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Nesting and Biology of *Alastor mocsaryi* (Hymenoptera, Vespidae: Eumeninae)

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Abstract—The nest structure of *Alastor mocsaryi* in trap nests was studied in Crimea. Fifteen nests were examined, located inside hollow reed stems 3.0–4.8 mm in inner diameter. The nests contained 1–9 cells separated by partitions. These were made of gravel cemented with soil mastic or sand. The bottom partitions (present in 14 nests) and final plugs (present in 2 nests) also contained loose gravel particles. The mean cell length was greater in the nests made in narrow cavities than in those made in broad cavities. The mean length of a cell with a female exceeded that of a cell with a male. Females provisioned the nest cells with weakly paralyzed larvae of curculionid beetles. The cocoon looked as whitish cobweb-like film and could be detached from the cell walls. The prepupae retained a high level of mobility during winter hibernation. Adult feeding was recorded on flowers of 12 plant species belonging to 9 families. Only 3 of them had nectar accessible to *A. mocsaryi* while 9 species were specialized melittophilous (7 species) or psychophilous plants (2 species). The wasps obtained nectar from flowers of the latter plants through holes in the perianth which they gnawed out with their mandibles. The nest partitions were found to contain monosaccharides; this indicates that wasp females use nectar as building material, to moisten and bond dry soil and sand particles. Water collection by female *A. mocsaryi* was recorded only once. The species is univoltine. The sex ratio is female-biased. Attachment behavior of the females to the point of their emergence from mother nests (philopatry) was recorded. The nests were infested with the parasitoid wasps *Melittobia acasta* and *Hoplocryptus coxator*, a larva of the beetle *Trichodes apiarius*, and a puparium of an unidentified tachinid fly. The progeny mortality was 38.8%. Nesting of *A. mocsaryi* is discussed in relation to the phylogenetic position of the genus *Alastor*. The use of nectar as building material may be related to nectar robbing from the flowers of many plant species; this feature may also be characteristic of some other members of the subfamily Eumeninae.

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The genus *Alastor* Lepeletier de Saint Fargeau, 1841 (Hymenoptera, Vespidae, Eumeninae) is distributed in the Palaearctic, Afrotropical, and Oriental zoogeographic regions. Its world fauna comprises 79 species in 4 subgenera: *Alastor* s. str., *Alastorellus* Giordani Soika, 1991, *Megalastor* Blüthgen, 1951, and *Parastalor* Blüthgen, 1939. The nominotypical subgenus is distributed in all the three zoogeographic regions, the subgenus *Alastorellus*, only in the Afrotropical Region, and the remaining two subgenera, only in the Palaearctic. The genus *Alastor* is represented in the Palaearctic fauna by 28 species, one of which, *Alastor* (*Alastor*) *mocsaryi* (André, 1884) (= *A. biegelebeni* Giordani Soika, 1942) occurs in the territory of Russia (Antropov and Fateryga, 2017).

The specific biological features of members of the genus *Alastor* are rather scantily studied. There are data in the literature on the nesting of *Alastor* (*Alastor*) *atropos* Lepeletier de Saint Fargeau, 1841 in the south of Europe (Grandi, 1961) and of *Alastor* (*Alastor*) *ricae* Giordani Soika, 1934 in South Africa (Gess and Gess, 2008). Nests of *A. atropos* were found in hollow reed stems on roofs of village buildings. Nests of this species contain several cells separated by partitions made of fine gravel and soil mastic. *Alastor atropos* stores larvae of weevils of the genus *Gymnetron* Schonherr, 1825 (Coleoptera, Curculionidae) as provision. The female wasp weakly paralyses the prey; the weevil larvae extracted from the cells were capable of developing into pupae, and sometimes even into adults (Grandi, 1961). Little is known of the biology of *A. ricae*: this species nests in empty snail shells and uses fine gravel and sand cemented with unknown substance as building material (Gess and Gess, 2008). Nesting of *A. mocsaryi* is practically unknown; there is only one record of a nest of this species found inside a reed stem in Fabre’s hive (Ivanov et al., 2009).

According to the results of the latest phylogenetic reconstruction (Bank et al., 2017), the genus *Alastor* has an isolated position within the subfamily Eumeninae and is a sister group to all the other genera of the tribes Odynerini and Eumenini (sensu Hermes et al., 2014). Correspondingly, the biology of members of this genus is of special interest. The goal of this work was to study the nest structure, trophic associations, and other biological features of *A. mocsaryi*.

MATERIALS AND METHODS

Research was carried out in Crimea in 2002–2017. One nest of *A. mocsaryi* was found in 2002 in the environs of Yalta (44°31′10″N, 34°10′50″E), in an old nest of the bee *Ceratina chalybea* Chevrier, 1872 (Hymenoptera, Apidae) built inside a stem of *Rubus* sp. (Rosaceae). To obtain more nests, we used trap nests and special Fabre's hives (Ivanov et al., 2009) made of hollow stems of the reed *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae). The standard trap that was used most often consisted of a bundle of 20–25 reed stem segments 15–25 cm long and 3–12 cm in diameter. The trap nests were installed in 80 localities embracing all the landscape zones of the Crimean Peninsula. Nests of *A. mocsaryi* were obtained from 5 localities: Karadag Nature Reserve (44°56′00″N, 35°12′30″E), two nests in Fabre's hives (2005 and 2013); the south suburb of Simferopol (44°55′40″N, 34°07′40″E), four nests in trap nests on branches of various shrubs (2012 and 2013); Gvardeyskoye urban community (45°06′35″N, 33°59′55″E), three nests in a trap nest, on a balcony of a multistorey building (2012); Cherdakly-Bair Mt. (44°36′30″N, 33°47′50″E), one nest in a trap nest in a tree (2012); sand spit of Lake Donuzlav (45°19′10″N, 33°00′05″E), five nests in trap nests in shrubs of *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae). Altogether, 15 nests built in hollow reed stems were obtained and studied.

The structure and composition of the nests were analyzed in the laboratory in winter. The reed stem was split with a knife, and the upper part was detached from the tube. A schematic drawing of the opened nest was made on a sheet of paper. The size of the inner cavity of the reed stem (its length and greatest diameter), the number of nest cells, the lengths of their inner cavities, and the mass of prepupae were recorded on the same sheet. Measurements were carried out with a vernier caliper, compasses, and ruler; weighing was done with torsion balance. The preimaginal stages of wasps and other insects found in the nest cells were placed in short glass tubes tightly stopped at both ends with cotton wool and labeled with the nest and cell numbers. After emergence of adult wasps they were sexed, other insects were identified to species, and this information was added to the schematic drawing of the corresponding nest. The structure of partitions between the cells was studied under an MBS-9 binocular microscope equipped with an eyepiece graticule and documented as drawings on plotting paper.

The presence of sugars in the nest partition material was detected by a qualitative test for monosaccharides using α-naphthol (Shapiro, 1976). For this purpose, we sampled partitions from several nests of *A. mocsaryi*, with a total mass of 720 mg. These partitions were soaked for 24 h in 3 ml of distilled water, then the mixture was shaken up and filtered into a glass test tube via paper filter. Three drops of 0.2% solution of α-naphthol in 96% ethyl alcohol were added and the test tube was shaken up again. Then, an approximately equal amount of concentrated sulfuric acid was poured down the wall of the tube and allowed to gravitate to the bottom. The presence of monosaccharides was assessed by the appearance of reddish quinoid compound at the boundary of the layers of sulfuric acid and aqueous extract. For control, the same test was performed with extracts of identical quantities (720 mg) of nest partitions of *Euodynerus velutinus* Blüthgen, 1951 (Hymenoptera, Vespidae, Eumeninae) and the nest cell material of *Sceliphron curvatum* (F. Smith, 1870) (Hymenoptera, Sphecidae), and also with 0.4% aqueous solution of glucose and with distilled water.

The correlations between the nest cavity diameter, the cell length, and the structure of the bottom nest partition were assessed using Pearson's correlation coefficient r and Spearman's correlation coefficient r_S (Lakin, 1990). The confidence intervals of parameters were calculated for 95% confidence level ($p = 0.05$).

A special experiment was conducted to assess the degree of attachment of wasp females to the place of their emergence from maternal nests. At the end of May 2013, several days before the estimated date of adult emergence, prepupae of *A. mocsaryi* were returned to the cells of all the nests obtained in 2012, and these nests were placed into a Fabre's hive installed in the Karadag Nature Reserve. Attachment of the females to the place of their emergence was estimated by the number of nests that were founded in the same hive in 2013.

Table 1. The main parameters of structure and composition of *Alastor mocsaryi* nests built in hollow reed stems

Parameter	n	Range (min–max)	$\overline{x} \pm S_{\overline{x}}$
Cavity diameter, mm	15	3.0–4.8	3.90 ± 0.28
Cavity length, cm	15	7.2–25.5	14.93 ± 2.86
Number of cells	15	1–9	4.47 ± 1.47
Cell length, mm	63	9–26	13.35 ± 0.67
Length of cells with females, mm	16	10–21	13.31 ± 1.25
Length of cells with males, mm	6	9–13	11.83 ± 1.47
Mass of female prepupa, mg	15	26–40	18.29 ± 4.84
Mass of male prepupa, mg	4	19–26	14.94 ± 7.24

n is the sample size (number of studied nests or cells); $\overline{x} \pm S_{\overline{x}}$ are the mean and confidence interval ($p = 0.05$).

Observations of the trophic associations of *A. mocsaryi* were carried out in different Crimean localities in 2002–2017. The names of plants are mainly given according to the checklist of Yena (2012). The photographs were made with a Canon PowerShot A570 IS digital camera. The drawings of the cells, partitions, and flowers were produced by tracing of photographs and sketches made on plotting paper.

The adult flight phenology was studied using the collection material kept at the Taurida Academy of V.I. Vernadsky Crimean Federal University (Simferopol), the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), the Zoological Museum of M.V. Lomonosov Moscow State University (Moscow), I.I. Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine (Kiev), Taras Shevchenko National University of Kiev (Kiev), Kharkov Entomological Society (Kharkov), the State Natural History Museum of V.N. Karazin Kharkov National University (Kharkov), Odessa State Zoo (Odessa), and also private collections of S.A. Mosyakin (Simferopol), D.V. Puzanov (Yevpatoriya), and A.V. Amolin (Donetsk). Altogether, 348 specimens of *A. mocsaryi* collected in Crimea in 1900–2017 were studied; 342 specimens had collection dates in their labels.

RESULTS

Structure and Composition of Nests

The reed stems containing *A. mocsaryi* nests were of different length while their inner diameter varied within a relatively narrow range (Table 1). The nests consisted of one or several cells arranged in a row and separated by transverse partitions (Fig. 1*a*). Despite high variation in the nest cavity length and the number of cells, no correlation was revealed between these parameters.

The partitions consisted of fine gravel and usually of soil mastic (with the exception of nests from the sand spit of Lake Donuzlav). The gravel particles were about 1–3 mm in size, 1.7 ± 0.7 mm on average (based on measuring 3 rows of 30 particles), and had a mass of 1–6 mg (3.8 ± 0.6 mg on average). Almost every nest (14 out of 15) had a bottom partition that served as the bottom of the first cell. This partition differed from the rest in that it had some uncemented gravel at its base (Fig. 2*a*). It may be supposed that the wasp builds this partition in the following way: first it lays gravel particles to fill the inner cavity of the reed stem, then fastens them together. If, for some reason, the gravel particles cannot be placed properly on the first try the attempts are repeated, resulting in a great number of loose particles. Most nests contained 1–17 loose gravel particles in their bottom partitions but one nest had 106 such particles (the lower nest in Fig. 1*a*). Successful laying of gravel may be hindered by movements of the nest (for instance, when the trap nest was installed on a thin branch swinging in the wind) or by a too big inner diameter of the nest cavity. However, a positive correlation between the cavity diameter and the number of loose gravel particles in the bottom partition existed as a trend but was statistically nonsignificant ($r_S = 0.31$).

In most cases, the bottom nest partition was located close to the bottom (i.e., the dead end) of the reed stem cavity. This partition was positioned at some distance (49–133 mm) from the cavity end only in 5 nests, including all the 4 nests constructed in the longest stems

Fig. 1. Biology of *Alastor mocsaryi*: (*a*) dissected nests in hollow reed stems containing prepupae and a tachinid fly puparium (arrow); (*b*) female paralyzing a weevil larva extracted from the infructescence of *Plantago lanceolata*; (*c*) female feeding on a flower of *Polygonum patulum*; (*d*) female gnawing out a hole in the spur of *Linaria genistifolia*; (*e*) male gnawing out a hole in the calyx of *Salvia nemorosa* subsp. *pseudosylvestris*.

(over 20 cm), and 1 nest constructed in a relatively short stem (13.2 cm). One nest had no bottom partition at all, so that the bottom of the stem cavity served as the bottom of the first cell.

Partitions between the cells consisted only of fixed gravel and soil mastic (Fig. 2*a*). If the partition is constructed between cells, considerably fewer gravel particles seem to be needed to fill the inner stem lumen. This is related to the fact that before sealing the cell the wasp fills it tightly with provision consisting of weevil larvae (see below). Provision provides support for the gravel as it is cemented, similar to the pile of loose gravel before the bottom nest partition.

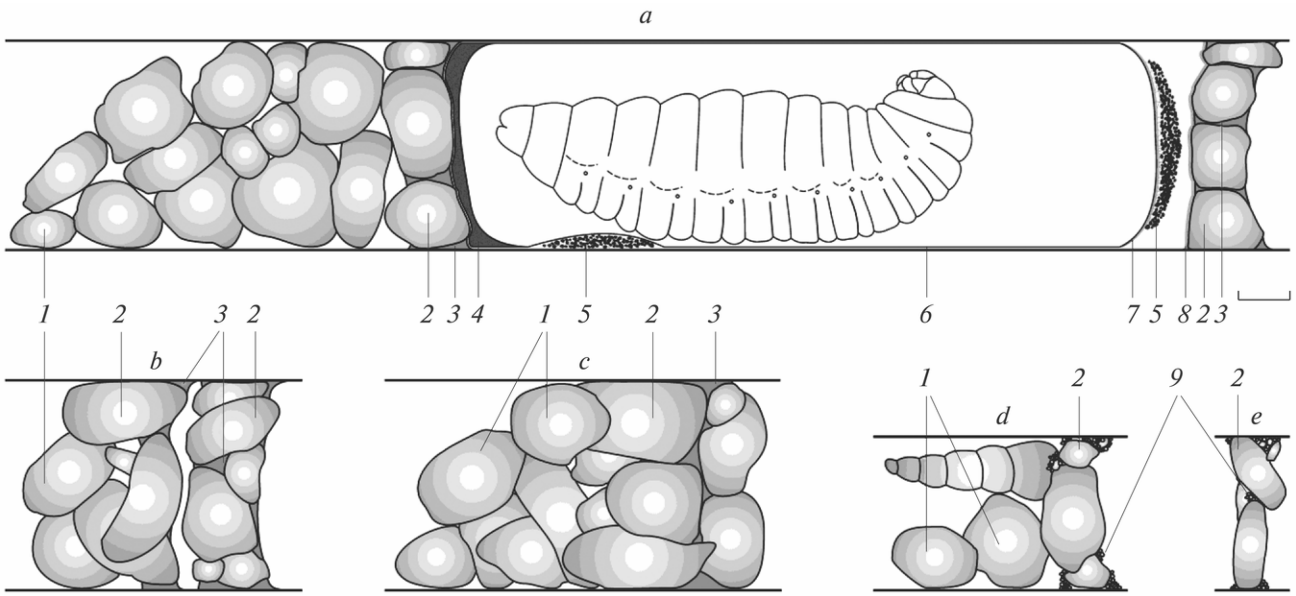

Fig. 2. Structure of the cell and partitions of *Alastor mocsaryi* nests built in hollow reed stems: (*a*) bottom partition and the first cell containing a prepupa in a cocoon; (*b*) plug of the last cell; (c) final plug in the nest having a vestibule; (*d*) bottom partition in the nest constructed without using soil mastic; (*e*) partition between cells in the same nest; *1*, loose gravel particles; *2*, cemented gravel particles; *3*, soil mastic; *4*, meconium; *5*, prey' feces; *6*, inner cocoon layer (for clarity, it is shown as detached from the cell walls, whereas in reality it tightly adheres to them); *7*, free part of the inner cocoon layer; *8*, external cocoon layer; *9*, sand grains. Scale bar 1 mm.

In most cases, the outer partition of the last cell also served as the final plug for the whole nest. This partition was usually thicker than the regular partitions between the cells; it often consisted of two parts and sometimes also contained 1–2 loose gravel particles (Fig. 2*b*). At the same time, two nests were found to contain empty vestibule cells between the outer partition of the last true cell and the final plug. The vestibule cells in these nests were 36 and 51 mm long while their final plugs resembled the bottom partitions and contained a considerable number of loose gravel particles (Fig. 2*c*).

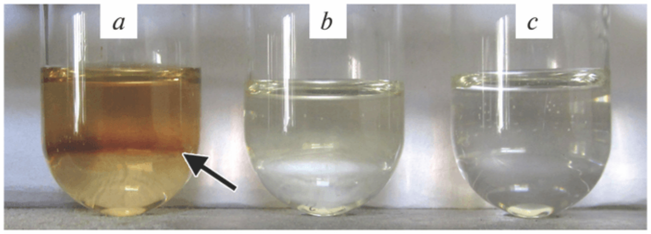

Fig. 3. Qualitative test for monosaccharides in aqueous extracts: (*a*) nest partitions of *Alastor mocsaryi*; (*b*) nest partitions of *Euodynerus velutinus*; (*c*) nest cells of *Sceliphron curvatum*. The reddish quinoid compound (arrow) formed at the boundary of layers of sulfuric acid and extract mixed with α-naphthol solution indicates the presence of monosaccharides in the extract.

Nests from the sand spit of Lake Donuzlav contained fragments of shells of various mollusks and even whole tiny shells instead of gravel, and cemented fine sand grains instead of soil mastic (Figs. 2*d*, 2*e*). Wasp females probably used nectar for cementing these sand grains as well as for making soil mastic. Most eumenine wasps collect dry earth and moisten it with water with addition of saliva (Cowan, 1991). However, throughout the whole study period (2002–2017) collection of water by a female of *A. mocsaryi* was recorded only once. At the same time, the nest partitions of this species were found to contain monosaccharides that form an obligatory component of nectar (Fig. 3*a*). By contrast, no monosaccharides were detected in the nest partitions of *E. velutinus*, which regularly visit water sources, or in the nest cells of *S. curvatum*, which collect naturally occurring mud (Figs. 3*b*, 3*c*). Since the nest partitions of *A. mocsaryi* did not fall apart when soaked and retained their structural strength after drying, females must have used not only nectar but also some saliva containing protein.

The length of cells in *A. mocsaryi* nests varied more than 2.5-fold (Table 1). The cells containing females were longer than those with males. At the same time, the mean length of all the measured cells proved to be somewhat greater than the mean length of the cells containing females, due to the fact that the total number of cells considerably exceeded that of cells for which the sex of the progeny was determined; moreover, the latter parameter remained unknown for the longest cells. The results of measuring all the cells revealed a significant correlation between the cell length and the reed stem diameter: the cells were slightly shorter in wide cavities than in narrow ones ($r = -0.34$, $p \leq 0.01$).

No significant change in the length of successive cells within one nest was revealed. In particular, the mean length of the first cell was 13.27 ± 1.09 mm, and that of the last (the ninth) one was 12.44 ± 3.46 mm. It is evident that more data are needed to reveal any significant correlations in this case. However, an interesting trend was observed: when the mean length values were calculated for the cells starting from the nest end, the last cell was the longest (14.00 ± 2.28 mm) and the ninth cell from the end was the shortest (12.67 ± 1.31 mm).

The cells of *A. mocsaryi* nests dissected in winter contained wasp prepupae in cocoons (Fig. 1*a*). The cocoon had an unusual structure and consisted of two layers (Fig. 2*a*). The outer layer was formed by yellowish lamellar threads closely adjacent to the inner surface of the cell plug and inseparable from it. The inner layer looked like whitish cobweb-like film. It closely adhered to the bottom and the side walls of the cell but could be separated from them. At some distance from the cell plug the inner cocoon layer separated from its walls and closed in the shape of a convex meniscus. This free part of the inner cocoon layer was a little thicker than the part lining the cell walls. The walls between the free part of the inner cocoon layer and the cell plug were not lined with the cocoon material. Feces of the prey (weevil larvae) were positioned outside the inner cocoon layer, on a side wall of the cell close to its bottom, and between the free part of the inner cocoon layer and the cell plug. The meconium occurred inside the inner cocoon layer, at the cell bottom.

The prepupae were elongated and yellow (Fig. 1*a*). Throughout the whole diapause they retained an unusually high degree of motility and responded to any mechanical stimulation by rapid spinning movements. The female prepupae had a greater body mass than the male ones (Table 1). The cocoons were noticeably larger than the prepupae so that the latter were rather loosely packed inside the inner cocoon layer (Fig. 2*a*). In the nests containing progeny of both sexes, cells with females were located at the beginning, and those with males, at the end of the nest. However, the position of cells with progeny of different sex could not be analyzed in greater detail since the entire progeny was sexed only in one nest which happened to contain a single cell with a female. In all the other nests the sex of the progeny remained unknown, at least in part of the cells.

Table 2. Species composition of plants on which feeding of *Alastor mocsaryi* was recorded in Crimea

Plant species	Females	Males
Caprifoliaceae		
Centranthus ruber (L.) DC.	+	+
Euphorbiaceae		
**Euphorbia glareosa* Pall. ex. M. Bieb.	+	–
Fabaceae		
**Dorycnium pentaphyllum* subsp. *herbaceum* (Vill.) Rouy	+	+
Lamiaceae		
Salvia nemorosa subsp. *pseudosylvestris* (Stapf) Bornm.	–	+
Satureja montana subsp. taurica (Velen.) P.W. Ball	+	+
Stachys annua (L.) L.	+	–
Lythraceae		
Lythrum salicaria L.	+	+
Plantaginaceae		
Linaria biebersteinii Besser s. l.	+	+
Linaria genistifolia (L.) Mill. s. l.	+	+
Polygonaceae		
**Polygonum patulum* M. Bieb.	+	–
Ranunculaceae		
Consolida regalis subsp. *paniculata* (Host.) Soó	+	–
Scrophulariaceae		
Buddleja davidii Franch.	+	+

* plants with open or shallow nectaries. *Euphorbia glareosa* was earlier (Fateryga, 2010) misidentified as *Euphorbia stepposa*.

Trophic Associations

Eggs died in 2 cells from 2 nests of *A. mocsaryi* obtained from the environs of Simferopol in 2013. These cells were found to contain larvae of the weevil *Tychius breviusculus* Desbrochers des Loges, 1873 (Coleoptera, Curculionidae), some of which were at different stages of the pupation process. This testifies to weak paralyzation of the prey by wasp females.

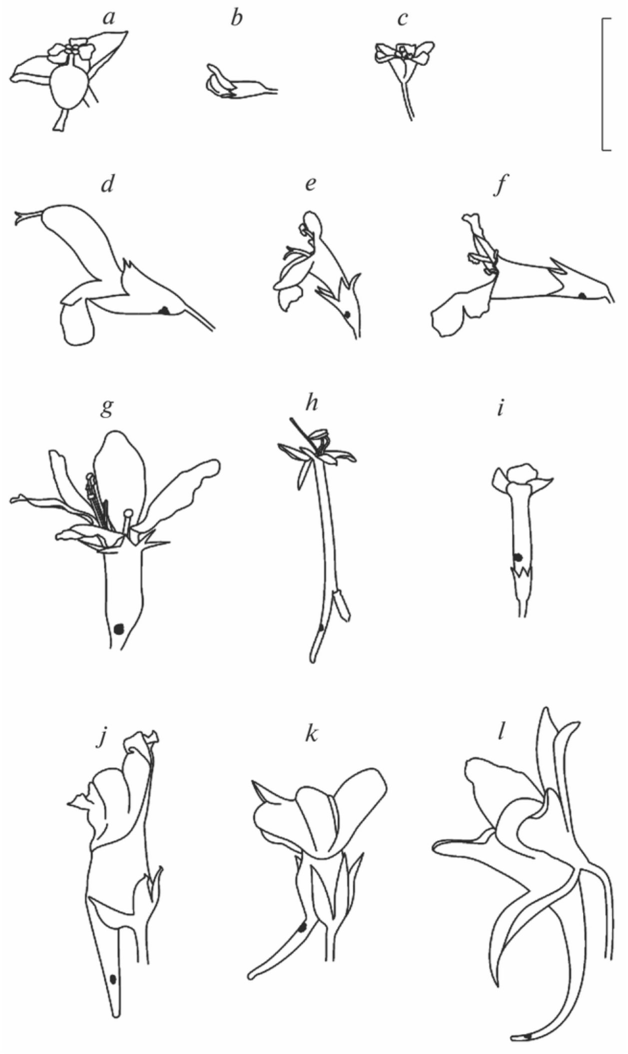

Fig. 4. Flowers of food plants of *Alastor mocsaryi* in Crimea: (*a*) *Euphorbia glareosa*; (*b*) *Dorycnium pentaphyllum* subsp. *herbaceum*; (*c*) *Polygonum patulum*; (*d*) *Salvia nemorosa* subsp. *pseudosylvestris*; (*e*) *Satureja montana* subsp. *taurica*; (*f*) *Stachys annua*; (*g*) *Lythrum salicaria*; (*h*) *Centranthus ruber*; (*i*) *Buddleja davidii*; (*j*) *Linaria biebersteinii*; (*k*) *Linaria genistifolia*; (*l*) *Consolida regalis* subsp. *paniculata*. The black spots mark the holes in the perianth gnawed out by wasps. Scale bar 1 cm.

Besides, one adult weevil was found in each cell, which allowed us to identify the larvae to species. The total number of victims in the cells was 36 and 54, the provision being very tightly packed.

Adult *T. breviusculus* weevils were found on *Melilotus officinalis* (L.) Pall. (Fabaceae) close to the nesting site of *A. mocsaryi* on the outskirts of Simferopol. At the same time, in the Karadag Nature Reserve and in other Crimean localities we recorded *A. mocsaryi* females examining the infructescences of *Plantago lanceolata* L. (Plantaginaceae). Once we observed a successful hunt when the female wasp extracted a weevil larva from such an infructescence (Fig. 1*b*). It may thus be supposed that larvae of weevils of the genus *Gymnetron* which inhabit infructescences of *Plantago* (see Grandi, 1961) may be also stored as provision by *A. mocsaryi*. According to observations made in the Karadag Nature Reserve, one *A. mocsaryi* female also examined an infructescence of *Sanguisorba minor* subsp. *balearica* (Nyman) Muñoz Garm. et C. Navarro (Rosaceae) that is externally similar to that of *P. lanceolata*.

In Crimea, feeding of *A. mocsaryi* adults was recorded on flowers of 12 plant species from 9 families (Table 2). Of these, only 3 species had flowers with open (Fig. 4*a*) or not very deep nectaries (Figs. 4*b*, 4*c*) accessible to this wasp species, and feeding of wasps on such flowers proceeded in the usual way (Fig. 1*c*). The nectaries of the remaining 9 plant species were located deep inside the corolla tube (Figs. 4*d*–4*f*, 4*i*), calyx (Fig. 4*g*), or spur (Figs. 4*h*, 4*j*–4*l*). Seven species (Figs. 4*d*–4*g*, 4*j*–4*l*) are specialized melittophilous plants pollinated by bees, and two species (Figs. 4*h*, 4*i*) are psychophilous, pollinated by butterflies (Faegri and van der Pijl, 1982). Flowers of these plant species are not usually visited by small wasps with short proboscides, such as *A. mocsaryi*. To get to the nectar of these plants, *A. mocsaryi* wasps gnawed out holes in the perianth with their mandibles (Figs. 1*d*, 1*e*). Depending on the flower structure, holes were made in the calyx and corolla (Figs. 4*d*–4*f*), only in the calyx (Fig. 4*g*), the spur (Figs. 4*h*, 4*j*–4*l*), or the corolla tube (Fig. 4*i*).

The flowers of most plant species were visited by wasps of both sexes (Table 2). An exception was *Salvia nemorosa* subsp. *pseudosylvestris* (Stapf) Bornm. on which many males were found and not a single female. Only females were recorded on flowers of four more plant species, but since *A. mocsaryi* was represented there only by single individuals, the absence of recorded males may have been the result of insufficient observation data. Males were also observed engaging females that were feeding on *Centranthus ruber* (L.) DC. and *Linaria genistifolia* (L.) Mill. s. l.; yet mating was not observed.

Progeny Development, Phenology, and Sex Ratio

The prepupae obtained from *A. mocsaryi* nests pupated from the middle till the end of April. Emergence of adults from nests was observed 4–5 weeks after pupation. The exact dates of emergence could not be recorded since most of the pupae were placed in a Fabre's hive at the end of May 2013 in order to assess the degree of the female's attachment to the place of their emergence (see above). Altogether, 15 females were reared in that year, 2 of which subsequently nested in separate reed stems of the same Fabre's hive. Nesting of the first female was observed from June 10 till June 28, when it constructed and provisioned a nest with five cells; during the last days of nesting the female mostly stayed inside the nest doing nothing in particular. The second female was also recorded in a reed stem on June 10, but then it disappeared. This female had built only the bottom partition of the nest and had not started provisioning. It appears that the environmental conditions under which Fabre's hive was installed in the Karadag Nature Reserve in 2013 were not suitable for nesting of *A. mocsaryi*. The spring of that season was abnormally dry with almost no precipitation in the territory of the reserve, and this could have negatively affected the trophic resources of the wasps. This assumption is indirectly supported by the low building activity of the first female which constructed only 5 cells in 19 days. Since two females did nest in the same Fabre's hive despite unfavorable conditions, *A. mocsaryi* wasps demonstrate a certain degree of philopatry, i.e., attachment to the place of their emergence from maternal nests.

According to the examined collection material, the flight of *A. mocsaryi* females was recorded in Crimea from May 28 till August 17, and that of males, from May 21 till July 21 (Fig. 5). Thus, wasps of this species are characterized by distinct proterandry. Since the flight lasts not longer than three months and males are completely absent in the August collections, it can be asserted that *A. mocsaryi* has only one annual generation. This was confirmed by our observations of progeny development in the nests. In particular, in 2014 we observed emergence of the progeny of the first female that had nested in a Fabre's hive in early June 2013.

The examined collections of *A. mocsaryi* were found to contain more than 2.5 times as many females (252) as males (96). This proportion in the collection specimens does not necessarily correspond to the actual sex ratio in nature, which can be determined only by examination of a great number of nests (Ivanov and Fateryga, 2006). In our material, only 16 females and 6 males were reared from the nests; therefore, the observed sex ratio was also strongly female-biased but these data cannot be regarded as significant due to the small sample size.

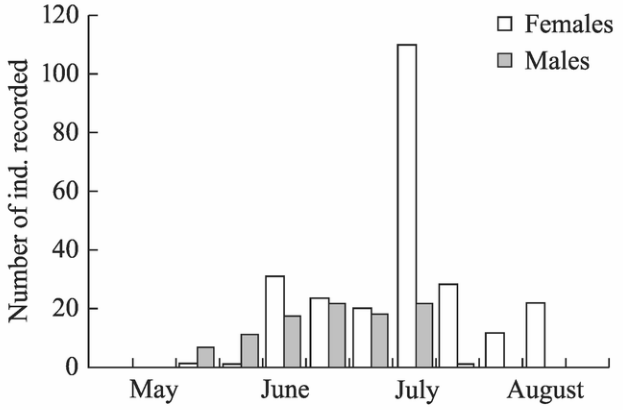

Fig. 5. Flight phenology of *Alastor mocsaryi* in Crimea.

Table 3. Mortality of *Alastor mocsaryi* progeny due to parasites and other factors

Parasite species or other mortality factors	Number of cells	Proportion of cells, %
Melittobia acasta (Walker)	11	16.4
Hoplocryptus coxator (Tschek)	5	7.5
Trichodes apiarius (Linnaeus)	4	6.0
Tachinidae gen. sp.	1	1.5
Death of egg for unknown cause	2	3.0
Death of prepupa for unknown cause	3	4.5
Total	26	38.8

Nest Parasites and Reproductive Success

The studied *A. mocsaryi* nests were infested with the parasitoid wasps *Melittobia acasta* (Walker, 1839) (Hymenoptera, Eulophidae) and *Hoplocryptus coxator* (Tschek, 1871) (Hymenoptera, Ichneumonidae), the predatory larva of the checkered beetle *Trichodes apiarius* (Linnaeus, 1758), and a tachinid fly (Diptera, Tachinidae) (Fig. 1*a*). The first species was found in 2 nests, and others, only in 1 nest each. According to the result of analysis of all the nests, the reproductive success of *A. mocsaryi* was 61.2% (Table 3).

DISCUSSION

The new data considerably extend our knowledge of the biology of members of the genus *Alastor*. Earlier it has been known that wasps of this genus nest in preexisting cavities and build their nests of fine gravel and earth or sand cemented with an unknown substance (Grandi, 1961; Gess and Gess, 2008), and also that they hunt weevil larvae (Grandi, 1961). Data on the structure of the bottom partition of *A. mocsaryi* nest allow us to draw a number of additional conclusions. First of all, it should be noted that the main building material is fine gravel while earth is used in very limited quantities. Actually, *A. mocsaryi* females build partitions of gravel particles cementing only some of them with earth or sand moistened with nectar and saliva. Therefore, it does not seem quite correct to consider the genus *Alastor* among wasps that use plastic materials for nest construction (Iwata, 1976). The main building material in wasps of the tribes Odynerini and Eumenini (sensu Hermes et al., 2014) is soil mastic (Cowan, 1991), which is practically never used by members of the genus *Alastor*.

The cocoon and prepupa of *A. mocsaryi* are also rather unusual for Eumeninae. As a rule, the cocoons of eumenine wasps are not detachable from the cell walls and do not look like white cobweb-like film. The prepupae of other genera are not as motile as those of *A. mocsaryi*. Thus, biology of the genus *Alastor* is fairly unique, which is consistent with its isolated phylogenetic position (Bank et al., 2017).

It is widely known that most eumenine wasps using soil mastic make it by mixing dry earth and water obtained from different sources. Some species are also known to use hemolymph of their prey or naturally occurring mud (Cowan, 1991), while others can obtain liquid from excretion of spittlebugs (Homoptera, Aphrophoridae) (Miotk, 1979), from glandular hairs of plants (Amolin, 2006) or succulent leaves (Fateryga et al., 2017). Females of *A. mocsaryi* have practically never been observed collecting water but they have been recorded in great quantities on flowers. In addition, the presence of monosaccharides in the nest partitions confirms the use of nectar as building material. Nectar has not been earlier recorded as building material in any species of Eumeninae. However, it is widely used for this purpose by some members of Masarinae (Hymenoptera, Vespidae) (Torchio, 1970; Gess, 1996). Besides nectar, *A. mocsaryi* females obviously add some saliva to the building material; this is typical of most of the studied species of Eumeninae (Cowan, 1991). Wasps of the genus *Alastor* may use nectar not only directly for mixing mastic but also for replenishing the inner reserves of water needed to produce saliva. Due to the small quantity of mastic used in building nest partitions, *A. mocsaryi* wasps need only little liquid which they can obtain from nectar without visiting water sources. This feature is important in arid biotopes where the genus *Alastor* has the greatest species diversity.

The use of fine gravel in nest building is also typical of some other genera of Eumeninae. According to Parker (1966), these are *Leptochilus* de Saussure, 1853, *Microdynerus* Thomson, 1874, *Maricopodynerus* Viereck, 1908, and *Hypalastoroides* de Saussure, 1856. Of them, nesting biology is best studied in species of the genus *Leptochilus* (Parker, 1966; Fateryga, 2013a). These wasps also almost never use plastic materials. Partitions of their nests mainly consist of small gravel particles which may be partly cemented with masticated stem pith, plant resin or saliva and sometimes a small quantity of earth. On the whole, the nests of *Leptochilus* wasps are fairly similar to those of *Alastor*, although the presence of nectar in the partitions has so far been demonstrated only for *A. mocsaryi*. Besides, the North American species *Odynerus cinnabarinus* R. Bohart, 1939 uses gravel or coarse sand grains for plugging the nest (Parker, 1984), although most other members of the genus *Odynerus* Latreille, 1802 use only soil mastic prepared by mixing water and dry earth (Fateryga, 2013b). Besides the above genera, the use of gravel is characteristic of the genus *Katamenes* Meade-Waldo, 1910 from a different tribe (Eumenini). However, *Katamenes* uses coarser gravel (20–40 mg on average) and, which is more important, also great quantities of real soil mastic (Fateryga and Ivanov, 2009).

In the accepted classification (Hermes et al., 2014) the subfamily Eumeninae is divided into three tribes: Zethini, Eumenini, and Odynerini. All the above genera except *Katamenes* belong to the tribe Odynerini. However, according to the latest phylogenetic reconstruction based on molecular data (Bank et al., 2017), the tribe Zethini should be placed in a separate subfamily (or two subfamilies), and three more tribes should be singled out from Odynerini: the first to comprise the genus *Alastor*, the second, the genus *Odynerus* proper and also *Pterocheilus* Klug, 1805 and closely related genera, and the third one, the genera *Microdynerus* and *Leptochilus*. It should be noted that these genera were not included in the previous phylogenetic reconstruction based on morphological data (Hermes et al., 2014), where "Odynerini" were represented by a group of genera forming a sister clade to "(*Microdynerus* + *Leptochilus*) + Eumenini" (Bank et al., 2017). Data on the specific traits of nesting biology agree well with the isolated positions of the genus *Alastor* and the clade uniting *Odynerus*, *Pterocheilus*, and related genera. The latter also form a distinct group with regard to nesting biology which is characterized by primarily ground nesting in the earth (see Fateryga et al., 2017). However, considering the very similar nest structure in species of the genera *Alastor* and *Leptochilus*, their remote position in the cladogram (Bank et al., 2017) looks strange. Further biological studies of *Leptochilus* and related genera may throw light on this situation.

Another notable phenomenon is the "robbing" of nectar by *A. mocsaryi* wasps through holes gnawed out in the perianth. Although such behavior is widespread among Hymenoptera and other anthophilous animals (Rojas-Nossa et al., 2016), it is little known among eumenine wasps due to lack of observation data. Until recently, nectar robbing through holes in the perianth gnawed out by the wasps themselves was recorded and described in detail only for three European species of Eumeninae: *Pterocheilus phaleratus* (Panzer, 1797), *Ancistrocerus scoticus* (Curtis, 1826), and *A. oviventris* (Wesmael, 1836) (Haeseler, 1980, 1997). Now, these species may be supplemented with *A. mocsaryi* and also *O. cinnabarinus*, which gnaws out holes in calyces of *Astragalus holmgreniorum* Barneby (Fabaceae) (Barlow and Pavlik, 2017). Robbing of nectar by *A. mocsaryi* females may be related to its use as building material. Of course, all the eumenine wasp species store nectar as provision, but as far as is known, none of them are trophically associated with so many plant species whose nectar would only be obtainable by robbing. It should be also noted that *O. cinnabarinus*, similar to *A. mocsaryi*, uses large sand grains cemented with some "liquid substance" (Parker, 1984). This substance may also be nectar. In this case, *O. cinnabarinus*, as well as *A. mocsaryi*, may resort to robbing nectar in order to use it in nest construction.

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