

ON THE BIOLOGY OF TWO SPECIES OF GROUND-NESTING EUMENINE WASPS (HYMENOPTERA: VESPIDAE: EUMENINAE) AND THEIR CUCKOO-WASP PARASITES (HYMENOPTERA: CHRYSIDIDAE) FROM THE TARKHANKUT NATURE PARK, CRIMEA

Alexander V. Fateryga^{1,*}, Valentina V. Fateryga¹, Maxim V. Onchurov²

¹*T.I. Vyazemsky Karadag Scientific Station – Nature Reserve of RAS, Russia*

**e-mail: fater_84@list.ru*

²*V.I. Vernadsky Crimean Federal University, Russia*

Received: 24.06.2025. Revised: 21.08.2025. Accepted: 16.09.2025.

Hemipterochilus bembeciformis and *Tropidodynerus interruptus* nest in ground with rather similar soil characteristics (light to medium clay loam). Two nests of the former species and four of the latter were excavated. Both species used water to moisten the ground. Females of *H. bembeciformis* surmounted the nest entrance with a 1–4 mm high mud collar; the nest entrance of *T. interruptus* was simple but temporarily closed with mud pellets by the wasps. One nest of *H. bembeciformis* was abandoned, while another contained two brood cells as ends of a branched burrow; all nests of *T. interruptus* were one-celled. A caterpillar of *Acontia trabealis* (Lepidoptera: Noctuidae) was recorded as a prey of *H. bembeciformis*, while females of *T. interruptus* hunted on larvae of *Rhinocyllus conicus* (Coleoptera: Curculionidae) extracting them from fading capitula of *Carduus nutans* subsp. *leiophyllus*. Cuckoo wasps *Chrysis cylindrica* and *Ch. valesiana* were observed at nests of both species, while only cocoons of the former species were recorded in the brood cells of both *H. bembeciformis* and *T. interruptus*. *Chrysis cylindrica* is recorded as a parasitoid, since its larva consumes the host larva and its cocoons were found inside cocoons of the host-wasp species. The cocoon of *T. interruptus* is described. *Hemipterochilus bembeciformis* and *T. interruptus* form a Müllerian mimicry ring with at least two other eumenine-wasp species co-occurring in the Tarkhankut Nature Park: *Paragymnomerus signaticollis* and *Pseudepipona herrichii*. The biology of all four species is discussed; all of them are confined to threatened steppe habitats and require our attention and conservation efforts.

Key words: brood parasites, *Chrysis cylindrica*, *Hemipterochilus bembeciformis*, mimicry ring, nest structure, trophic relationships, *Tropidodynerus interruptus*

Introduction

The subfamily Eumeninae is the most diverse group of the family Vespidae, numbering (in the broad sense, including Raphiglossinae and Zethinae) more than 3900 described species worldwide (Luo et al., 2022). Females of the eumenine wasps either nest in pre-existing cavities, excavate their own nest burrows in the ground (or rarely in wood), or construct aerial nests of mud or plant material (rarely combining them) (Spradbery, 1973; Iwata, 1976; Cowan, 1991). These wasps provision their nest cells with paralysed larvae of phytophagous insects: moths and butterflies, beetles, or rarely sawflies. Meanwhile, adult wasps principally feed at flowers, where they consume nectar as the main source of carbohydrates (Mauss et al., 2019). Although the biology of some eumenine-wasp species is rather well studied, it is poorly known or even unknown for the majority of their diversity. Cavity-nesting groups are the best studied since they are com-

mon dwellers of trap nests (e.g. Krombein, 1967; Budrienė et al., 2004; Buschini & Woiski, 2008; Ivanov et al., 2019). At the same time, the biology of the ground-nesting species is less studied. Conservation of the eumenine wasps rarely receives attention in scientific papers (e.g. Mader, 2000; Fateryga & Ivanov, 2013), although many representatives of these insects are confined to endangered habitats such as dry grasslands (Fateryga & Zhidkov, 2012). The present contribution deals with two species of ground-nesting eumenine wasps from the Crimean steppes: *Hemipterochilus bembeciformis* (Morawitz 1867) and *Tropidodynerus interruptus* (Brullé 1832).

The biology of *H. bembeciformis* was only briefly studied previously. According to Ferton (1908), a nest of this species was made in dense soil and had a linear-branched structure, an egg was suspended in a cell with a thread, and the provision was small unidentified caterpillars. Grandi (1957, 1961) reported that females col-

lected water, sometimes landing directly on its surface, as well as that the nest burrow was up to 10 cm deep, the nest entrance was surmounted by a mud turret 2–6 mm high, and the provision was caterpillars of the family Noctuidae. According to Blüthgen (1943, 1961), caterpillars of *Evergestis frumentalis* (Linnaeus 1761) (Crambidae) were recorded as a prey of this wasp species, while *Spinolia dallatorreana* (Mocsáry 1896) (Hymenoptera: Chrysididae) was recorded as its nest parasite. Imagines of *H. bembeciformis* were observed feeding at flowers of *Ferula caspica* M. Bieb. (Apiaceae), *Scabiosa argentea* L. (Caprifoliaceae), and *Nigella arvensis* L. (Ranunculaceae) (Blüthgen, 1961; Fateryga, 2020).

The biology of *T. interruptus* was rather better studied previously, although some details remained still unknown. Arens (1999) and Fateryga (2009) concluded that females of this species made nest aggregations in solid soil, the nests contained one cell each, there was no entrance turret, and females used mud pellets, extracted from the nest burrow during its excavation, to temporarily close the nest entrance before each departure for hunting. The prey was weevil larvae (Coleoptera: Curculionidae). The most interesting observation was that every time a female returned with a new victim, it extracted nearly the whole content of the nest cell except the egg: not only the temporary closure consisting of the mud pellets but also the whole food supply stored in the cell previously. By this way, weevil larvae were placed on the ground near the nest entrance and examined by the wasp. After that, it placed all prey items (including the newly delivered one) in the cell again and closed it again with mud pellets. Only after delivering of 4–10 weevil larvae, the female finally closed the nest with a mud plug. Fateryga (2009) also observed that the species was univoltine, with two-year diapause in some individuals, as well as that females used sea water to moisten the substrate during the nest construction and the egg was deposited on the bottom of the cell without a thread. Arens (1999) observed *Chrysis jaxartis* Semenov 1910 (Hymenoptera: Chrysididae) as a nest parasite of *T. interruptus*, while Fateryga (2009) observed two other species, later identified as *Ch. cylindrica* Eversmann 1857 and *Ch. valesiana* Frey-Gessner 1887 (Martynova & Fateryga, 2015); the latter species is closely related to *Ch. jaxartis*. Details of their host–parasite relationships remained unknown, although *Ch. valesiana* was supposed to be a kleptoparasite, according to observations on this

species in nests of other species of the eumenine wasps (Fateryga & Ivanov, 2013; Martynova & Fateryga, 2015; Fateryga, 2018). All three species of cuckoo wasps were observed at least partially (with metasoma only) penetrating into the cells of *T. interruptus* at the provisioning stage, due to their ability to remove the temporary closure of the nest, consisting of mud pellets. Imagines of *T. interruptus* were recorded feeding at flowers of plants of the family Brassicaceae, *Butomus umbellatus* L. (Butomaceae), *Euphorbia* sp. (Euphorbiaceae), *Thymra capitata* (L.) Cav. and *Thymus tauricus* Klokov & Des.-Shost. (both Lamiaceae), and *Malva thuringiaca* (L.) Vis. (Malvaceae) (Białynicki-Birula, 1926; Blüthgen, 1961; Arens, 1999; Fateryga, 2020; Fateryga & Fateryga, 2025).

Despite the research summarised above, several aspects of the biology of *H. bembeciformis* and *T. interruptus* remained unknown: a detailed study of the nest substrate was not carried out previously, nest and cocoon structures were insufficiently illustrated, the prey was not always completely identified, and the host–parasite relationships of these wasps with their specific cuckoo wasps were not ascertained. Thus, the purpose of the present contribution is to study these biological details of *H. bembeciformis* and *T. interruptus* under the conditions of the Tarkhankut Nature Park (Crimean Peninsula).

Material and Methods

Field observations were carried out in Crimea, at three localities in the Tarkhankut Nature Park: Bolshoy Kastel Bay (45.46° N, 32.55° E; Fig. 1A) on 22–25.07.2015, 06–08.07.2018, and 20.06.2019; Kalosha Bay (45.47° N, 32.57° E) on 08.07.2022, 10–11.07.2022, and 06.08.2022; Kipchak Bay (45.48° N, 32.59° E; Fig. 1B) on 19–23.06.2019, 08.07.2022, 10.07.2022, and 06.08.2022. Wasp nests were discovered largely by accident. After a female was observed returning to or flying out from its nest, the nest was marked with four triangular pieces of red plastic set into the ground at equal distances from the entrance.

The wasps' activity was observed with the naked eye and documented with digital cameras. Photographs were taken mainly with a Canon EOS RP or a Canon EOS M6 digital cameras and a Sigma AF 105 mm f/2.8 macro lens (scale up to 1:1), except for some taken with a Canon PowerShot SX160 IS digital camera. The nests were excavated after they had been sealed by females or when we could be certain that they had been abandoned.



Fig. 1. Nesting sites of eumenine wasps in the Tarkhankut Nature Park. Designations: A – Bolshoy Kastel Bay; B – Kipchak Bay.

A total of two nests of *H. bembeciformis* (both excavated) and 17 nests of *T. interruptus* (four of them excavated) were observed during the study. The nests were excavated by the following method. First, the grass cover near the nest was removed with scissors. Then, the nest was extracted together with the surrounding lump of soil measuring about 25 cm in diameter and height. To do this, the earth around the nest area was removed with a shovel, and the remaining soil column was cut from below and gently lifted. The extracted lump of soil was transported to the laboratory, where the nest had to be exposed by cutting the soil off layer by layer in a plane perpendicular to the upper soil surface. Cutting was done with extreme care when approaching the approximate location of the nest, i.e. the centre of the cylindrical soil lump.

The excavated nest was documented with photographs and with diagrams drawn on graph paper at a scale of 1:1 using compasses. The drawings of nests and cells presented herein were made by tracing of photos and sketches on graph paper. Soil samples were collected from each

nesting site for analysis of granulometric composition, specific gravity of the solid phase, physical fractions by the method of Rutkovsky, and granulometric classification using the system of Kachinsky (see Vadyunina & Korchagina, 1986). The preimaginal stages of both the host wasps and cuckoo wasps found in the cells were placed in short glass tubes with cotton-wool stoppers, labelled with the nest and cell numbers, and kept in an unheated room until the emergence of adults. The prey extracted from the brood cells of the excavated nest were fixed in 96% ethanol. In order to identify the prey, the surrounding vegetation was examined for living larvae. The larvae found on the plants were photographed. Some of them were kept in the laboratory in an attempt to rear the adults, and some were preserved in ethanol and then compared with those from the nest cells, using a stereomicroscope. The reference material of the wasps and their prey is kept in the collection of Alexander V. Fateryga.

Results

Biology of Hemipterochilus bembeciformis

The first nest of *H. bembeciformis* was found in the Bolshoy Kastel Bay on 22.07.2015. It was situated between two tracks of a dirt road (Fig. 1A). The soil at this nesting site was a medium clay loam with a low percentage of gravel and a considerable amount of loess and silt (Table 1, Table 2). There was a well about 100 m west of the nesting site and females of this wasp species were observed collecting water flowing on the ground from a bucket used by humans (Fig. 2A). The nesting female of *H. bembeciformis* was discovered at about 12:10 h (solar time), when its nest burrow was about 0.5 cm deep. The nest entrance was not surmounted by a mud turret but there was a short mud collar about 1 mm high. The female arrived to its nest burrow with water in its crop and regurgitated a drop in the nest burrow. Then, it formed a remarkably loose mud pellet with its mouthparts and extracted it from the nest entrance holding in mandibles and additionally supported with labial palpi (Fig. 2B). The female flew with this pellet and dropped it away. By extracting pellet by pellet, the nest burrow was deepened. After extracting several mud pellets, the female flew away for water. Unfortunately, this female left out its nest soon and never returned to this nesting site (our observations were interrupted and the exact time was not measured, but the

nest was abandoned before our next inspection at 15:00 h). Next day, the nest burrow was occupied by *Hoplitis perezi* (Ferton 1894) (Hymenoptera: Megachilidae) (see Fateryga et al., 2024). The bee finished its nesting and the nest was excavated on 25.07.2015. Examination of

the nest burrow in the laboratory revealed that the wasp was stopped by a stone and probably therefore abandoned this nest. The burrow was about 3 cm deep, sub-vertical at the beginning and then inclined, probably in a failed attempt to avoid the stone (Fig. 3A; on the left).

Table 1. Granulometric composition of soil at the nesting sites of *Hemipterochilus bembeciformis* and *Tropidodynerus interruptus* from the Tarkhankut Nature Park

Nesting site, year of sampling	Granulometric composition, %						
	> 10 mm	10–7 mm	7–5 mm	5–3 mm	3–1 mm	1–0.5 mm	< 0.5 mm
Bolshoy Kastel Bay, 2015	0.40	3.55	4.46	10.36	36.62	14.56	29.86
Kalosha Bay, 2022	6.15	12.90	9.78	15.41	30.19	5.09	19.66
Kipchak Bay, 2022	4.12	4.75	2.97	6.60	27.06	10.28	43.89

Table 2. Soil characteristics at the nesting sites of *Hemipterochilus bembeciformis* and *Tropidodynerus interruptus* from the Tarkhankut Nature Park

Nesting site, year of sampling	Specific gravity of the solid phase, g/cm ³	Physical fraction content by Rutkovsky's method, %				Granulometric class in Kachinsky's system
		> 0.5 mm (sand)	0.5–0.05 mm (loess)	0.05–0.005 mm (silt)	< 0.005 mm (clay)	
Bolshoy Kastel Bay, 2015	2.43	8.90	42.05	41.26	7.79	Medium clay loam
Kalosha Bay, 2022	2.35	15.50	44.64	30.35	9.51	Medium clay loam
Kipchak Bay, 2022	2.79	22.17	25.54	45.95	6.34	Light clay loam

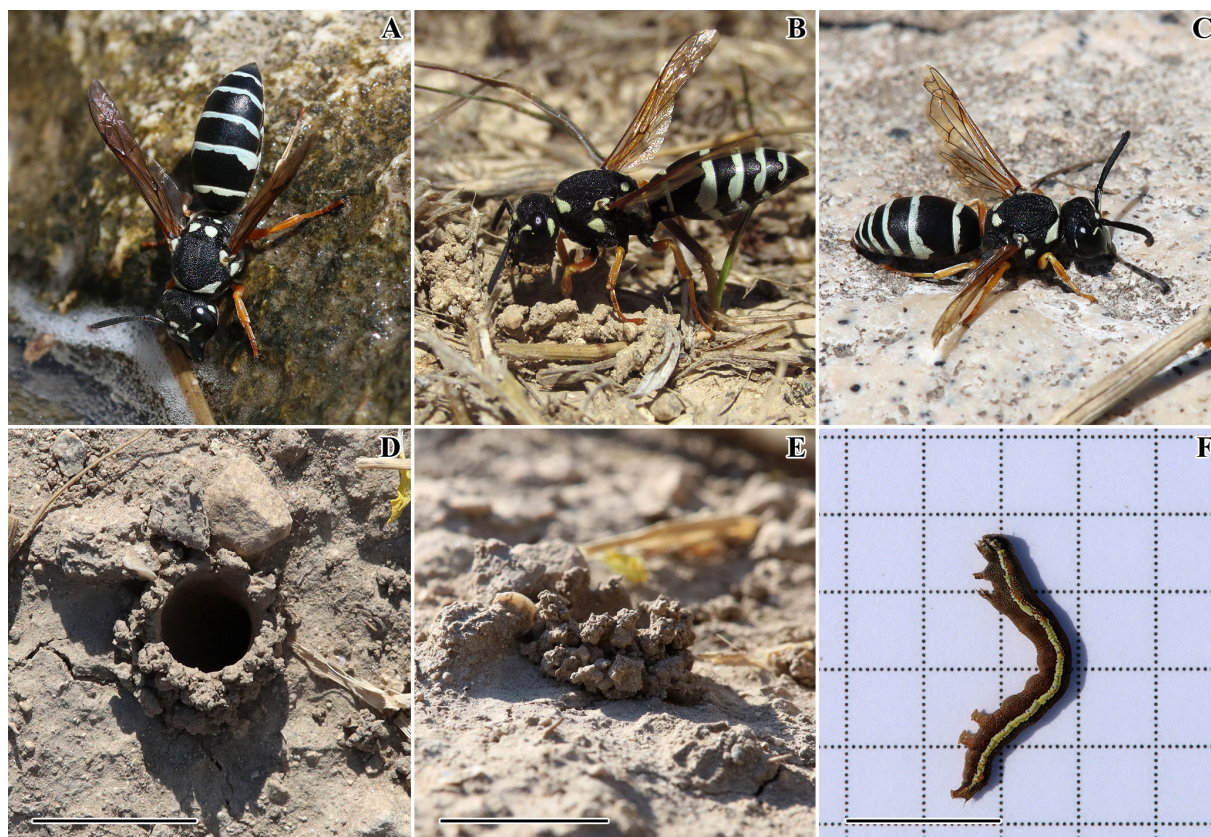


Fig. 2. Biology of *Hemipterochilus bembeciformis* (Morawitz 1867) in the Tarkhankut Nature Park. Designations: A – female collecting water; B – female excavating nest burrow; C – male perching on a stone at a water-collecting site; D – nest entrance from above; E – the same in lateral view; F – caterpillar of *Acontia trabealis* (Scopoli 1763) extracted from the nest cell. Scale bars (D–F) = 1 cm.

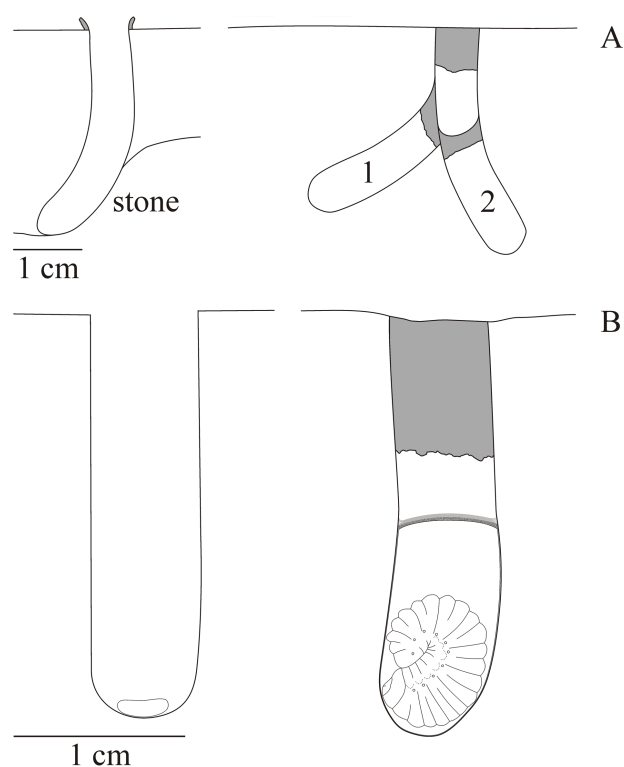


Fig. 3. Schematic plans of nests of eumenine wasps from the Tarkhankut Nature Park. Designations: A – *Hemipterochilus bembeciformis* (Morawitz 1867), an open abandoned nest (left) and a complete nest (right) with two cells (1, 2) containing cocoons of *Chrysis cylindrica* Eversmann 1857 (not shown); B – *Tropidodynerus interruptus* (Brullé 1832), an open nest with an egg (left) and a complete nest with a prepupa in a cocoon (right).

The second nest of *Hemipterochilus bembeciformis* was found in the Kalosha Bay on 08.07.2022, also between two tracks of a dirt road. The soil at this nesting site was also a medium clay loam, similarly to that in the Bolshoy Kastel Bay, but with a slightly larger amount of physical clay, as well as with a large percentage of gravel (Table 1, Table 2). There was no well in this bay and females collected water from the sea 50 m north of the nesting site. The nesting female was discovered after 15:00 h when it arrived to the nest. The nest entrance was surmounted by a mud collar about 4 mm high (Fig. 2D,E). The female entered the nest burrow and stayed inside it during about 30 min. After that, it flew away for a while and again entered the nest, with the metasoma first. The observations were continued on 10.07.2022. There was no entrance collar that day because it was broken by a biker. The wasp entered the nest with the head first on 15:12 h. On 15:34 h it flew away for a while and entered the nest with the metasoma first. At night, the female was visible (with the help of a flash light) in the nest with the head directed outside. Next day, the female performed five long flights from the nest from 8:07 h to 9:19 h, returning and enter-

ing the nest each time just for a while. On 9:19 h, the wasp returned to the nest with a caterpillar of *Acontia trabealis* (Scopoli 1763) (Lepidoptera: Noctuidae) (Fig. 2F). After deposition of the prey into the cell, it stood in the nest burrow with the head directed outside for 13 min. From 9:42 h to 11:13 h, the wasp performed five more long flights from the nest; after two of them it was also standing in the burrow with the head directed outside for 14 min and 15 min. This characteristic behaviour of the female looked like a typical hunting activity in conditions of scarce prey resources (see Ivanov & Fateryga, 2006). Then, our observations were finished.

The nest was excavated on 06.08.2022. It was somewhat more than 3 cm deep; the burrow was branched and each branch was terminated by a cell. The first cell was sub-horizontal, while the second cell was sub-vertical. Both cells were sealed with own mud plugs and there was an empty space between the plug of the second cell and the closing plug of the nest, which was thicker than the plugs of the cells (Fig. 3A; on the right). Despite a cuckoo wasp *Ch. valesiana* was observed near the nest at the provisioning stage (Fig. 4A), both cells contained cocoons of another species, *Ch. cylindrica*. In each case, the cocoon of the cuckoo wasp was inside a cocoon of the host wasp. Therefore, we can conclude that *Ch. cylindrica* is a parasitoid, with its larva consuming the host-wasp's larva. Imagines of *Ch. cylindrica* emerged from both cocoons in 2023, after a winter diapause.

Numerous males of *H. bembeciformis* were observed perching on stones at water-collecting sites (Fig. 2C) and performing slow constant flights around both nesting sites. However, mating was not documented.

Biology of *Tropidodynerus interruptus*

Since nesting of this species was studied previously in the Tarkhankut Nature Park (Fateryga, 2009), it is only briefly described here, with a focus on details not known until now. Two nests of this species were found in the Bolshoy Kastel Bay on 06.07.2018 and 20.06.2019 at the same nesting site where the first nest of *H. bembeciformis* was observed. Fifteen other nests were found in the Kipchak Bay on a side of a dirt road (Fig. 1B) on 19.06.2019 (ten nests) and 08.07.2022 (five nests). The soil at this nesting site was a light clay loam with a heavier solid phase, in comparison with the two previous sites, a slightly less amount of physical clay, and a considerable percentage of sand (Table 1, Table 2). Females of *T. interruptus* were observed collecting water at a well about 20 m south-west of the nesting site in the Kipchak Bay

or from the sea about 120 m north of it (Fig. 5A). The wasps usually nested closely to each other making a nest aggregation. There was no mud turret or collar at the nest entrance (Fig. 5B,C,D,E). A female excavating its nest burrow merely deepened it using regurgitated water to moisten the soil and forming mud pellets, which were extracted and put near the nest entrance (Fig. 5B). When the nest burrow reached a depth of about 2.5–3.0 cm, the wasp laid an egg on its bottom, without attaching it by any thread (Fig. 3B, on the left). Then, the female temporarily closed the nest with mud pellets, available around the entrance (Fig. 5C), and flew away for hunting. When the wasp returned with a prey, it extracted the mud pellets and put the prey into the nest burrow. After that, it again temporarily closed the nest with mud pellets and flew for the next victim. Every time the wasp returned with the next weevil larva, it extracted not only the mud pellets but also all previously stored victims and examined them (Fig. 5D,E). After a necessary number of delivering the prey, the wasp put all of them into the nest burrow for the last time and closed it with a thick mud plug. To construct this plug, it not merely put mud pellets into the burrow but moistened them with regurgitated water. All nests contained just one cell. Females of *T. interruptus* spent nights in their nests, cleaned from the mud pellets, with their heads directed outside. Females of the cuckoo wasps *Ch. cylindrica* and *Ch. valesiana* were regularly observed at nests of *T. interruptus*. Both removed the temporary closures of the nests, consisting of mud pellet, when the host wasps were absent; the former species was especially common (Fig. 4B,C).

The prey of *T. interruptus* was identified as larvae of *Rhinocyllus conicus* (Frölich 1792) (Coleoptera: Curculionidae). Females hunted for them at

fading capitula of *Carduus nutans* subsp. *leiophyllus* (Petrovič) Stoj. & Stef. (Fig. 5F) about 20 m southwest of the nesting site (near the well). One of the studied complete nests excavated on 08.07.2018 contained three larvae of this weevil that was probably the minimal number for this wasp species (the previously reported one was 4–10, according to Arens, 1999 and Fateryga, 2009). A male wasp emerged from this nest in 2019, after a winter diapause. Three other nests were excavated on 06.08.2022. Two of them contained cocoons of *T. interruptus* with prepupae (Fig. 5G). The cocoon was previously described as consisting of a single thick layer (Fateryga, 2009), which was actually not true (see Fateryga, 2021). Detailed examination of the cocoons in the present study revealed that they actually have a sandwich-like structure, similar to that in the cocoon of *Parkerodynerus erythrogaster* (Bohart 1939) (Parker, 1984; Fateryga, 2021), but present only at the free part (= proximal end) of the cocoon instead of over its whole surface. The outer layer of the cocoon is made of a loose chaotic interweaving of silk strands and films in the form of a convex meniscus at a distance from the inner surface of the cell plug (= the closing plug of the nest). The middle layer consisting of soil is present directly under the outer layer. The inner layer consisting of mostly broad silk strands is present over the whole cocoon surface (Fig. 3B; on the right). Fateryga (2021) supposed that the middle layer was present also over the whole cocoon surface but it was not recognisable anywhere except the free part of the cocoon, according to the present data. The inner surface of the cell plug was not covered with silk. It is also interesting that neither meconium nor prey excrements were found in the cells of *T. interruptus* in the present study.



Fig. 4. Cuckoo wasps at nests of eumenine wasps in the Tarkhankut Nature Park. Designations: A – *Chrysis valesiana* Frey-Gessner 1887 perching on a stone at a nesting site of *Hemipterochilus bembeciformis* (Morawitz 1867); B, C – *Ch. cylindrica* Eversmann 1857 removing the temporary closure of mud pellets of a nest of *Tropidodynerus interruptus* (Brullé 1832).



Fig. 5. Biology of *Tropidodynerus interruptus* (Brullé 1832) in the Tarkhankut Nature Park. Designations: A – female collecting water; B – female excavating nest burrow; C – female temporary closing the nest entrance with mud pellets; D, E – female extracting and examining the provision from the nest cell; F – larvae of *Rhinocyllus conicus* (Frölich 1792) in a capitula of *Carduus nutans* subsp. *leiophyllus* (Petrovič) Stoj. & Stef.; G – dissected nest cell with a prepupa in a cocoon; H – cocoon of *Chrysis cylindrica* Eversmann 1857 inside a cocoon of *T. interruptus*. Scale bars (G, H) = 1 cm.

The last nest excavated on 06.08.2022 contained a cocoon of *Ch. cylindrica* inside a cocoon of the host wasp (Fig. 5H). Therefore, we can conclude that *Ch. cylindrica* is a parasitoid in the nests of *T. interruptus*, like in the nests of *H. bembeciformis*. An imago of this cuckoo wasp emerged in 2023, after a winter diapause, together with two imagines of *T. interruptus*.

Males of *T. interruptus* were observed much more rarely than those of *H. bembeciformis*. A few males were recorded at the water collecting site on the sea shore and just once a male was found performing a slow constant flight around the nesting site in the Kipchak Bay.

Discussion

New data on the biology of Hemipterochilus bembeciformis, Tropidodynerus interruptus, and their parasites

Although nests of both *H. bembeciformis* and *T. interruptus* were described previously (Ferton, 1908; Grandi, 1957, 1961; Arens, 1999; Fateryga, 2009), the present contribution enlarges the knowledge of their biology and provides some new details. Particularly, a caterpillar of *Acontia trabealis* has been recorded as a prey of *H. bembeciformis* for the first time. The prey of *T. interruptus* (larvae of *Rhinocyllus conicus*) has also been identified for the first time. The structure of the cocoon of *T. interrup-*

tus was properly described. Also for the first time, a cuckoo wasp species *Ch. cylindrica* has been recorded as a nest parasite of *H. bembeciformis*. The only host previously known for this species was *T. interruptus* (Martynova & Fateryga, 2015). For the first time, the host–parasite relationships of *Ch. cylindrica* with both *T. interruptus* and *H. bembeciformis* have been ascertained. The species is a parasitoid, i.e. its larva consumes the host larva already enclosing in the cocoon. It is remarkable that another species of cuckoo wasps found at nests of *T. interruptus*, namely *Ch. valesiana*, is a kleptoparasite, i.e. its larva feeds on the stored food supply. The known hosts of this parasite include also three other species of ground-nesting eumenine wasps (Fateryga & Ivanov, 2013; Martynova & Fateryga, 2015; Fateryga, 2018): *Paravespa rex* (von Schulthess 1924) hunting on noctuid caterpillars and two species of the genus *Paragymnomerus* Blüthgen 1938 hunting on sawfly larvae, i.e. the prey somewhat different from the curculionid larvae stored by *T. interruptus*. Due to such a large food range able to be consumed by the larva of *Ch. valesiana*, we can speculate that it parasitises *H. bembeciformis* as well, especially taking into account that a specimen of this cuckoo wasp was recorded at a nest of this eumenine-wasp species in the present study. Thus, both *T. interruptus* and *H. bembeciformis* may be parasitised by both parasitoidic *Ch. cylindrica* and kleptoparasitic *Ch. valesiana* co-occurring in the same habitat.

Host–parasite relationships between studied eumenine and cuckoo wasps

A situation of a parasitoid and a kleptoparasite of the family Chrysididae being associated with the same host is known in the eumenine wasps. Chapman (1869) studied *Chrysis viridula* Linnaeus 1761 (= *Ch. bidentata* Linnaeus 1767) and *Pseudochrysis neglecta* (Shuckard 1837) in nests of *Odynerus spinipes* (Linnaeus 1758) and found that the former species, which is closely related to *Ch. cylindrica*, was a parasitoid consuming the host larva enclosing in the cocoon, while the second one was a kleptoparasite consuming the food supply (curculionid larvae). It is remarkable that a female of *Ch. viridula* laid an egg into a sealed nest cell of *O. spinipes* through a perforation in the cell plug made by the parasite (Chapman, 1869). In the case of *T. interruptus*, females of *Ch. cylindrica* were not able to penetrate a sealed nest, while they always tried to lay an egg at the provisioning stage, partially removing the temporary closure of the nest (Fateryga, 2009; present study). We can speculate that the first-instar larva

of *Ch. cylindrica* has a delayed development and begins to feed only after the host larva has fully grown.

It is worth mentioning that *Ch. viridula* was recorded at nests of *Tropidodynerus flavus* (Lepelletier 1841) (= *Odynerus nobilis* de Saussure 1856), a species with nearly identical nesting habits as *T. interruptus*, where the parasite also tried to remove the temporary closure of the nests (Ferton, 1895). Therefore, we can speculate that either the egg or the first-instar larva of *Ch. viridula* also has a delayed development that is partially corroborated by Chapman (1869), who reported that an egg of this species developed more slowly than that of *P. neglecta*. However, Ferton (1895) could have misidentified another species of the *Ch. viridula*-group as *Ch. viridula*, which is a common situation in old literature (Rosa et al., 2019), especially taking into account that he often misidentified even the host species (Berland, 1927). In the case of Chapman (1869), working in Great Britain, the identification of *Ch. viridula* was apparently correct because there are no other similar species over there (Morgan, 1984).

Mimicry ring of steppe eumenine wasps and their biology

Hemipterochilus bembeciformis forms a Müllerian mimicry ring with at least two other eumenine-wasp species co-occurring in the Tarkhankut Nature Park: *Paragymnomerus signaticollis* (Morawitz 1888) and *Pseudepipona herrichii* (de Saussure 1856). These three species have a similar body size and a nearly identical colouration: a black body with a whitish pattern and ferruginous legs (Fig. 6). Such mimicry rings are a common phenomenon in vespidae wasps (Bequaert, 1918; Pauly et al., 2003; Garcete-Barrett, 2014; Selis, 2020). *Tropidodynerus interruptus* can be also included in this mimicry ring, although its colouration is slightly different in that the whitish pattern is less rich (the clypeus of the female is completely black, whitish spots on dorsal mesepisternum, scutellum, and metanotum are reduced, whitish bands on metasomal terga are interrupted medially, and the tegula is ferruginous instead of whitish). All four species are ground-nesting. The biology of *P. signaticollis* was studied previously in the Tarkhankut Nature Park, and the species also nests in light to dense clay loam of dirt roads (Fateryga, 2018). The biology of *P. herrichii* was previously studied mainly in Great Britain by Mortimer (1908) and Spooner (1934) (summarised by Fateryga, 2022); one nest from the Iberian Peninsula was illustrated by Baldock et al. (2020). Ac-

cording to these literature data, it nests in rather sandy soil, while soil preferences of the other three species mentioned above are quite similar. At the same time, *P. herrichii* and *H. bembeciformis* hunt for moths caterpillars (Depressariidae in the former species; Crambidae and Noctuidae in the latter one), while *T. interruptus* hunts for weevil larvae (Curculionidae) and *P. signaticollis* hunts for sawfly larvae of the family Megalodontesidae. Such details of the biology of these four co-occurring species certainly help them in the differentiation of their ecological niches. It is also noteworthy that all four species have a different nest structure, particularly the nest entrance. *Pseudepipona herrichii* has a simple nest entrance, *H. bembeciformis* has the nest entrance surmounted by a short collar, while it is surmounted by a relatively long mud turret in *P. signaticollis*. In the case of *T. interruptus*, the entrance is simple but temporary closed with mud pellets. Besides this, nests of *T. interruptus* are always one-celled, while those of the other three species can contain several brood cells.



Fig. 6. Water-collecting females of eumenine-wasp species from the mimicry ring of *Hemipterochilus bembeciformis* (Morawitz 1867) in the Tarkhankut Nature Park. Designations: A – *Paragymnomerus signaticollis* (Morawitz 1888); B – *Pseudepipona herrichii* (de Saussure 1856).

Function of the nest turret and the temporary closure

The function of the entrance turret is not entirely clear (Grandi, 1961; Cowan, 1991). There are indications that it can prevent some of the natural enemies, primarily ants, from entering the nest (Hacker, 1918; Fateryga, 2013; Fateryga & Ivanov, 2013; Catarineu et al., 2024), while the temporary closure, consisting of mud pellets, in the nests of *Tropidodynerus* spp. serves the same purpose (Fateryga, 2009). The entrance turret or at least a collar can also partially keep rainwater from getting into the nest in some eumenine-wasp species (Gess & Gess, 1976). It is, however, evident that none of these structures prevent nests from cuckoo wasps (Chapman, 1869; Bristowe, 1948; Gess & Gess, 1976; Fateryga, 2009; Fateryga & Ivanov, 2013). As for the unusual behaviour of *Tropidodynerus* spp., namely extracting and inspecting the whole food supply every time a new victim is delivered, Ferton (1895) supposed that the female malaxated the extracted victims to prevent their spoilage, while Arens (1999) concluded that by this way it merely evaluate the amount of the provision stored in the nest cell. Baldock et al. (2020) suggested that a careful inspection of the stored weevil larvae may be a precaution against eggs of satellite flies (Diptera: Sarcophagidae: Miltoigramminae), which were often a constant presence around active nests of *T. flavus*. However, there were no satellite flies at nests of *T. interruptus* in the present study.

Measures for conservation of the studied eumenine wasps

Fateryga (2009) already paid attention to the fact that *T. interruptus* is a threatened species requiring conservation. Some details of its biology, particularly extracting the whole food supply every time a new victim is delivered, make it vulnerable to an anthropogenic pressure even in Protected Areas such as the Tarkhankut Nature Park. There is no overgrazing in this area, while its territory is largely used for recreation. Both walking humans and vehicles can damage the provision exposed by the wasp near the nest entrance, especially taking into account that the nests are situated on road sides or even between tracks of dirt roads. Since *T. interruptus* is extinct in the Crimean foothills (Simferopol and Bakhchisaray districts and the Sevastopol area), it is

regionally protected (Ivanov & Fateryga, 2016; Red Data Book of Sevastopol, 2018). The present study suggests that *H. bembeciformis* may be a threatened species as well. Although it is somewhat more common than *T. interruptus* and does not have any protected status, it also nests on dirt roads where its nest entrances can relatively easily be damaged, as was observed in the case with bikers. By this way, the nesting success of the species can be decreased. Therefore, the whole complex of the eumenine wasps confined to steppe habitats requires our attention and conservation efforts. We recommend a better control of motorbikes, as well as off-road, all-terrain, and other similar vehicles, which are declared to be prohibited in the Tarkhankut Nature Park but actually often used through their territory without permission of the administration.

Conclusions

We have collected new data on the biology of *H. bembeciformis* and *T. interruptus*, including new prey records for these species and new details of their host–parasite relationships with two species of cuckoo wasps: *Ch. cylindrica* and *Ch. valesiana*. These cuckoo wasps demonstrate two different strategies, where the first species is a parasitoid with an apparently delayed development of the first-instar larva, while the second is a kleptoparasite feeding primary on the food supply stored by the host wasp. With two other eumenine-wasp species, *H. bembeciformis* and *T. interruptus* form a Müllerian mimicry ring of threatened ground-nesting steppe species, which members demonstrate somewhat differentiated ecological niches. Particularly, they hunt for different prey and use not equal but functionally similar strategies to protect their nests from natural enemies.

Acknowledgements

Vladimir Savchuk (Feodosiya) identified *Acontia tra-bealis* and Ilya Zabaluyev (Moscow) identified *Rhinocyllus conicus*. The research of Alexander V. Fateryga and Valentina V. Fateryga was carried out within the state assignment of the Ministry of Science and Higher Education of the Russian Federation №124030100098-0.

References

- Arens W. 1999. Zum Verhalten von *Tropidodynerus interruptus* (Brullé 1832) (Vespoidea, Eumenidae) und seines Brutparasiten *Chrysis jaxartis* Sem. am Nest. *Linzer Biologische Beiträge* 31(1): 147–158.
- Baldock D.W., Castro L., Cross I., Schmid-Egger C., Smit J., Wood T.J. 2020. *The vespiform wasps of Portugal (Hymenoptera: Scolioidea, Tiphioidea, Pompiloidea & Vespoidea)*. *Monografías S.E.A. Vol. 14*. Zaragoza: Sociedad Entomológica Aragonesa. 73 p.
- Bequaert J.C. 1918. A revision of the Vespidae of the Belgian Congo based on the collection of the American Museum Congo expedition, with a list of Ethiopian diplopterous wasps. *Bulletin of the American Museum of Natural History* 39: 1–384.
- Berland L. 1927. Rectification de quelques noms d'Odynères employés par Ferton. *Annales de la Société Entomologique de France* 96(1): 92. DOI: 10.1080/21686351.1927.12279973
- Białynicki-Birula A. 1926. Ein Beitrag zur Kenntniss der paläarktischen *Hoplomerus*-Arten (Hymenoptera – Diploptera). *Bulletin de l'Académie des Sciences de l'URSS* 20(10–11): 885–906.
- Blüthgen P. 1943. Taxonomische und biologische Notizen über paläarktische Faltenwespen (Hym. Vespidae). *Stettiner Entomologische Zeitung* 104: 149–158.
- Blüthgen P. 1961. Die Faltenwespen Mitteleuropas (Hymenoptera, Diploptera). *Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin. Klasse für Chemie, Geologie und Biologie* 1961(2): 1–252. DOI: 10.1515/9783112537084
- Bristowe W.S. 1948. Notes on the habits and prey of twenty species of British hunting wasps. *Proceedings of the Linnean Society of London* 160(1): 12–37. DOI: 10.1111/j.1095-8312.1948.tb00502.x
- Budrienė A., Budrys E., Nevronytė Ž. 2004. Solitary Hymenoptera Aculeata inhabiting trap-nests in Lithuania: nesting cavity choice and niche overlap. *Latvijas Entomologs* 41: 19–31.
- Buschini M.L.T., Woiski T.D. 2008. Alpha-beta diversity in trap-nesting wasps (Hymenoptera: Aculeata) in Southern Brazil. *Acta Zoologica* 89(4): 351–358. DOI: 10.1111/j.1463-6395.2008.00325.x
- Catarineu C., Castro L., Cuesta-Segura A.D. 2024. Sobre la biología de *Stenancistrocerus hispanicus* (Dusmet, 1903) (Hymenoptera: Vespidae), cleptoparasitismo de *Tetramorium semilaeve* André, 1883 y *Aphaenogaster iberica* Emery, 1908 (Hymenoptera: Formicidae) y otras relaciones en torno a sus agregaciones reproductivas. *Boletín de la Sociedad Entomológica Aragonesa* 75: 83–88.
- Chapman T.A. 1869. On the oeconomy of the chrysid parasitic on *Odynerus spinipes*. *Entomologist's Monthly Magazine* 6: 153–158.
- Cowan D.P. 1991. The solitary and presocial Vespidae. In: K.G. Ross, R.W. Matthews (Eds.): *The social biology of wasps*. Ithaca; London: Cornell University Press. P. 33–73. DOI: 10.7591/9781501718670-005
- Fateryga A.V. 2009. The observations on the nesting behavior of the solitary wasp *Tropidodynerus interruptus* (Brullé, 1832) (Hymenoptera, Vespidae, Eumeni-

- nae) in Crimea. *Euroasian Entomological Journal* 8(4): 381–385. [In Russian]
- Fateryga A.V. 2013. Nesting biology of *Odynerus albopictus calcaratus* (Morawitz, 1885) and *Odynerus femoratus* de Saussure, 1856 (Hymenoptera: Vespidae: Eumeninae). *Journal of Insects* 2013(1): 597583. DOI: 10.1155/2013/597583
- Fateryga A.V. 2018. Nesting biology of *Paragymnomerus signaticollis tauricus* (Kostylev, 1940) (Hymenoptera: Vespidae: Eumeninae). *Zootaxa* 4378(3): 429–441. DOI: 10.11646/zootaxa.4378.3.10
- Fateryga A.V. 2020. New data on trophic relationships of eumenine wasps (Hymenoptera, Vespidae: Eumeninae) with angiosperm plants in Crimea. *Entomological Review* 100(4): 497–509. DOI: 10.1134/S0013873820040077
- Fateryga A.V. 2021. Two new Nearctic genera in the tribe Odynerini s. str. revealed on the bionomics and morphology, with a comment on the cocoons of the eumenine wasps (Hymenoptera: Vespidae: Eumeninae). *Far Eastern Entomologist* 427: 1–19. DOI: 10.25221/fee.427.1
- Fateryga A.V. 2022. Revision of the *Pseudepipona herichii*-group of the eumenine wasps (Hymenoptera: Vespidae: Eumeninae) with the description of two new species from China and Russia. *Zootaxa* 5154(2): 101–126. DOI: 10.11646/zootaxa.5154.2.1
- Fateryga A.V., Fateryga V.V. 2025. A third contribution on the trophic relationships of eumenine wasps (Hymenoptera, Vespidae: Eumeninae) with angiosperm plants in Crimea. *Entomological Review* 104(8): 502–511. DOI: 10.1134/S0013873824080025
- Fateryga A.V., Ivanov S.P. 2013. Nesting biology of *Paravespa rex* (von Schulthess 1924) (Hymenoptera: Vespidae: Eumeninae) in the Crimea, Ukraine. *Zootaxa* 3721(6): 589–600. DOI: 10.11646/zootaxa.3721.6.5
- Fateryga A.V., Zhidkov V.Yu. 2012. Vespoid wasps (Hymenoptera, Vespidae) of the National Nature Park “Charivna Gavan”. *Zapovidna Sprava v Ukraini* 18(1–2): 81–87. [In Russian]
- Fateryga A.V., Proshchalykin M.Yu., Abakumov E.V. 2024. A new species and new records of *Hoplitis Klug* (Hymenoptera, Megachilidae) from Russia. *Journal of Hymenoptera Research* 97: 1417–1433. DOI: 10.3897/jhr.97.139623
- Ferton C. 1895. Observations sur l’instinct de quelques Hyménoptères du genre *Odynerus* Latreille. *Actes de la Société Linnéenne de Bordeaux* 48: 219–230.
- Ferton C. 1908. Notes détachées sur l’instinct des Hyménoptères mellifères et ravisseurs (4^e série) avec la description de quelques espèces. *Annales de la Société Entomologique de France* 77: 535–586.
- Garcete-Barrett B.R. 2014. *Stenonartonia tekoraava* sp. nov. (Hymenoptera: Vespidae: Eumeninae), a new member of a typical Amazonian mimicry ring. *Zootaxa* 3860(1): 97–100. DOI: 10.11646/zootaxa.3860.1.7
- Gess F.W., Gess S.K. 1976. An ethological study of *Parachilus insignis* (Saussure) in the eastern Cape Province of South Africa. *Annals of the Cape Provincial Museums. Natural History* 11(5): 83–102.
- Grandi G. 1957. Contributi alla conoscenza degli Imenotteri meliferi e predatori. XXVII. *Bollettino dell’Istituto di Entomologia della Università degli Studi di Bologna* 22: 307–398.
- Grandi G. 1961. Studi di un entomologo sugli Imenotteri superiori. *Bollettino dell’Istituto di Entomologia della Università degli Studi di Bologna* 25: 1–661.
- Hacker H. 1918. Entomological contributions. *Memoirs of the Queensland Museum* 6: 106–111.
- Ivanov S.P., Fateryga A.V. 2006. The nesting biology of solitary wing folded wasp, *Syneuodynerus egregius* (Hymenoptera, Vespidae, Eumeninae) in Crimea. *Vestnik Zoologii* 40(4): 341–349. [In Russian]
- Ivanov S.P., Fateryga A.V. (Eds.). 2016. *Red Book of the Republic of Crimea. Animals. 2nd ed.* Simferopol: Arial. 440 p. [In Russian]
- Ivanov S.P., Fateryga A.V., Zhidkov V.Yu. 2019. Aculeate Hymenoptera (Hymenoptera, Aculeata) inhabiting trap nests in Crimea. *Entomological Review* 99(2): 163–179. DOI: 10.1134/S0013873819020040
- Iwata K. 1976. *Evolution of instinct. Comparative ethology of Hymenoptera*. New Delhi: Amerind Publishing Co. Pvt. Ltd. 536 p.
- Krombein K.V. 1967. *Trap-nesting wasps and bees: life histories, nests, and associates*. Washington: Smithsonian Press. 570 p. DOI: 10.5962/bhl.title.46295
- Luo L., Carpenter J.M., Chen B., Li T.J. 2022. First comprehensive analysis of both mitochondrial characteristics and mitogenome-based phylogenetics in the subfamily Eumeninae (Hymenoptera: Vespidae). *Insects* 13(6): 529. DOI: 10.3390/insects13060529
- Mader D. 2000. Nistökologie, Biogeographie und Migration der synanthropen Delta-Lehmwespe *Delta unguiculatum* (Eumenidae) in Deutschland und Umgebung. *Dendrocopos* 27(2): 1–245.
- Martynova K.V., Fateryga A.V. 2015. Chrysidid wasps (Hymenoptera, Chrysididae) – parasites of eumenine wasps (Hymenoptera, Vespidae: Eumeninae) in Crimea. *Entomological Review* 95(4): 472–485. DOI: 10.1134/S0013873815040090
- Mauss V., Kuba K., Krenn H.W. 2019. Evolution of the multifunctional mouthparts of adult Vespidae. In: H.W. Krenn (Ed.): *Insect mouthparts. Zoological Monographs* 5. Cham: Springer. P. 443–478. DOI: 10.1007/978-3-030-29654-4_14
- Morgan D. 1984. *Handbooks for the identification of British insects. Vol. 6, part 5. Cuckoo-wasps. Hymenoptera, Chrysididae*. London: Royal Entomological Society of London. 37 p.
- Mortimer C.H. 1908. *Odynerus basalis* in Dorset. *Entomologist’s Monthly Magazine* 44: 236.
- Parker F.D. 1984. Nests and nest associates of two “red” *Odynerus* wasps (Hymenoptera: Eumeni-

- dae). *Journal of the Kansas Entomological Society* 57(3): 521–525.
- Pauly A., Vago J.L., Wahis R. 2003. La couleur vert pomme chez les Hyménoptères de Madagascar (Vespidae, Apidae, Pompilidae, Leucospidae). *Annales du Musée Royal de l'Afrique Centrale. Zoologie* 291: 91–98.
- Red Data Book of Sevastopol. Kaliningrad; Sevastopol: ROST-DOAFK, 2018. 432 p. [In Russian]
- Rosa P., Lelej A.S., Belokobylskij S.A., Vinokurov N.N., Zaytseva L.A. 2019. *Illustrated and annotated checklist of the Russian cuckoo wasps (Hymenoptera, Chrysididae)*. *Entomofauna, Supplement* 23. Ansfielden. 360 p.
- Selis M. 2020. On generic placement of *Odynerus dictatorius* Giordani Soika and its mimicry ring (Hymenoptera: Vespidae: Eumeninae). *Zootaxa* 4845(1): 83–96. DOI: 10.11646/zootaxa.4845.1.6
- Spooner G.M. 1934. Observations on *Odynerus (Lionotus) herrichi* Sauss. in Dorset. *Entomologist's Monthly Magazine* 70: 46–54.
- Spradbery J.P. 1973. *Wasps; an account of the biology and natural history of solitary and social wasps*. Washington: University of Washington Press. 408 p.
- Vadyunina A.F., Korchagina Z.A. 1986. *Methods of the studying of physical properties of soils*. 3rd ed. Moscow: Agropromizdat. 416 p. [In Russian]

К БИОЛОГИИ ДВУХ ГНЕЗДЯЩИХСЯ В ЗЕМЛЕ ВИДОВ ОС-ЭВМЕНИН (HYMENOPTERA: VESPIDAE: EUMENINAE) И ПАРАЗИТИРУЮЩИХ НА НИХ ОС-БЛЕСТЯНОК (HYMENOPTERA: CHRYSIDIDAE) В ПРИРОДНОМ ПАРКЕ «ТАРХАНКУТСКИЙ» (КРЫМ)

А. В. Фатерыга^{1,*} , В. В. Фатерыга¹ , М. В. Ончуров² 

¹Карадагская научная станция имени Т.И. Вяземского – природный заповедник РАН, Россия

*e-mail: fater_84@list.ru

²Крымский федеральный университет имени В.И. Вернадского, Россия

Hemipterochilus bembeciformis и *Tropidodynerus interruptus* гнездятся в земле с довольно сходными почвенными характеристиками (легкий или средний суглинок). Было раскопано два гнезда первого вида и четыре – второго. Оба вида использовали воду для размягчения грунта. Самки *H. bembeciformis* выстраивали на входе в гнездо ободок из грязи, имеющий высоту 1–4 мм; вход в гнездо *T. interruptus* был простым, но самки временно закладывали его комочками из грязи. Одно гнездо *H. bembeciformis* было брошенным, другое содержало две ячейки, которыми оканчивался разветвленный гнездовой ход; все гнезда *T. interruptus* были одноячейковыми. В качестве добычи *H. bembeciformis* была обнаружена гусеница *Acontia trabealis* (Lepidoptera: Noctuidae); самки *T. interruptus* охотились на личинок *Rhinocyllus conicus* (Coleoptera: Curculionidae), извлекая их из увядающих корзинок *Carduus nutans* subsp. *leiophyllus*. У гнезд обоих видов были обнаружены осы-блестянки *Chrysis cylindrica* и *Ch. valesiana*, однако коконы лишь первого из них были найдены в ячейках как *H. bembeciformis*, так и *T. interruptus*. *Chrysis cylindrica* – паразитоид, личинка которого питается личинкой хозяина, поскольку его коконы были найдены внутри коконов вида осы-хозяйки. Описан кокон *T. interruptus*. *Hemipterochilus bembeciformis* и *T. interruptus* образуют кольцо мюллеровской мимикрии с, как минимум, двумя другими видами ос-эвменин, обитающими вместе с ними в природном парке «Тарханкутский»: *Paragymnomerus signaticollis* и *Pseudepipona herrichii*. Обсуждается биология всех четырех видов; все они приурочены к уязвимым степным местообитаниям и требуют нашего внимания и мероприятий по их сохранению.

Ключевые слова: *Chrysis cylindrica*, *Hemipterochilus bembeciformis*, *Tropidodynerus interruptus*, гнездовые паразиты, кольцо мимикрии, строение гнезд, трофические связи