

A further study of the nesting biology of *Leptochilus* (*Neoleptochilus*) *regulus* (de Saussure, 1855) (Hymenoptera, Vespidae, Eumeninae)

Alexander V. Fateryga¹, Valentina V. Fateryga¹

¹ T.I. Vyazemsky Karadag Scientific Station – Nature Reserve of RAS – Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Kurortnoye 298188, Feodosiya, Russia

Corresponding author: Alexander V. Fateryga (fater_84@list.ru)

Academic editor: M. Proshchalykin | Received 30 March 2021 | Accepted 5 May 2021 | Published 24 August 2021

<http://zoobank.org/000B65DE-0DBF-4B28-8321-9B67E664EB64>

Citation: Fateryga AV, Fateryga VV (2021) A further study of the nesting biology of *Leptochilus* (*Neoleptochilus*) *regulus* (de Saussure, 1855) (Hymenoptera, Vespidae, Eumeninae). In: Proshchalykin MYu, Gokhman VE (Eds) Hymenoptera studies through space and time: A collection of papers dedicated to the 75th anniversary of Arkady S. Lelej. Journal of Hymenoptera Research 84: 75–86. <https://doi.org/10.3897/jhr.84.66652>

Abstract

Two females of *Leptochilus regulus* (de Saussure, 1855) were observed nesting in reed stalks of a Fabre's hive serving as a block of trap nests in Crimea, with the timekeeping of all their nesting behaviours. The building material used by the females to separate the nesting cavity into the cells consisted of pellets of dry soil, gravel particles, and small fragments of tree bark, leaves, and thin stems. Females rapidly carried these items collected in 1.0–1.5 m from the nests. They bonded only the last portions of the building material in each “partition” with a very small amount of mud. An additional amount of unbonded building material items was deposited into the nest after sealing the last nest cell. Females hunted exclusively for small larvae of an anobiid beetle (Coleoptera, Anobiidae); they stored 19–37 prey items per cell. Hunting and provisioning occupied the largest portion of the females' time budget. Duration of hunting flights was different between the females. The nests of both females contained three brood cells. Cocoons of *Chrysis ragusae* De Stefani, 1888 (Hymenoptera, Chrysididae) were found in the nests; females of this cuckoo wasp species were also recorded entering the host nests at the stage of provisioning, acting apparently as inquilines. The cocoon ultrastructure of *L. regulus* is illustrated and discussed.

Keywords

Crimea, *Chrysis ragusae*, cocooning behaviour, eumenine wasps, host-parasite association, nesting activity, solitary wasps

Introduction

The genus *Leptochilus* de Saussure, 1853 is the largest one in the subfamily Eumeninae (sensu Bank et al. 2017 and Piekarski et al. 2018). The genus includes 201 described species in six subgenera and is distributed in most zoogeographical regions except of the Australian, while most species (191) occur in the Holarctic (according to Fateryga et al. 2020, combined with a newly described species by Schmid-Egger et al. 2021). The bionomics of *Leptochilus* are rather poorly known. Sixteen species of the subgenus *Zendalia* Robertson, 1928 were studied in detail in the Nearctic region (Parker 1966). In a recent paper by Fateryga et al. (2020), the data on seven Palaearctic species were summarized with a detailed description of the habits of an eighth one. The authors, however, did not notice an important note by Berland (1927), who postulated that Fabre (1891) and Ferton (1895) had misidentified *Leptochilus* (*Euleptochilus*) *duplicatus* (Klug, 1835) [= *Odynerus sazi* Dusmet, 1909] as *L. (Lionotulus) alpestris* (de Saussure, 1855) [= *O. alpestris* de Saussure, 1855]. Ferton (1914) also provided a putative note on a nest of *Odynerus punctizona* Ferton, 1914, a tentative synonym of *Leptochilus* (*Neoleptochilus*) *medanae* (Gribodo, 1886) (van der Vecht and Fischer 1972). Taking this into account, at least 25 species of *Leptochilus* have been studied bionomically to date (this number includes both detailed bionomical accounts and brief data such as the nesting substrate only).

Leptochilus (*Neoleptochilus*) *regulus* (de Saussure, 1855) is a rather broadly distributed Mediterranean species known from Western, Southern, and Eastern Europe, North Africa, the Caucasus, and the Middle East (Antropov and Fateryga 2017). Its nests were for the first time observed by Ferton (1901, 1914) in France (under the name *Odynerus gallicus* de Saussure, 1855) and in Algeria. The author reported this species to nest in various pre-existing cavities such as holes in wood or pithy stems, stone caverns, and empty snail shells. The building materials used to separate the nesting cavity into the cells were gravel particles, pellets of soil, and tiny plant fragments; these materials laid loosely in a part of the nests while they were bonded with mud in the rest of the nests. Nests from Algeria were provisioned by both moth (Lepidoptera) and anobiid beetle (Coleoptera, Anobiidae) larvae; two kinds of prey were mixed even within the same nest cell. Fateryga (2013, 2014) described two nests of *L. regulus* in reed stalks of trap nests from Crimea. Both nests contained nine cells separated by “partitions” corresponding in structure to Ferton’s descriptions. Burger and Hahnefeld (2016) reported this species to nest in small caverns of concrete walls and sandstones in Germany; this paper was overlooked by Fateryga et al. (2020). Burger and Reder (2018) also speculated that *L. regulus* was a host of *Chrysis ragusae* De Stefani, 1888, a species of cuckoo wasps (Hymenoptera, Chrysididae).

The purpose of the present contribution is to report new data on the bionomics of *Leptochilus regulus*, particularly, the nesting activity of the females. We also take this opportunity to provide some additions to the previously described cocoon of this species (Fateryga 2013).

Material and methods

Nesting of *Leptochilus regulus* was observed at the T.I. Vyazemsky Karadag Scientific Station in Crimea (44°54.8'N, 35°12.1'E), in a garden. Two females (A and B) were recorded nesting in a Fabre's hive serving as a block of trap nests (Ivanov et al. 2019). The hive contained stalks of a reed, *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae) of varying diameter and pithy stems of a willow, *Salix caprea* L. (Salicaceae); in the ends of the latter ones, holes were bored into the pith. The females were first recorded on 25.VI.2020 in the afternoon, both in reed stalks. The next day, they were observed with the timekeeping of all their nesting behaviours from 8:00 to 18:00 (solar time). The nest of female A was extracted from the hive and dissected on 26.VI.2020, that of female B on 11.VII.2020. Stalks with both nests were split longitudinally and the nest structure and the contents were examined. Cocoons of a cuckoo wasp found in nest B were kept under outdoor conditions till 1.III.2021 and then transferred to incubation under 27 °C. Cocoons of *L. regulus* examined in this study were taken from a nest collected in Crimea in 2010 (Fateryga 2013).

Photographs were taken with a Canon EOS M6 camera and a Sigma 105 mm macro lens (scale up to 1:1) except a photograph of the nest collected in 2010 taken with a Canon PowerShot A570 IS camera. SEM micrographs of the cocoons were taken using a Hitachi SE3500 Scanning Electron Microscope. The cocoon fragments were not critical-point dried; they were simply mounted on stubs and coated with gold and palladium.

Results

Nesting activity

The observations started at 13:07 (solar time) when female A provisioned its nest while female B sealed a cell. The building materials used by female B were pellets of dry soil and gravel particles. The female collected these items on the ground surface in 1.0–1.5 m from the hive. Each portion of the building material was carried with the mandibles (Fig. 1) and rapidly put into the nest hole. The prey items used by female A were small larvae of an anobiid beetle (Coleoptera, Anobiidae) (Figs 2, 3). They were also transported with the mandibles only. When female A was disturbed by the observer after its landing with a prey item, it turned the body and stood for some seconds towards the disturber (Fig. 3). Otherwise, the female quickly entered the nest (Fig. 2). This female brought in a total of ten anobiid larvae and finished its activity at 15:47 when it entered the nest hole backwards. Female B finished its building activity after an hour of observations, returned head first, and entered the nest hole backwards at 14:26. It came out at 14:29; during these three minutes it apparently laid an egg. After that, it subsequently brought in four prey items and entered the nest hole backwards (finished its activity) at 15:58.



Figures 1–6. Bionomics of *Leptochilus regulus* (de Saussure, 1855) **1** female arriving with a portion of the building material **2,3** female arriving with a prey item **4** female inspecting a willow stem while searching a place for a new nest **5** male perching in front of the nest **6** female of *Chrysis ragusae* De Stefani, 1888 waiting at the nest site.

The next day, activity of female B started at 8:50 while the activity of female A started at 9:09 (Fig. 7). Both females continued their hunting. Female A subsequently brought in 13 anobiid larvae and started sealing the nest at 10:52. It brought in 66 portions of the building material (pellets of dry soil, gravel particles, and small fragments of tree bark, leaves, and thin stems) and then flew away at 14:43. Nest sealing

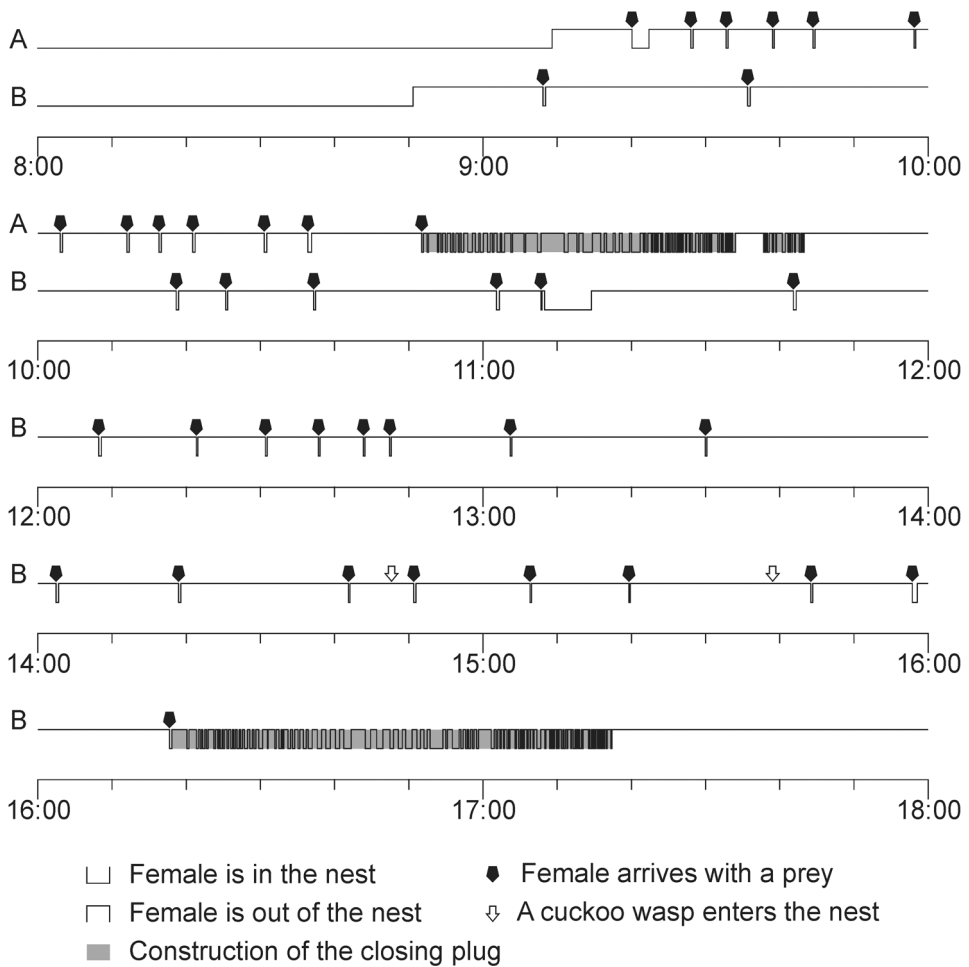


Figure 7. Chronogram of the activity of two females (**A, B**) of *Leptochilus regulus* (de Saussure, 1855) on 26.VI.2020 (solar time).

was interrupted for three minutes from 11:34 to 11:37 when the female was absent from the nest (after that, it arrived without a portion of the building material). This female also returned to the hive once in the afternoon (not shown in the Fig. 7) when it was searching for a place for a new nest. It investigated empty reed stalks and willow stems (Fig. 4) but did not start nesting there. Female B subsequently brought in 25 anobiid larvae. It had a rest for six minutes from 11:08 to 11:14 when it was standing inside the nest hole with its head directing towards the entrance (it had entered backwards). The provisioning was completed at 16:20. After that, the female brought in 85 portions of the building material and then flew away at 17:17 (Fig. 7). No females of *Leptochilus regulus* were recorded at the hive during subsequent days suggesting that both nests had been finished by the wasps on 26.VI.2020.

Table 1. Duration (minutes) of some nesting behaviours of two females of *Leptochilus regulus* (de Saussure, 1855) (n = sample size; CI = confidence interval, p = 0.05).

Parameter	n	Minimum – maximum	Mean ± CI
Hunting and transport of a prey item	32	3.35–42.65	14.24 ± 5.86
the same, for female A only	11	4.00–13.38	6.95 ± 1.85
the same, for female B only	21	3.35–42.65	18.06 ± 6.00
Deposition of a prey item into the nest	31	0.17–2.28	0.34 ± 0.22
Collecting and transport of a portion of the building material	117	0.08–3.08	0.41 ± 0.23
Deposition of a portion of the building material into the nest	117	0.03–1.72	0.31 ± 0.15

Hunting and provisioning evidently occupied the largest portion of the females' time budget. Hunting and provisioning flights of female A were nearly three times shorter than those of female B (Table 1), the difference was significant (Student's t-test: $t = 4.62$; $p \leq 0.01$). Duration of a deposition of a prey item into the nest was very short and took usually much less than a minute; the same was true for the building behaviours: collecting and transporting a portion of the building material and depositing it into the nest (Table 1). All these activities were not different between the females ($t = 0.99, 0.46$, and 0.97). In both females, the length of the time intervals spent for the deposition of a single portion of the building material was longer in the middle of the nest sealing process while it was very short both at the beginning and at the end (Fig. 7). Apparently, the females initially merely put portions of the building material into the nest hole, then did some manipulations after carrying each portion, and finally again merely deposited these portions without any processing. It is also worthy to mention that the longest flights for the building material preceded the longest deposition acts (Fig. 7). This may indicate that the females selected a certain type of the building material (such as pellets of dry soil or gravel particles) in the middle of the nest sealing phase while otherwise took any items of a suitable size (including plant fragments).

Male behaviour

A male of *Leptochilus regulus* was observed near the nests. It was recorded at the hive three times on 25.VI.2020 and three times during the next day. Each time it investigated several reed stalks and willow stems, but paid considerably more attention to the nest of female A (Fig. 5).

Associated insects observed

Three females of the cuckoo wasp *Chrysis ragusae* were recorded at the nest site. All of them were rapidly walking on walls of the hive and inspecting them with their antennae (Fig. 6). Females of *Ch. ragusae* entered the nest of female B two times during the observations. Both times the host female was hunting and thus absent from the nest (Fig. 7).

Nest structure and contents

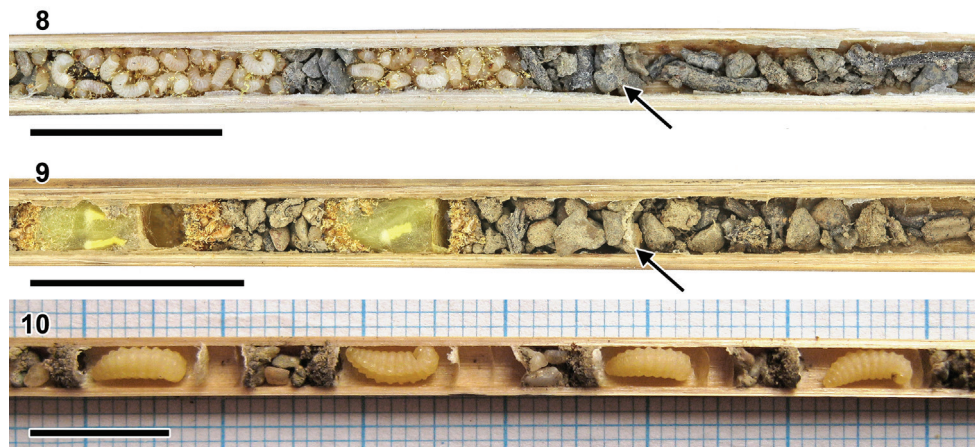
The nest of female A was built in a reed stalk 16 cm long and 3.0 mm in the inner diameter. There was a trace of an old nest of the same species at the inner end of the reed stalk. This may explain the presence of a male at the nest site: it may have emerged from that old nest and returned to the site of its emergence for mating. The same could be true for the females as well. The nest of female A contained three brood cells separated by large amounts of gravel particles and soil pellets. Most of them laid loosely except some gravel particles on the outer surface of each “partition”, which were bonded with a very small amount of mud (Fig. 8). The closing plug consisted of the same “partition” and an additional amount of loosely laying materials such as gravel particles, soil pellets, and plant fragments. This explains why the longest acts of the deposition of the building material occurred in the middle of the construction of a closing plug (see above): those acts included bonding of gravel particles with mud. Apparently, the mud was prepared by moistening dry soil pellets with saliva and this took place inside the nest since the females did not do this while they were collecting the building material.

The first cell in the nest of female A contained prey remains characteristically damaged by a fly maggot but the immature fly itself was not found. The second cell contained 37 prey items and no immature wasp (apparently, it was also damaged by that supposed maggot penetrating through the “partition” between the first and second cells). The third cell contained 33 prey items and a dead wasp larva of the first instar. Another smaller hymenopteran larva was found in the same cell; apparently, it killed the host larva. Unfortunately, the second larva also died the next day. We can just speculate that it was a larva of *Chrysis ragusae*.

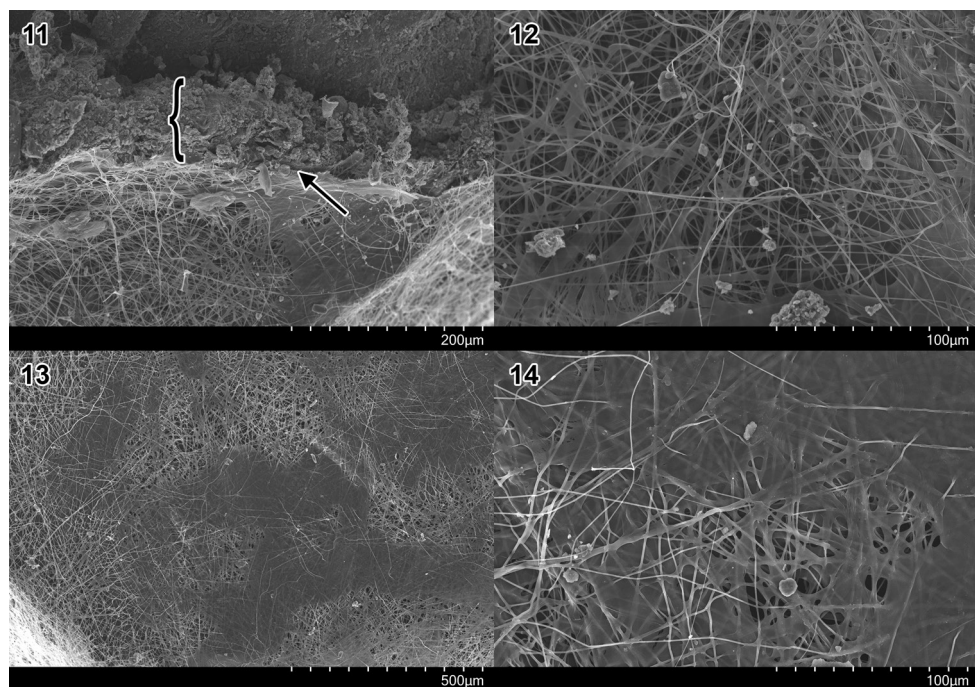
The nest of female B was built in a reed stalk which was 15 cm long and 3.2 mm in the inner diameter. This nest also contained three cells. The structure of the “partitions” and the closing plug was similar to that in the previous nest (Fig. 9). The first cell contained 19 prey items and a dead larva of the first instar. A dead adult female of *Melittobia acasta* (Walker, 1839) (Hymenoptera, Eulophidae) was also found in that cell. Two other cells contained cocoons of *Chrysis ragusae* (Fig. 9). Two females of this cuckoo wasp emerged on 23 and 25.III.2021 (on 23rd and 25th days of incubation).

Cocoon structure

The nest described in an earlier paper (Fateryga 2013) contained cocoons of *Leptochilus regulus* with prepupae inside (Fig. 10). The cocoons consisted of three to four layers. The outer layer, tightly adhering to the cell walls and “partitions”, consisted of silk strands of various widths, which were sometimes covered from inside by a smooth, presumably airtight, thin film of silk (Figs 11–12). The inner layer was made distantly from the inner surface of the outer “partition” of the cell. It was combined with the outer layer at the bottom (i.e., on the outer surface of the inner cell “partition”) and along lateral walls of the cell while it had a form of a transverse septum in its free, outer part. The inner layer was not principally different from the outer one in its ultrastructure; it also con-



Figures 8–10. Nests of *Leptochilus regulus* (de Saussure, 1855) **8** part of the nest of female A (two cells provisioned with anobiid larvae and the closing plug) **9** part of the nest of female B (two cells with cocoons of *Chrysis ragusae* De Stefani, 1888 and the closing plug) **10** part of the nest collected in 2010 (four cells with prepupae in cocoons). Scale bars 1 cm; arrows indicate a small amount of bonded soil in the closing plugs.



Figures 11–14. SEM micrographs of two cocoon layers of *Leptochilus regulus* (de Saussure, 1855) **11** dissection of the outer layer with a part of the inner surface of the outer cell “partition” **12** the same layer from inside, close up **13** the inner layer (free part) from inside **14** the same, close up. Arrow indicates the cocoon on the dissection; figure parenthesis indicates the material of the “partition”.

sisted of silk strands and smooth films (Figs 13, 14). The meconium was located inside the inner cocoon layer, on the bottom of the cell. One or two middle cocoon layers were present between the outer “partition” of the cell (covered with the outer layer) and the inner layer. They had the same structure as the inner layer in its free part.

Discussion

Fateryga et al. (2020) speculated that the method of nest construction of *Leptochilus regulus* is the same as that of *L. (Euleptochilus) limbiferus* (Morawitz, 1867). The latter species is known to nest in empty snail shells; it seals the shell opening with a large amount of pellets of dry soil and then puts in some gravel particles which are finally bonded. To bond the gravel particles, the wasp licks the soil pellets between them with its glossa secreting saliva with a significant proportion of nectar. That species often collects nectar by robbing it from flowers with spurs (Fateryga et al. 2020). *Leptochilus regulus* is known to visit flowers of *Anthemis* sp., *Erigeron annuus* (L.) Desf., *Leucanthemum vulgare* Lam. (Asteraceae) (Burger and Hahnefeld 2016), *Mentha longifolia* (L.) L. (Lamiaceae), and *Nigella arvensis* L. (Ranunculaceae) (Fateryga 2020). It was apparently not recorded robbing nectar but it also uses a very small amount of liquid to bond some gravel particles while sealing the cells. Different from *L. limbiferus*, *L. regulus* adds an additional amount of unbonded building material items after sealing the last nest cell. Other habits of *L. regulus* concerning the building material are indeed similar to those of *L. limbiferus*: both species use pellets of dry soil and gravel particles and deposit them in a form of a pile (without bonding of each item). Therefore, we can confirm the previous speculation that these two species are similar in their building behaviour. Nests of *L. regulus* are, however, variable. They can be made in various kinds of pre-existing cavities; their “partitions” can be either rather thick and look like an unbonded pile of materials (Ferton 1901), or thinner and look like several bonded gravel particles resembling a true partition (Ferton 1914). We can explain this by various diameters of the nest hole and various amounts of the building material items used to construct each “partition”. The method of the construction is, however, always the same: the wasp first deposits several building material items and after that bonds only the outer surface of the produced pile. We can now also explain how soil appears between the cocoon and the prey feces in the nests of *L. regulus* (Fateryga 2013): the larva crumbled and moved the pellets of dry soil from the outer “partition” towards the inner one, similarly as the larva of *L. limbiferus* does (Fateryga et al. 2020).

The present study also confirms the host-parasite association between *Leptochilus regulus* and *Chrysis ragsae* previously assumed by Burger and Reder (2018). Following the classification of the cuckoo wasps associated with the eumenine wasps (Martynova and Fateryga 2015), *Ch. ragsae* can be considered an inquiline. The females of inquilines deposit an egg in the host cell at the stage of provisioning; the few existing data point to the fact that the young inquiline larvae kill the egg or the young host larva and after that feed on the stored provisions. This seems to be characteristic of *Ch. ragsae*

in the nests of *L. regulus*. It is interesting that the distributional range of *Ch. ragusae* is narrower than that of *L. regulus* and does not include the Caucasus and the Middle East (Agnoli and Rosa 2021).

The cocoon ultrastructure of *Leptochilus regulus* is quite similar to that previously illustrated for *L. limbiferus* (Fateryga et al. 2020). In both species, the cocoons consist of several rather thin layers: the outer layer adhering to the cell walls, followed by at least one but up to three middle layers in the form of transverse septa, and the inner layer surrounding the developing wasp. The only difference is that the inner cocoon layer of *L. limbiferus* is thicker than the middle ones while they are equal in thickness in *L. regulus*. In both species, all cocoon layers consist of silk strands and films; no building materials are incorporated into them. Thus, these cocoons are typical of the eumenine wasps but different from some Nearctic representatives of the genus *Leptochilus* (subgenus *Zendalia*). Larvae of some of them reinforce the outer layer of their cocoons with embedded sand grains, and in doing so distribute the outer “partition” material over the whole surface of the cell walls. Besides, before spinning the cocoon proper, larvae of some species (the group of *L. rufinodus* Cresson, 1868) build an additional transverse partition using sand from the outer “partition” of the cell. Larvae of some other species of *Zendalia*, however, merely line the cell walls with silk while cocooning (Parker 1966).

Such a polymorphism in the cocoon structure within the genus *Leptochilus* may suggest that it is not a monophyletic group. Two genera were recently segregated from another eumenine wasp genus *Odynerus* Latreille, 1802 on the base of the cocoon structure besides the morphology (Fateryga 2021). In our opinion, the genus *Leptochilus* should be also thoroughly studied morphologically (and possibly also genetically) to ascertain its phylogeny in relation to the closely related genera such as *Stroudia* Gribo, 1892, *Labochilus* Blüthgen, 1939, *Cyrtolabulus* van der Vecht, 1969, etc.

Acknowledgments

We thank Arkady S. Lelej, a great and famous Russian entomologist, for his permanent support of the solitary wasp studies, conducted by the first author, and express our best wishes for his 75th birthday anniversary.

Kateryna V. Martynova (Kyiv, Ukraine) confirmed the identification of the cuckoo wasp. Petr Bogusch (Hradec Králové, Czech Republic) and an anonymous reviewer provided helpful suggestions on the first version of this paper. Anagnostis P. Agelarakis (New York, USA) kindly improved our English. The reported study was a part of the State research project No. 121032300023-7.

References

Agnoli GL, Rosa P (2021) Chrysis.net website. Interim version. <https://www.chrysis.net/> [accessed 22 March 2021]

- Antropov AV, Fateryga AV (2017) Family Vespidae. In: Lelej AS, Proshchalykin MYu, Loktionov VM (Eds) Annotated Catalogue of the Hymenoptera of Russia. Volume I. Symphyta and Apocrita: Aculeata. Proceedings of the Zoological Institute RAS, Supplement 6: 175–196. <https://doi.org/10.31610/trudyzin/2017.supl.6.5>
- Bank S, Sann M, Mayer C, Meusemann K, Donath A, Podsiadlowski L, Kozlov A, Petersen M, Krogmann L, Meier R, Rosa P, Schmitt T, Wurdack M, Liu S, Zhou X, Misof B, Peters RS, Niehuis O (2017) Transcriptome and target DNA enrichment sequence data provide new insights into the phylogeny of vespid wasps (Hymenoptera: Aculeata: Vespidae). *Molecular Phylogenetics and Evolution* 116: 213–226. <https://doi.org/10.1016/j.ympev.2017.08.020>
- Berland L (1927) Rectification de quelques noms d'Odynères employés par Ferton. *Annales de la Société Entomologique de France* 96: 92.
- Burger R, Hahnefeld M (2016) Erste Nachweise der Zwerg-Mauerwespen-Art *Leptochilus regulus* in Rheinland-Pfalz. Verbreitung, Ökologie und Nistweise in Südwestdeutschland. *Pollichia-Kurier* 32(1): 14–17.
- Burger R, Reder G (2018) Erstnachweis von *Chrysis ragusae* De Stephani, 1888 in Deutschland und Hinweise auf den Wirt (Hymenoptera: Chrysididae). *Ampulex* 10: 24–26.
- Fabre J-H (1891) Souvenirs entomologiques. Études sur l'instinct et les mœurs des insectes. Quatrième série. Librairie Ch. Delagrave, Paris, 330 pp.
- Fateryga AV (2013) On the nest structure in two species of the genus *Leptochilus* (Hymenoptera, Vespidae, Eumeninae). *Vestnik Zoologii* 47(5): 469–473. <https://doi.org/10.2478/vzoo-2013-0045>
- Fateryga AV (2014) Notes on the nesting habits of *Leptochilus regulus* (Hymenoptera, Vespidae, Eumeninae). *Vestnik Zoologii* 48(2): 190.
- Fateryga AV (2020) New data on trophic relationships of eumenine wasps (Hymenoptera, Vespidae: Eumeninae) with angiosperm plants in Crimea. *Entomological Review* 100(4): 497–509. <https://doi.org/10.1134/S0013873820040077>
- Fateryga AV (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. <https://doi.org/10.25221/fee.427.1>
- Fateryga AV, Popovich AV, Podunay YuA, Fateryga VV (2020) First data on the bionomics of *Leptochilus* (*Euleptochilus*) *limbiferus* (Morawitz, 1867) (Hymenoptera: Vespidae: Eumeninae), with taxonomic notes and new records. *Zootaxa* 4851(2): 289–304. <https://doi.org/10.11646/zootaxa.4851.2.4>
- 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 (1901) Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs avec la description de quelques espèces. *Annales de la Société Entomologique de France* 70: 83–148. [+ pls 1–3.]
- Ferton C (1914) Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs (8^e série) avec la description de quelques espèces nouvelles. *Annales de la Société Entomologique de France* 83: 81–119. [+ pls III–V.]

- Ivanov SP, Fateryga AV, Zhidkov VYu (2019) Aculeate Hymenoptera (Hymenoptera, Aculeata) inhabiting trap nests in Crimea. Entomological Review 99(2): 163–179. <https://doi.org/10.1134/S0013873819020040>
- Martynova KV, Fateryga AV (2015) Chrysidid wasps (Hymenoptera, Chrysididae) – parasites of eumenine wasps (Hymenoptera, Vespidae: Eumeninae) in Crimea. Entomological Review 95(4): 472–485. <https://doi.org/10.1134/S0013873815040090>
- Parker FD (1966) A revision of the North American species in the genus *Leptochilus* (Hymenoptera: Eumenidae). Miscellaneous Publications of the Entomological Society of America 5: 151–229.
- PiekarSKI PK, Carpenter JM, Lemmon AR, Lemmon EM, Sharanowski BJ (2018) Phylogenomic evidence overturns current conceptions of social evolution in wasps (Vespidae). Molecular Biology and Evolution 35(9): 2097–2109. <https://doi.org/10.1093/molbev/msy124>
- Schmid-Egger C, Gusenleitner J, Liebig W-H, Jacobs H-J (2021) New records of Vespidae (Hymenoptera) from Iran with descriptions of three species. Linzer Biologische Beiträge 52(2): 1105–1121.
- van der Vecht J, Fischer FCJ (1972) Hymenopterorum Catalogus. Pars 8. Palaearctic Eumenidae. N.V. Junk, 's-Gravenhage, 199 pp.