protruding over rim of puncture; interstices finely shagreened, moderately covered with very tiny, decumbent, pale setae, all setae orientated towards caudal end. Tergum VI with sides converging almost as straight lines, posterior margin with curved protrusion over central two-thirds (Fig. 5), laterally transverse, forming distinct angle to side.

Metasomal sternum I shiny, finely shagreened, with tiny setae but without punctures. Sterna II–V posteriorly with broad stripe of asetose, translucent cuticula adjacent to posterior margin of more strongly sclerotized cuticula; small sparse band of setae along posterior sclerotized margin somewhat projecting over anterior part of translucent strip of cuticula; sclerotized cuticula shiny, finely shagreened, on posterior half of sternum II–V with dense to moderate punctuation of shallow micropunctures from which short pale setae arise, becoming sparser anteriorly, on sternum II antero-laterally with a few shallow macropunctures, on sternum III–V anteriorly with moderate to sparse shallow macropunctuation. Sternum VI tapering towards distal end; with outer margin raised to bulged rim, posteriorly protruded into little blunt spine; cuticula with rather narrow smooth mid-line slightly raised to weak keel at distal end, at sides with strong macropunctures from which pale setae arise.

Male. Colour: Resembles female, except as follows (Fig. 1a). White (less yellowish than female); basal spot on mandible (absent in one specimen); labrum; clypeus except small reddish brown ventral margin; sinuate band at frons laterally extending towards upper inner margin of eye where it bends ventrally into ventral half of ocular sinus (shortly to broadly interrupted medially in two specimens); humeral spot postero-laterally extended to posterior margin of pronotum (except in one specimen), dorso-medially lengthened towards enlarged anterior part of stripe along dorso-medial margin of pronotum (fused with it into complete dorso-anterior pronotum band in two specimens); stripe along lateral part of dorso-medial margin of pronotum interrupted in the middle by zone of black colour; posterior bands on terga II–VI interrupted on each side of middle into median and two lateral markings; broad band on posterior four-fifth of sternum II; (in one specimen postero-lateral spot on each side of sternum III–IV). Antenna with A1–2 black; A3–6 anteriorly with whitish stripe otherwise dark brown at basal end changing continuously into reddish-brown to orange towards A6; A7 reddish-brown to orange; antennal club (A8–12) orange, ventrally with distinct blackish marking on A12 extending on distal parts of A11 well set off from orange of adjacent ventral area, orange on dorso-posterior parts of A8–A12 can be darkened to variable extend.

Structure: Resembles female, except as follows. Clypeus longer than broad, distal margin deeply emarginated; cuticula shiny, with moderately spaced, shallow macropunctuation, interstices on apical third weakly shagreened becoming smooth distally; pale stiff setae arising from macropunctures without distal “knob”, distal ends of setae

frequently curved in distal-medial direction. Frons with moderately spaced macro-punctuation; interstices densely obliquely shagreened; bearing pale stiff setae, mainly with curved distal end, in centre few with distal “knob” (Fig. 4); frontal line can be raised to form small carina or protuberance in centre of frons. Antenna with two oval shaped, perhaps sensory, depressions (tyloids) on concave, ventral side of club, situated within antennal articles A9 and A10. Midcoxa with small but distinct spine at distal end on anterior side close to anterior-medial angle. Posterior margin of tergum VII with three deep emarginations, resulting in two lateral lobes that continue laterally into lateral margins of tergum VII and two lanceolate medial projections (Fig. 6). Sternum VIII with distinct little spine on each side of posterior margin; even concavely emarginated, surface not much sunk in towards emargination (Fig. 7).

Male genitalia as in Figs 7, 8. Genital broad, in dorsal view distance between dorso-medial margins of stipites smaller than transverse width of adjacent part of stipes. Dorso-medial shovel-like lobe of harpide large, densely covered ventrally with long setae. Dorso-posterior margin of stipes only slightly curved, without distinct dorso-medial concavity. Stipes with dorso-medial margin running nearly parallel to sagittal plane. Sides of stipites converging continuously anteriorly towards cupula. Volsella large and broad reaching antero-medial margin of dorso-medial lobe of harpide; dorsal area with strongly sclerotized large, dark tubercles; distances between tubercles moderate; medial process large, trapeziform due to more or less truncate apex, continuing posteriorly into posterior process at a blunt angle. Sides of thyrsos only slightly converging towards posterior (apical) end of aedoeagus. Each thyrsos continues anteriorly into apodema thyrsos with a distinct outwardly directed curve. On ventral side cupula medially clearly protruded anteriorly, completely projecting over dorsal margin of cupula in ventral view of genital capsule.

Measurements. Measurements of the exoskeleton are listed in Table 1.

Geographic distribution and variation. The geographic range of *Celonites tauricus* is shown in Fig. 9. Based on morphological differences six intraspecific taxa can be separated (Table 2, Figs 10–13) belonging to different geographic regions (Fig. 9). Distinct population groups exist in the Crimea, Kos, western Asia Minor, eastern Asia Minor up to the Elburs mountains, south-east of the Taurus range and in Cyprus.

Individuals from western Asia Minor are large and strongly built (Fig 1a), their metasomal terga are coarsely punctured and bear distinct pointed spines at the posterior end that project well beyond the lower posterior margin (Fig. 10). The specimens are dark with reduced whitish markings and reddish brown legs (Fig. 1a). The posterior bands on the metasomal terga are laterally interrupted, usually from T2 to T5 but at least from T3 to T5. The population from the Crimea differs only slightly in that the individuals are a little less robust and the terga are somewhat less coarsely punctured. The population from Kos varies from the mainland population in that the crenulation along the posterior margin of the metasomal terga is reduced to short, weakly pointed, horizontal processes that do not project beyond the posterior margin (Fig. 12). The members of the populations to the south-east of the Taurus range are distinguished from individuals from western Asia Minor by their yellowish colour and considerably

Table 1. Measurements of the exoskeleton of imagines of *Celonites tauricus* from the Crimea (x = median; min = minimum, max = maximum; measurements were made with a Wild M3 stereomicroscope with maximum magnification 80×, maximum accuracy 0.011 mm, all distances in mm).

Parameter	Female				Male			
	x	min	max	n	x	min	max	n
lateral ocelli distance	0.42	0.40	0.45	5	0.39	0.32	0.41	5
front./lat. ocellus distance	0.17	0.14	0.17	5	0.14	0.11	0.14	5
compound eyes distance	1.28	1.17	1.33	5	1.06	0.92	1.10	5
A1 length	0.20	0.19	0.21	5	0.19	0.18	0.20	5
A3 length	0.30	0.25	0.31	5	0.23	0.21	0.25	5
A3 width	0.12	0.10	0.12	5	0.11	0.11	0.13	5
A4-5 length	0.14	0.11	0.21	5	0.19	0.17	0.21	5
A8-12 length	0.79	0.77	0.86	5	0.97	0.92	1.05	5
A8-12 width	0.37	0.35	0.39	5	0.47	0.44	0.51	5
antennal sockets distance	0.74	0.66	0.76	5	0.50	0.47	0.53	5
clypeus max. width	1.12	1.03	1.14	5	0.84	0.80	0.88	5
clypeus apical width	0.48	0.45	0.52	5	0.42	0.39	0.44	5
clypeus length	0.95	0.85	0.97	5	0.73	0.68	0.76	5
mesonotum width	2.81	2.55	2.90	5	2.32	2.16	2.46	5
mesoscutum length	2.07	1.82	2.13	5	1.51	1.41	1.68	5
wing length	5.61	5.11	5.68	5	4.90	4.83	5.04	3
R+Sc length	3.13	2.85	3.22	5	2.60	1.71	2.80	5
number of hamuli	10	8	12	5	10	8	10	5
femur I length	1.50	1.41	1.55	5	1.19	1.14	1.26	5
tibia I length	0.97	0.96	1.01	5	0.84	0.78	0.88	5
metatarsus I length	0.58	0.54	0.61	5	0.45	0.41	0.46	5
tergum I width	2.85	2.55	2.99	4	2.44	2.30	2.60	5
tergum I length	1.26	1.12	1.31	5	0.99	0.90	1.07	5
tergum II width	2.92	2.66	2.99	4	2.35	2.30	2.55	5
total length	7.8	7.1	8.3	5	7.5	6.8	7.8	4

more extensive markings (Fig. 1b), including a spot on the clypeus of the females. The individuals from eastern Asia Minor are smaller and daintier than individuals from the western populations. The macropunctures on their metasomal terga are much smaller and the crenulation along the posterior margins of the terga consists of short, horizontal, truncated processes (Fig. 13). The light colour is yellowish and the markings are more extensive than in specimens from the western populations with, at least, complete posterior bands on the terga T1 to T3 (Fig. 1b). Populations with at least some specimens intergrading between the taxa from western and eastern Asia Minor exist in a zone extending from the Taurus range in the south-west to north-east Turkey and Armenia (Fig. 9). Such individuals reveal an intergrading pattern of various morphological and colour traits, but also transient characters like, for example, little spines along the posterior margins of the metasomal terga or macropunctures of intermediate size on the metasomal terga. Likewise there are populations in south-east Turkey with

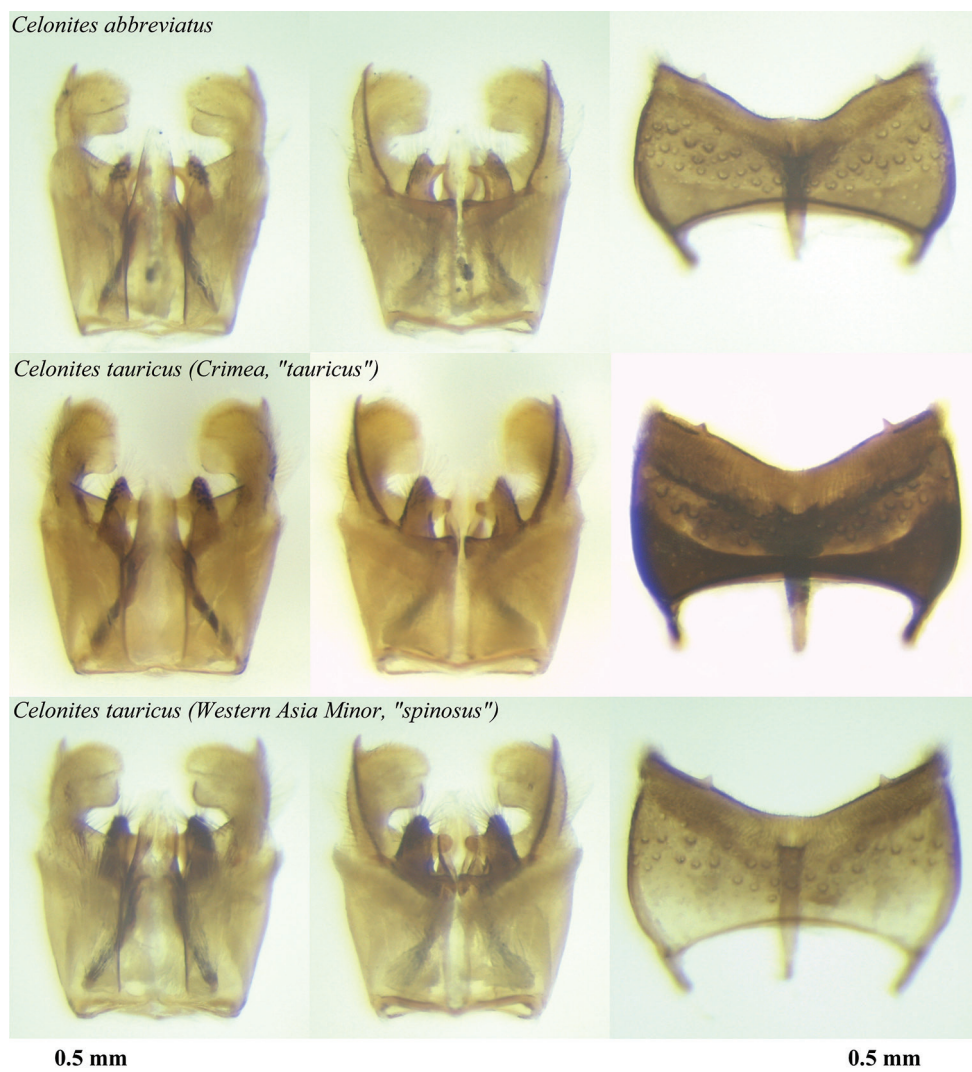


Figure 7. Male genitalia in dorsal (left) and ventral view (middle) and metasomal sternum VIII of male in ventral view (right) of *Celonites abbreviatus* (dbM No. 3451), *C. tauricus* from the Crimea (dbM No. 4307) and *C. tauricus* from Western Asia Minor (dbM No. 3431).

specimens, intergrading between the taxon from eastern Asia Minor and the taxon to the south-east of the Taurus range (Fig. 9), that are characterized by little spines along the posterior margins of the metasomal terga and a yellowish spot on the clypeus of the females. The specimens from Cyprus are distinguished by their small size, comparatively dark coloured dorsal side of the antennae (Fig. 1b), deeper yellow colour, and the crenulation of the metasomal terga that, at least laterally, consists of short but more or less pointed processes.

Table 2. Comparison of the morphological characters of six intraspecific taxa of *Celonites tauricus* from different geographic regions of its range.

Taxon No.	1 Crimea	2 Kos	3 Western Asia Minor	4 Eastern Asia Minor	5 SE of Taurus range	6 Cyprus
antenna	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club; four specimen with dorsal side dark reddish brown	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club; one specimen with dorsal side dark reddish brown	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club; one specimen with dorsal side dark reddish brown	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light proximal area of antennal club, on dorsal side fading gradually into dark reddish brown to dark brown colour of proximal area of club
shade of light colour	faintly yellowish-white	faintly yellowish-white	faintly yellowish-white; in two specimens light yellowish	light yellowish to yellow	light yellowish to yellow	light yellow to yellow
clypeus (female)	black; one specimen with two tiny spots	black	black	black	black with dorsal spot, that may reach the dorsal margin and can expand on ventral half of clypeus, at minimum little isolated spot	black
tempora	short stripe to completely black	short stripe	short stripe to completely black	long stripe to completely black	long stripe	long to short stripe
tegula	reddish brown	reddish brown	reddish brown	light yellowish to yellow with small reddish brown translucent centre or reddish brown	light yellowish to yellow; in two specimens with small reddish brown translucent centre	light yellowish to yellow with small reddish brown translucent centre
pronotum	narrow stripe along dorsal margin, brownish interrupted in the middle of dorso-lateral margin	narrow stripe along dorsal margin, blackish interrupted in the middle of dorso-lateral margin; in one specimen brownish interrupted	narrow stripe along dorsal margin, brownish or blackish interrupted in the middle of dorso-lateral margin	continuous stripe along dorsal margin; in three specimens brownish interrupted in the middle of dorso-lateral margin	continuous stripe along dorsal margin; in two specimens brownish interrupted in the middle of dorso-lateral margin	broad continuous stripe along dorsal margin

Taxon No.	1 Crimea	2 Kos	3 Western Asia Minor	4 Eastern Asia Minor	5 SE of Taurus range	6 Cyprus
scutellum	medium-sized medial spot	medium-sized medial spot	medium-sized to small medial spot	medium-sized or large laterally expanding medial spot; in one specimen completely black	large laterally expanding or medium-sized medial spot	medium-sized medial spot
metasomal terga	continuous posterior band on tergum I, posterior band on terga II–V laterally interrupted; in two specimens tergum II with continuous band; in seven specimens on tergum I interrupted; in one specimen band on tergum II continuous; in six specimens posterior band on tergum V reduced to medial stripe; in three specimens posterior band on terga III–V reduced to medial stripe	posterior band on terga I–V laterally interrupted; four specimens with continuous band on tergum I	continuous posterior band on tergum I, posterior band on terga II–V laterally interrupted; in two specimens tergum II with continuous band; in seven specimens on tergum I interrupted; in one specimen band on tergum II continuous; in six specimens posterior band on tergum V reduced to medial stripe; in three specimens posterior band on terga III–V laterally interrupted	broad continuous posterior band on terga I–V; in three specimens on tergum V laterally interrupted; in three specimens on terga IV–V laterally interrupted	broad continuous posterior band on terga I–V; in two specimens on tergum V laterally interrupted; in two specimens on terga III–V laterally interrupted	broad continuous posterior band on tergum I–V; in one specimen on tergum V laterally interrupted
metasomal tergum VI (female)	black	black	black	black	black, basally with narrow lateral stripe; in one specimen completely black	black, basally with narrow lateral stripe; in one specimen completely black
legs	reddish brown	reddish brown	reddish brown	reddish brown	yellowish	yellowish
size, physique	large, strong	large, strong	large, very strong to strong	medium-sized to small, more dainty	large, strong	small, more dainty
macropunctuation of terga II–IV	coarse	coarse	coarse (in specimens from Antalya very coarse)	moderate	very coarse to coarse	moderate
Σ macropunctures along visible part of sagittal axis of tergum III	10	8–10	8–10	10	7–8	10

Taxon No.	1 Crimea	2 Kos	3 Western Asia Minor	4 Eastern Asia Minor	5 SE of Taurus range	6 Cyprus
sculpture of posterior margin of tergum II–IV	crenate, crenulation produced into distinct spines raised at an angle of approximately 30° distinctly projecting beyond the translucent lower posterior margin of terga (spines approximately as long as diameter of macropunctures)	crenate, crenulation consists of short ± pointed horizontal processes, posteriorly not projecting beyond the translucent lower posterior margin; in one specimen a few processes on tergum III projecting beyond posterior margin	crenate, crenulation produced into distinct spines raised at an angle of approximately 30° distinctly projecting beyond the translucent lower posterior margin of terga (spines approximately as long as diameter of macropunctures); in seven specimens spines projecting only slightly beyond posterior margin	crenate, crenulation consists of very short horizontal processes, posteriorly truncated not projecting over the translucent lower posterior margin so that the translucent margin remains completely exposed	crenate, crenulation produced into distinct spines raised at an angle of approximately 30° distinctly projecting beyond the translucent lower posterior margin of terga (spines approximately as long as diameter of macropunctures); in one specimens spines projecting only moderately beyond posterior margin	crenate, at least laterally crenulation consists of short horizontal ± pointed processes, posteriorly not projecting beyond the translucent lower posterior margin, medially processes posteriorly truncate to variable extend

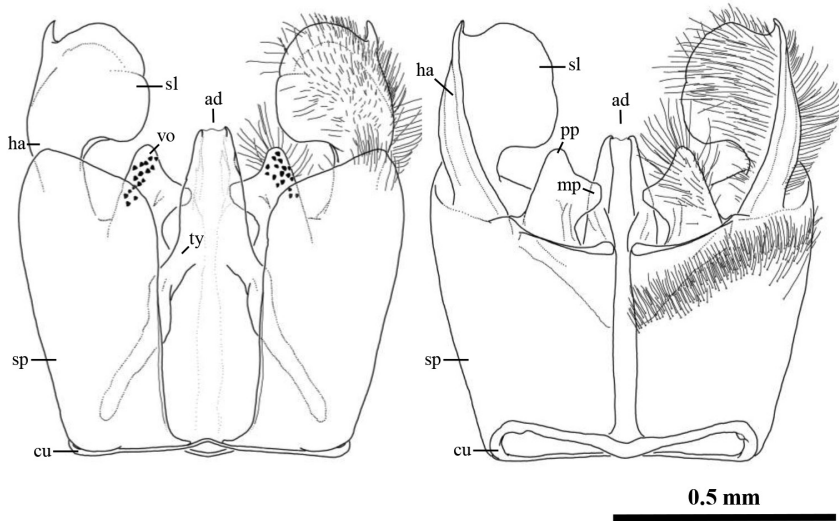


Figure 8. Male genitalia of *C. tauricus* (dbM No. 4307) in dorsal (left) and ventral view (right). (Setae only shown on one side of each drawing; Nomenclature follows that of Birket-Smith (1981): ad, aedoeagus; cu, cupula; ha, harpide; mp, medial process of volsella; pp, posterior process of volsella; sl, shovel-like dorso-medial lobe of harpide; sp, stipes; ty, thyrsos; vo, volsella).

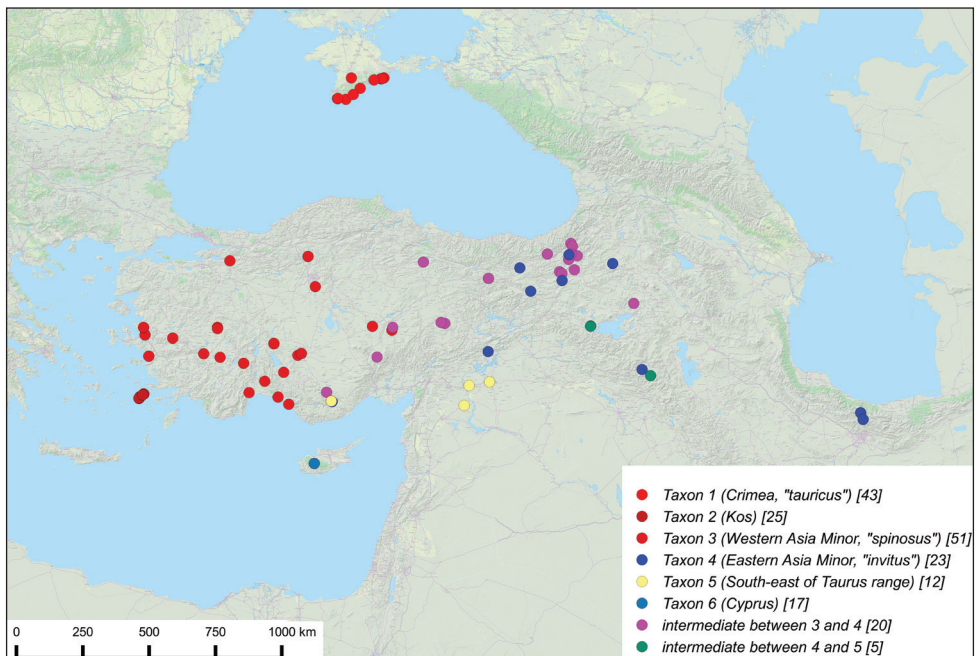
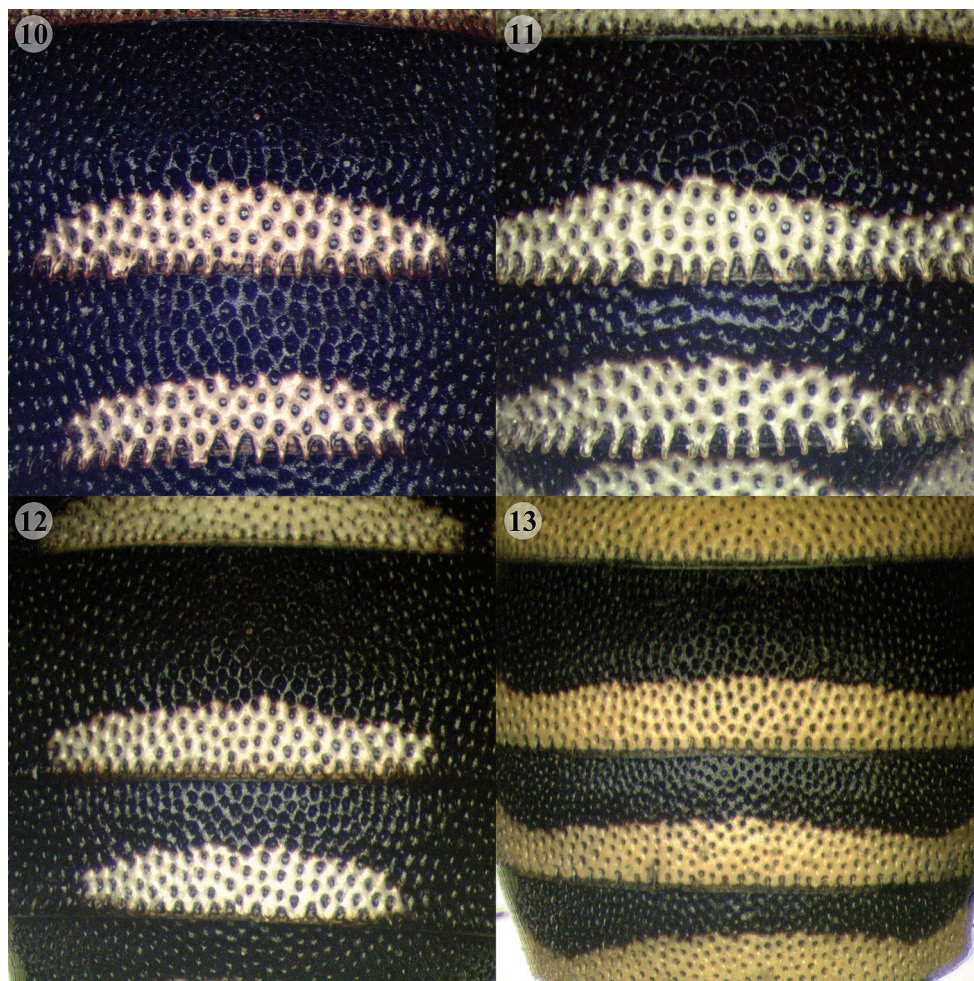


Figure 9. Geographical records of *Celonites tauricus*. The intraspecific taxon affiliation of the local populations is marked by different colours; a population is regarded as “intermediate” when at least one individual shows intermediate character states. [OpenStreetMap contributors]



Figures 10–13. Cuticula structure of metasomal terga II and III of females belonging to different intraspecific taxa of *Celonites tauricus* in dorsal view. **10** Western Asia Minor (dbM No. 4681) **11** South-east of Taurus range (dbM No. 4673) **12** Kos (dbM No. 3607) **13** Eastern Asia Minor (dbM No. 3653).

Bionomics of *Celonites tauricus*

Habitat

Eight out of nine localities of *Celonites tauricus* in the Crimea are situated in the habitat zone of submediterranean vegetation of the south coast (Fig. 14), and it can be presumed that the taxon is distributed along the whole south coast of the peninsula. A single record comes from the zone of forest steppes of the Crimean foothills. In the Crimea *C. tauricus* is confined to dry light forests and shrubs or rocky steppe and phrygana slopes (Fig. 15). The highest abundance of the taxon was recorded in Lisya Bay where in some years 1.5–2 foraging females per 100 m² were observed on average



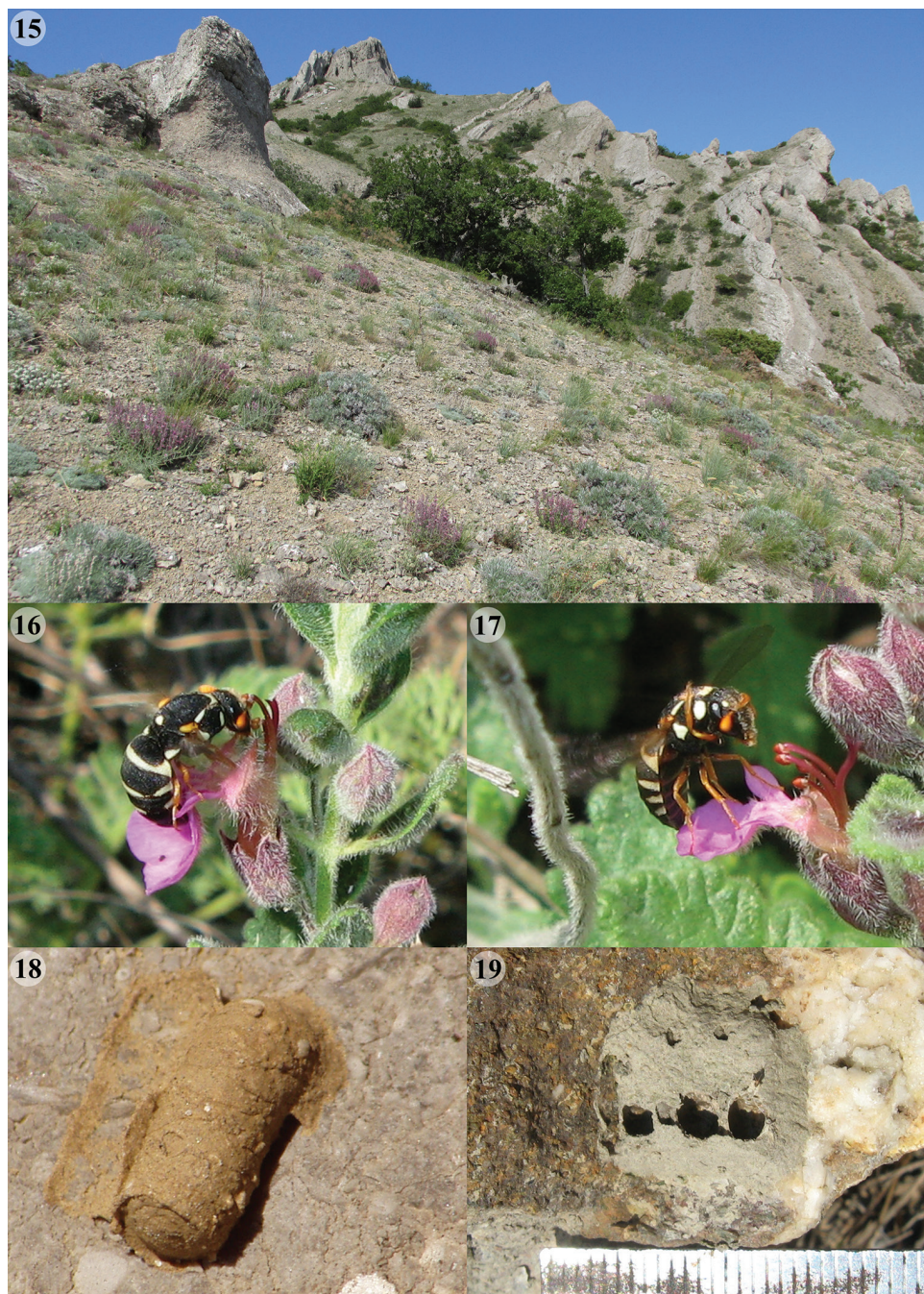
Figure 14. Distribution of localities of *Celonites tauricus* in different habitat zones in the Crimea.

at the same time (the size of the whole sample area was 2500 m²). The distribution of *Celonites tauricus* in the Crimea seems to be not only affected by the distribution of *Teucrium chamaedrys*, as its main forage plant, since this plant is very common and abundant on the entire peninsula. Probably *C. tauricus* does not occur both in higher altitudes of the mountains and in the plains of the Crimea for climatic reasons, since e.g. the mean winter temperatures are lower in these regions in comparison with the foothills and slopes on the south coast (Ved' 2000).

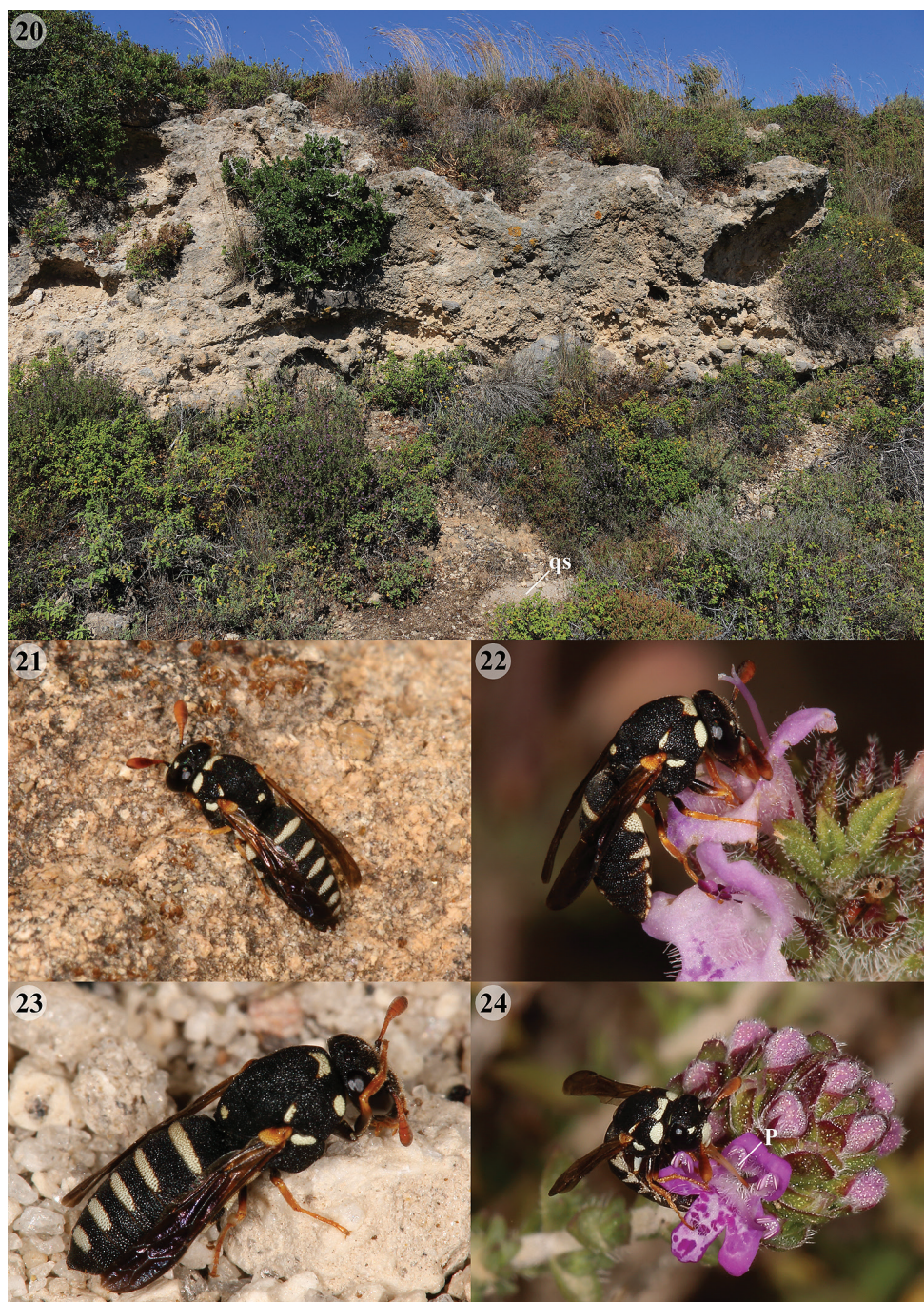
In Kos *Celonites tauricus* was found in areas from 20 to 110 m above sea level that were covered with phrygana vegetation characterized by larger patches of flowering plants of *Satureja thymbra* (Fig. 20).

Flower associations

Flower visiting records of *Celonites tauricus* are summarized in Table 3. In all investigated populations males and females of *C. tauricus* were exclusively recorded from flowers of Lamiaceae, but there are distinct regional differences with regard to the species of Lamiaceae utilized. In the Crimea females of *Celonites tauricus* visiting flowers were primarily observed to collect pollen and nectar from flowers of *Teucrium chamaedrys* (Figs 16, 17). This flower association was confirmed at all localities where *C. tauricus* was studied and in every study period. Occasionally females were also recorded at



Figures 15–19. Bionomics of *Celonites tauricus* in the Crimea **15** Habitat **16** Female visiting flower of *Teucrium chamaedrys* **17** Female brushing pollen from the frons towards the mouthparts by alternating movements of the fore legs subsequent to regular flower visit at *Teucrium chamaedrys* **18** Nest under construction on the underside of a stone (brood cell on the left removed) **19** Old nest attached to the underside of a stone with emergence holes of *Celonites* imagines in the walls of three brood cells.



Figures 20–24. Bionomics of *Celonites tauricus* in Kos **20** Habitat (qs = potential quarry site of females) **21** Male perching on stone **22** Male visiting flower of *Satureja thymbra* **23** Female standing on the ground near a plant of *Satureja thymbra* brushing with the fore legs over her frons **24** Male visiting flower of *Thymus capitatus* (p = protruded proboscis).

Table 3. Flower-visiting records of males and females of *Celonites tauricus* from different geographic regions.

plant taxon	Σ sightings of flower visiting individuals					
	Crimea		Palandöken		Kos	
	♀	♂	♀	♂	♀	♂
Lamiaceae						
<i>Satureja thymbra</i> L.					52	11
<i>Teucrium chamaedrys</i> L.	35	10				
<i>Teucrium polium</i> L.	1	2				
<i>Thymus capitatus</i> (L.) Hoffmanns. & Link					1	6
<i>Thymus tauricus</i> Klovov & Des.-Shost.	8					
<i>Ziziphora clinopodioides</i> Lam.			1*			
other plant taxa						

*dbM No. 2795

flowers of *Thymus tauricus* and *Teucrium polium*. However, visiting flowers of these two plant species is probably not typical for *C. tauricus* in the Crimea and was only observed in Lisy Bay in 2013. In that year the spring was unusually dry and flowering plants of *Teucrium chamaedrys* were very scarce whereas flowering *Thymus tauricus* were much more abundant and widespread. In five out of the eight visits to *Thymus tauricus* and also in the visit to *Teucrium polium* the females switched over to these plants from *Teucrium chamaedrys* and afterwards returned to visit flowers of *T. chamaedrys*. Females of *C. tauricus* were only observed to visit plants of *Thymus tauricus* growing in close proximity to flowering plants of *Teucrium chamaedrys*. Males of *C. tauricus* also were observed mainly at flowers of *T. chamaedrys* at Cape Aya in 2004 and in Lisy Bay in each year of observation. In contrast, the Kos population was mainly associated with *Satureja thymbra* and to minor extend also with *Thymus capitatus*, though in addition, at least at some localities two *Teucrium* species (*T. divaricatum* and *T. polium*) were in flower. However, the proportion of visits to *Thymus capitatus* may increase during the on-going flight season, since at the end of the investigation period *Th. capitatus* had just started flowering whereas *S. thymbra* was nearly over.

During flower visits at *Satureja thymbra* and *Teucrium chamaedrys* the females always stood on the lower lip of a flower and took up nectar and pollen simultaneously. The proboscis was protruded deeply into the corolla tube while the female performed at a high frequency slight back and forth movements of the anterior parts of her body, rubbing her head over the nototribic anthers (Figs 16, 25, 26). In this manner pollen grains were removed from the pollen sacs with the stiff knobbed setae on the frons, which form a pollen-collecting apparatus, accumulating on frons and clypeus (Fig. 27). The median duration of the visits of females to flowers of *Satureja thymbra* was 2.6 s (range 0.8–6.3 s, n = 43). At *Thymus capitatus* the flower visiting behaviour was very similar to the behaviour described above, except that the female orientated her body axis at an angle to the longitudinal plane of the zygomorphic flower both to the left and to the right so that her frons was directed towards the anthers that are situated



Figures 25–30. Flower visiting behaviour of *Celonites tauricus* at *Satureja thymbra* in Kos **25–26** Regular flower visit for the simultaneous uptake of nectar and pollen with the proboscis protruded into the corolla tube and the knobbed setae on the frons making contact with the nototribic anthers **25** Viewed from ventral-posterior **26** Viewed from dorso-lateral **27** Proboscis partly retracted shortly before leaving the flower, in lateral view **28–29** Female standing on the lower lip and an adjacent flower brushing pollen from her frons with alternating movements of her fore legs **30** The fore legs are brought between the mouthparts for pollen ingestion during pollen transfer from the frons by brushing movements towards the mouthparts.

further laterally in this flower. Periodically flower visiting was interrupted and the pollen grains were transferred from the frons to the mouthparts by alternating brushing movements of the fore legs (Figs 17, 28, 29) which were brought between the mouth-

parts while the pollen was being ingested (Fig. 30). This frons brushing behaviour took place on flowers (Figs 17, 28, 29) and also on the ground in the close vicinity of the plants (Fig. 23).

On the Crimea, individual females of *C. tauricus* usually visited flowers over a period of 20–40 minutes. After about 10–15 minutes they regularly interrupted flower visiting and alighted on stones or grass. They remained there for several minutes repeatedly regurgitating and withdrawing again a mass of pollen and nectar that became visible as a drop of liquid between the mouthparts. This behaviour probably served to thicken the pollen and nectar mass.

During flower visits males always inserted their proboscis into the corolla tube (Figs 22, 24) indicating the uptake of nectar. At flowers of *Satureja thymbra* males, like the females, performed slight back and forth movements in addition rubbing with their frons over the anthers, so that they probably collected pollen as well. This rubbing behaviour was not observed at flowers of *Thymus capitatus*.

More than 99% of the pollen from the crops of females from Kos consisted of hexacolpat pollen grains of Lamiaceae. This pollen type occurs in several genera of Lamiaceae including *Satureja* and *Thymus*.

Nesting

Three nests of *Celonites tauricus* were recorded in the Crimea. The first nest was investigated on 2 July 2004 in the vicinity of the village of Veseloye near Sudak. The nest site was a rocky slope with steppe vegetation predominated by *Melica taurica* K. Koch and *Teucrium chamaedrys* along with individual trees of *Celtis glabrata* Steven ex Planch. The nest was located in a small cavity underneath a stone situated in the shadow of one of the *Celtis* trees. The nest under construction contained two brood cells. The cells were placed on the underside of the stone and were made of fine clayey soil with a few tiny stones (Fig. 18). The cells were cylindrical, rounded at the closed (basal) and truncate at the open (apical) end (Fig. 18) measuring 9 mm in length and 4 mm in width. The cell wall was 0.25 mm thick. The outer cell surface, typically for *Celonites*, showed a distinct “fish scale” pattern. The first cell was sealed with mud. The cell seal was positioned slightly in from the edge of the cell opening and was of the same thickness as the cell wall. The cell was provisioned with a pollen loaf and contained an egg at the basal end. Basally the loaf was situated close to the egg, while the apical end of the loaf was further away from the seal resulting in an empty space between the pollen loaf and the seal at the apical end of the cell. The pollen loaf was attached to the cell wall with numerous spike-like projections. The second cell was open and contained the female owning the nest.

The second nest was studied on 2 July 2011 in Lisya Bay. The nest site was a slope covered with phrygana vegetation predominated by *Elytrigia caespitosa* subsp. *nodosa* (Nevski) Tzvelev, *Atraphaxis replicata* Lam., *Thymus tauricus* and *Teucrium chamaedrys*. The nest was also situated in a small cavity on the underside of a small stone. The

nest was old and contained three cells covered with an additional layer of mud forming a nest covering (Fig. 19). All cells were sealed at the apical end and had a large frontal opening that covered the apical third of the cell, which had probably been made by an emerging imago of *Celonites tauricus* (Fig. 19). Every cell contained an empty, thin, whitish *Celonites* cocoon and a meconium.

The third nest was found in Lisya Bay on 11 July 2013. It was also situated on the underside of a small stone and it was also old. The nest consisted only of a single cell covered with an additional layer of mud. The cell was sealed at the apical end and had a frontal opening at the apical part, which had probably been made by an emerging imago of *C. tauricus*. Inside the cell were a *Celonites* cocoon and meconium.

Females of *C. tauricus* were never observed at water collection sites. Therefore the mud used for cell construction was probably made by mixing clay particles with regurgitated nectar.

Male behaviour

Males performed patrol flights along the preferred forage plants of the females, i.e. *Teucrium chamaedrys* in the Crimea as well as *Satureja thymbra* and *Thymus capitatus* in Kos, and over nearby stones in a low constant flight. Patrolling was regularly interrupted by perching in the immediate vicinity of the forage plants, mainly on stones but also on the ground or on the plants themselves (Fig. 21). Moreover, patrolling was occasionally interrupted by flower visits. On one occasion a male was observed pouncing on a female resting on a stone between consecutive flower visits. The male alighted on the back of the female for a short moment and flew off again. On another occasion a male pounced on a female while it was visiting a flower of *Satureja thymbra*. Courtship and copulation were not observed.

Phenology

The species is univoltine. In the Crimea males were observed from 5 June to 8 July and females from 7 June to 31 July indicating slight proterandry.

Discussion

The rediscovered *Celonites* taxon from the Crimea, assigned to *C. abbreviatus tauricus*, can be consistently identified as a member of the *Celonites abbreviatus*-complex (sensu Mauss 2013) by the existence of a pollen collecting apparatus composed of knobbed setae on clypeus and frons, the outstanding autapomorphic character of this group (Mauss 2013). Moreover, the Crimean taxon also shares all apomorphies of the *C. abbreviatus*-group (Mauss 2013), that is, the males have only two oval-shaped tyloids

on the antennal club, they bear a small spine at the distal end of the midcoxa, their tergum VII is posteriorly markedly lobed and the posterior margin of sternum VIII of the males is specifically emarginated.

Within the *Celonites abbreviatus*-complex the members of the taxon *Celonites a. tauricus* from the Crimea are in the main similar to individuals of *Celonites spinosus* from western Asia Minor in both the colouration and morphology of the exoskeleton and in the structure of the male genitalia. Because of this high degree of similarity it is hypothesized that both taxa are not reproductively isolated from each other and thus belong to the same biospecies (sensu Mayr 1967). The existence of populations of *Celonites* in Central and East Anatolia that include at least some individuals with intermediate characters between typical *spinosus*- and typical *invitus*-forms indicate that these eastern populations are not reproductively isolated from the western *spinosus*-like populations. This is in agreement with the findings of Gusenleitner (1985), who as a result formally synonymized both taxa. In the same way, the distinct yellowish populations that occur to the southeast of the Taurus range are connected to the northeastern *invitus*-form by populations that contain individuals with intermediate characters in southeast Anatolia. For that reason it can be hypothesized that they also are not reproductively isolated from the other taxon and therefore belong to the same biospecies. All members of this biospecies are characterized by an antennal club with dark tip and male genitalia with a broad stipes and a large medial process of the volsella. The colour pattern on the ventral side of the antennal club that is in contrast richly coloured might be associated with mate recognition, since it has been demonstrated by Mauss and Müller (2014) that in an allied *Celonites* species the tips of the male antennae are held above the female compound eyes for a short time during mating prior to the insertion phase. Therefore the colour pattern of the club could be part of a mating signal and therefore may act as a reproductive isolation mechanism. This is also likely for the observed differences in the proportion and structure of the male genitalia. Since the *Celonites* populations from Kos and from Cyprus are mainly similar in regard to these particular characters there is no evidence that they may be reproductively isolated from the mainland populations. For that reason, they are regarded as allopatric populations of a single biospecies. Due to priority the name of this biospecies has to be *Celonites tauricus*.

Celonites tauricus resembles *Celonites abbreviatus* in many characters and is therefore in all probability closely related to this species, as already established by Gusenleitner (1966). Despite some differences in specific characters of particular populations, both taxa differ mainly in the colour pattern on the ventral side of the antennal club and in the proportion of the stipes and the form of the volsella. As discussed above these characters are associated with the mating system and might act as a reproductive isolation mechanism. It is of note that neither *Celonites abbreviatus* nor any other species of the *C. abbreviatus*-complex could be demonstrated to occur within the geographic range of *C. tauricus*. All former records of *C. abbreviatus* from this region, for which voucher specimens were examined, turned out to belong to *C. tauricus*. Therefore *C. tauricus* and *C. abbreviatus* seem to be allopatric taxa that have evolved from a common stem species.

The areas inhabited by *Celonites tauricus* in the Crimea and in Kos are comparable to habitats of *Celonites abbreviatus* in Central Europe (Bellmann 1995, pers. obs.), southern France (pers. obs.), Spain (pers. obs.) or the Peloponnese (Mauss 2006). The flower associations of *C. tauricus* are very similar to those of *C. abbreviatus*, in that both taxa specialize in utilizing Lamiaceae with nototribic flowers that serve as the sole pollen source (Bellmann 1984, 1995, Mauss 2006, Müller 1996, Schremmer 1959). Moreover, as in *C. tauricus* in the Crimea, a *Teucrium* species seems to be of particular importance for the occurrence of *C. abbreviatus* in Central Europe (Bellmann 1995), and *Satureja thymbra*, which is the main forage plant of *C. tauricus* in Kos, is also the mainly visited plant of *C. abbreviatus* in the Peloponnese (Mauss 2006). The flower visiting behaviour of both species appears identical (cf. Bellmann 1984, 1995, Mauss 2006, Müller 1996, Schremmer 1959). The construction of the brood cell, the position and shape of the egg and the provision, as well as the frontal orientation of the emergence hole in old cells of *C. tauricus* are similar to *C. abbreviatus* (cf. Bellmann 1984, 1995). Nests constructed on the underside of stones, as in *C. tauricus*, do also exist in *C. abbreviatus* (Bellmann 1995), though nests of the latter, at least in Central Europe, are more frequently aerial, attached to stones or twigs (Bellmann 1995). Finally, males of both taxa search for females in the vicinity of forage plants (cf. Mauss 2006). In summary, the ecology and behaviour of *C. tauricus* and *C. abbreviatus* seem to be similar in all investigated parameters and their ecological niches are probably mainly identical. This is in congruence with the perceived allopatric distribution of both taxa, as their comparable ecological requirements should prevent sympatry.

The observed distribution pattern of the intraspecific taxa of *C. tauricus* in Asia Minor (Fig. 9) can be biogeographically explained by the isolation of small populations in cold periods of the Pleistocene in secondary glacial refuges that have already been characterized by Lattin (1967). The ancestors of the western *spinosus*-like populations probably subsisted in the eastern part of the Pontomediterranean refuge, the ancestors of the populations south-east of the Taurus range in the Syrian refuge and the ancestors of the eastern *invitus*-like populations in the Caspian refuge sensu Lattin (1967). As a result of the post glacial warming the three populations expanded their range again and hybridized with each other where they secondarily came into contact as is indicated by individuals with intergrading characters.

It can be hypothesized that *C. tauricus* colonized the Crimea from the west of Asia Minor, since the Crimean population of *Celonites tauricus* is morphologically much more similar to the *spinosus*-like populations of *C. tauricus* from the western parts of Asia Minor than to the *invitus*-like populations in the east. Probably, the colonization took place in a phase of low sea-level when today's extensive western shelf of the Black Sea was situated above the level of the ancient Black Lake, resulting in a large area along the western coast of the Black Lake covered with Sub-Mediterranean vegetation that connected the Sub-Mediterranean areas on the Crimea with the north-west end of Asia Minor (Yena et al. 2005, and references therein). During the Würm glacial this western costal zone was an extensive refuge harbouring the Mediterranean flora (Yena et al. 2005). Major et al. (2006) showed that intense meltwater pulses at the end of the

Würm glacial between 18 and 16 ka BP raised the level of the Black Lake, probably to its outflow, so that lower parts of the shelf were drowned. But during the following warm post glacial periods of the Bølling-Allerød (15–13 ka BP) and the Preboreal (11.6–9.4 ka BP) the complete shelf was again well above the sea level (Major et al. 2006). Consequently it seems likely that finally this entire area was inhabited by the western *spinosus*-like population of *C. tauricus*. The range was disrupted when the Black Sea shelf was flooded with water from the Marmara Sea as a result of the post glacial rise of the global sea level about 9.4 ka BP (Major et al. 2006). The flooding led to the separation of the recent relict population on the Crimea from the main *spinosus*-like population of *C. tauricus* in the western part of Asia Minor. A comparable biogeographical pattern exists, for example, in *Pinus brutia* Ten. (Yena et al. 2005) and some species of spiders (Kovblyuk 2014). Similarly, the population of *C. tauricus* in Kos probably has been isolated from the *spinosus*-like mainland population by the post-glacial rising of the sea level of the Aegean that separated the island from Asia Minor.

In contrast, Cyprus is a primarily oceanic island of volcanic origin, that probably has been connected to the mainland only for a period of approximately 600000 years during the Messinian Salinity Crisis of the upper Miocene (5.9–5.3 Ma BP), when a land bridge existed that joined the island with continental areas of Asia Minor and Syria (Poulakakis et al. 2013, and references therein). Since the re-flooding of the Mediterranean basin in the early Pliocene Cyprus has been separated from Asia Minor as the nearest mainland by a distance of at least 30 km (Hadjisterkotis et al. 2000). Therefore, the existence of a morphologically distinct Cyprian population of *C. tauricus* is probably the result of dispersal, but it is uncertain whether this occurred over a land bridge or transmarine, as the divergence time from the mainland population is unknown. Based on morphological similarity the migration probably started from an eastern, more *invitus*-like population of *C. tauricus*.

Acknowledgments

We are greatly indebted to Sergey P. Ivanov and Dmitriy V. Puzanov (Taurida Academy of the Vernadskiy Crimean Federal University, Simferopol) for help with collecting material in the field; to Alexander V. Antropov (Zoological Museum of the Lomonosov Moscow State University, Moscow) for help with access to the collection with Kostylev's type specimens in Moscow, to Sergey A. Belokobylskij (Zoological Institute of the Russian Academy of Sciences, Saint Petersburg) for help with access to the collection of the type specimens of Vespidae in Saint Petersburg, and James M. Carpenter (American Museum of Natural History, New York) for his consultation concerning the whereabouts of the type of *C. a. tauricus* and his careful review of the manuscript. Josef Gusenleitner (Linz), Erol Yildirim (Atatürk University, Department of Plant Protection, Erzurum), Christoph Saure (Berlin) and Christian Schmid-Egger (Berlin) generously provided material from their collections. Annette Rosenbauer (Stuttgart State Museum of Natural History, Stuttgart) identified the collected plants from Kos and

Andreas Müller (Zürich) determined the pollen samples. We are especially grateful to Sarah Gess (Albany Museum, Grahamstown) for valuable comments on the manuscript and improvement of our English.

References

- Bellmann H (1984) Beobachtungen zum Brutverhalten von *Celonites abbreviatus* Villers (Hymenoptera, Masaridae). Zoologischer Anzeiger 212: 321–328.
- Bellmann H (1995) Bienen, Wespen, Ameisen - Hautflügler Mitteleuropas. Kosmos Naturführer, Franckh-Kosmos, Stuttgart, 336 pp.
- Birket-Smith SJR (1981) The male genitalia of Hymenoptera - a review based on morphology in Dorylidae (Formicidae). Entomologica scandinavica Supplement 15: 377–397.
- Carpenter JM (1988) The phylogenetic systems of the Gayellini (Hymenoptera: Vespidae, Masarinae). Psyche 95: 211–241. doi: 10.1155/1988/45034
- Carpenter JM (2001) Checklist of species of the subfamily Masarinae (Hymenoptera: Vespidae). American Museum Novitates 3325: 1–40. doi: 10.1206/0003-0082(2001)325<0001:CO-SOTS>2.0.CO;2
- Fateryga AV (2010) Trophic relations between Vespid wasps (Hymenoptera, Vespidae) and flowering plants in the Crimea. Entomological Review 90: 698–705. doi: 10.1134/S0013873810060047
- Fateryga AV, Ivanov SP (2009) Results of the centennial studying of the vespoid wasps (Hymenoptera, Vespidae) of the Karadag Nature Reserve and adjacent territories. Zapovidna Sprava v Ukraini 15: 65–70. [In Russian]
- Fateryga AV, Ivanov SP (2010) Redbook-species of diplopterous wasps (Hymenoptera, Vespidae) on the Crimean map. Ekosistemy, ikh Optimizatsiya i Okhrana 3: 180–192. [In Russian]
- Gusenleitner J (1966) Vespidae, Eumenidae und Masaridae aus der Türkei. Teil I. Polskie Pismo Entomologiczne 36: 343–363.
- Gusenleitner J (1973) Über Masaridae aus dem nahen Osten (Vespoidea, Hymenoptera). Bolletino della Museo Civico di Storia Naturale di Venezia 24: 55–69.
- Gusenleitner J (1985) Bemerkenswertes über Faltenwespen VIII. (Hymenoptera, Vespoidea). Nachrichtenblatt Bayerischer Entomologen 34: 105–110.
- Hadjisterkotis E, Masala B, Reese D (2000) The origin and extinction of the large endemic Pleistocene mammals of Cyprus. Biogeographia Anatolia 21: 593–606.
- Ivanov SP, Fateryga AV (2009) New findings of the wasp, *Celonites abbreviatus tauricus* (Hymenoptera, Vespidae, Masarinae) in Crimea. Vestnik Zoologii 43: 354. [In Russian]
- Kostylev G (1928) Materialien zur Kenntnis der Vespidenfauna der östlichen Krim. Entomologische Mitteilungen 17: 398–407.
- Kostylev G (1935) Materialien zur Kenntnis der Masariden-Fauna der Paläarktis. Archives du Musée Zoologique de l'Université de Moscow 2: 85–116, 8 Figs. [In German and Russian]
- Kovblyuk MM (2014) Spiders (Arachnida, Aranei) of Crimea: Faunogenesis and hypothesis of Pontida. Ukrainska Entomofaunistyka 5: 29–53. [In Russian]
- Lattin G de (1967) Grundriß der Zoographie. Gustav Fischer, Stuttgart, 602 pp.

- Major CO, Goldstein SL, Ryan WBF, Lericolais G, Piotrowski AM, Hajdas I (2006) The co-evolution of Black Sea level and composition through the last deglaciation and its paleoclimatic significance. *Quaternary Science Reviews* 25: 2031–2047. doi: 10.1016/j.quascirev.2006.01.032
- Mauss V (2006) Observations on flower association and mating behaviour of the pollen wasp species *Celonites abbreviatus* (Villers, 1789) in Greece (Hymenoptera: Vespidae, Masarinae). *Journal of Hymenoptera Research* 15: 266–269. doi: 10.3897/jhr.31.4235
- Mauss V (2013) Description of *Celonites andreasmuelleri* sp. n. (Hymenoptera, Vespidae, Masarinae) from the Middle East with a key to the Palearctic species of the *C. abbreviatus*-complex of the subgenus *Celonites* s. str. *Journal of Hymenoptera Research* 31: 79–95. doi: 10.3897/JHR.31.4235
- Mauss V, Müller A (2014) First contribution to the bionomics of the pollen wasp *Celonites fischeri* Spinola, 1838 (Hymenoptera, Vespidae, Masarinae) in Cyprus. *Journal of Hymenoptera Research* 39: 119–153. doi: 10.3897/JHR.39.7841
- Mayr E (1967) *Artbegriff und Evolution*. Paul Parey, Hamburg, 617 pp.
- Müller A (1996) Convergent evolution of morphological specializations in Central European bee and honey wasp species as an adaptation to the uptake of pollen from nototribic flowers (Hymenoptera, Apoidea and Masaridae). *Biological Journal of the Linnean Society* 57: 235–252. doi: 10.1111/j.1095-8312.1996.tb00311.x
- Pils G (2006) *Flowers of Turkey - a photo guide*. Gerhard Pils Verlag, Linz, 409 pp.
- Poulakakis N, Kapli P, Kardamaki A, Skourtanioti E, Göcmen B, Ilgaz C, Kumlutas Y (2013) Comparative phylogeography of six herpetofauna species in Cyprus: late Miocene to Pleistocene colonization routes. *Biological Journal of the Linnean Society* 108: 619–635. doi: 10.1111/j.1095-8312.2012.02039.x
- Romeis B (1989) *Mikroskopische Techniken*, 17th ed. Urban und Schwarzenberg, Wien, 697 pp.
- Schmidt J (1984) *Erinnerungen an meine Sammelreisen in die Türkei (Anatolischer Raum)*. *Steirische Entomologenrunde* 18: 76–90.
- Schremmer F (1959) Der bisher unbekannte Pollensammelapparat der Honigwespe *Celonites abbreviatus* Vill. (Vespidae, Masarinae). *Zeitschrift für Morphologie und Ökologie der Tiere* 48: 424–438. doi: 10.1007/BF00408580
- Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1964–1980) *Flora Europae* 1–5. Cambridge University, Cambridge, England.
- Ved' IP (2000) *Klimaticheskiiy atlas Kryma*. Tavriya-Plyus, Simferopol, 120 pp., 110 Figs. [In Russian]
- Westrich P, Schmidt K (1986) Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera, Apoidea). *Linzer biologische Beiträge* 18: 341–360.
- Yena A, Yena A, Yena V (2005) “Stankiewicz pine” in Crimea: some new taxonomical, chronological and paleo-landscape considerations. *Dendrobiology* 53: 63–69.