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ON THE FORAGING BEHAVIOR OF TWO POLLEN WASP SPECIES OF THE GENUS *CELONITES* LATREILLE, 1802 (HYMENOPTERA: VESPIDAE: MASARINAE) FROM KAZAKHSTAN

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Summary. *Celonites tristiculus* Kostylev, 1935 and *C. montanus* Mocsáry, 1906 demonstrate two different foraging strategies. The first species is probably polylectic (or at most eclectically oligolectic). Females of *C. tristiculus* collect pollen (but not nectar) from flowers of *Allium caricifolium* Kar. & Kir. (Amaryllidaceae), consuming it directly from the anthers with the mouthparts and the foretarsi. They collect nectar from flowers of *Ziziphora tenuior* L. (Lamiaceae), which are hardly used for pollen uptake. Females of *C. montanus* collect pollen and nectar from nototribic flowers of the genera *Lagochilus* Bunge ex Benth. and *Moluccella* L. (Lamiaceae). They take up pollen with pollen-collecting setae on the frontal surface of the head, by rubbing it over the anthers; rubbing movements are alternated with pollen brushing from the head with the foretarsi, from which the pollen is finally consumed with the mouthparts. Males visit flowers of other plants (such as *Convolvulus fruticosus* Pall., Convolvulaceae) for nectar uptake only. The evolution of pollen uptake with pollen-collecting setae in the pollen wasps is discussed.

Key words: *Celonites tristiculus*, *Celonites montanus*, flower preferences, flower-visiting behavior, Central Asia.

А. В. Фатерыга. О фуражировочном поведении двух видов цветочных ос рода *Celonites* Latreille, 1802 (Hymenoptera: Vespidae: Masarinae) из Казахстана // Дальневосточный энтомолог. 2025. N 528. С. 7-20.

Резюме. *Celonites tristiculus* Kostylev, 1935 и *C. montanus* Mocsáry, 1906 характеризуются разными фуражировочными стратегиями. Первый вид – предположительно полилект (или, в крайнем случае, эклектический олиголект). Самки *C. tristiculus* собирают пыльцу (но не нектар) с цветков *Allium caricifolium* Kar. & Kir. (Amaryllidaceae), потребляя ее напрямую из пыльников с помощью ротовых органов и передних лапок. С цветков *Ziziphora tenuior* L. (Lamiaceae) самки берут нектар, практически не используя их для сбора пыльцы. Самки *C. montanus* берут пыльцу и нектар с нототрибических цветков растений родов *Lagochilus* Bunge ex Benth. и *Moluccella* L. (Lamiaceae). Они собирают пыльцу с помощью собирательных волосков на передней поверхности головы, путем трения ею о пыльники; трение чередуется со счисткой пыльцы с головы передними лапками, с которых она, в конце концов, потребляется с помощью ротовых органов.

Самцы посещают цветки других растений (таких, как *Convolvulus fruticosus* Pall., Convolvulaceae), но только для сбора нектара. Обсуждается эволюция сбора пыльцы с помощью собирательных волосков у ос-мазарин.

INTRODUCTION

The pollen wasp genus *Celonites* Latreille, 1802 has a disjunct distribution with 20 species occurring in the semi-arid to arid areas in the southwest of the Afrotropical region (Gess & Gess, 2010; although they claimed to report 21 species, their list contained 20 valid species and one synonym) and 42 species in the Palaearctic and adjacent dry areas in the north of the Afrotropical region (according to the list by Carpenter, 2001, combined with newly described or synonymized species by Gusenleitner, 2002, 2007, 2012, 2018; Mauss, 2013; Mauss *et al.*, 2016, 2022a; Mauss & Prosi, 2018; Fateryga & Fadeev, 2023; Fateryga, 2025a). It is the second largest genus of the subfamily Masarinae after *Quartinia* Andre, 1884. At least four Palaearctic species of the genus *Celonites* are still undescribed.

Most species of *Celonites*, for which flower visiting records are available, are either broadly or narrowly oligolectic (*sensu* Müller & Kuhlmann, 2008). In the Palaearctic region, members of the *C. abbreviatus*-complex and *C. sibiricus* Gusenleitner, 2007 independently evolved to collect pollen from nototribic flowers of Lamiaceae, on which they are broadly oligolectic, with specialized pollen-collecting setae on the frontal surface of the head. During flower visits, pollen accumulates on the frons and the clypeus of these species, being subsequently transferred with the foretarsi towards the mouth, where it is finally consumed with the mouthparts (Schremmer, 1959; Müller, 1996; Mauss, 2006; Mauss *et al.*, 2016; Fateryga, 2020; Fateryga *et al.*, 2022, 2023). Some other species are narrowly oligolectic on the genus *Heliotropium* Tourn. ex L. (Boraginaceae): *C. jousseaumei* du Buysson, 1906, members of the *C. cyprius*-group, and *C. pictus* Richards, 1962 from the Palaearctic region (Richards, 1962; Gess & Roosenschoon, 2016; Mauss *et al.*, 2022a, b, 2024), as well as *C. heliotropii* Gess, 2007 from Namibia (Gess, 2007; Gess & Gess, 2010). Such a trophic relationship evolved independently at least two times, with two fundamentally different behavioral patterns for pollen uptake from *Heliotropium* flowers with a narrow corolla tube: most studied species remove pollen from the concealed anthers with the proboscis, while *C. pictus* takes up pollen with elongated forelegs equipped with a tarsal pollen brush formed by hooked setae (Mauss *et al.*, 2024).

Other species of *Celonites*, including some in the Palaearctic region and most Afrotropical species, consume pollen directly from the anthers with their mouthparts and an unmodified pollen brush on the foretarsi. Palaearctic species can be narrowly oligolectic, as in the case of *C. fischeri* Spinola, 1838, exclusively visiting flowers of the genus *Echium* Tourn. ex L. (Boraginaceae with a broad corolla tube) (Mauss & Müller, 2014), or even polylectic sensu stricto (in the sense of Müller & Kuhlmann 2008), as in the case of *C. kozlovi* Kostylev, 1935 that has been observed to visit flowers of at least seven plant families and to ingest pollen from at least five of them (Fateryga *et al.*, 2023). Most Afrotropical species of *Celonites* are broadly oligolectic, visiting a few closely related genera of either Scrophulariaceae or Campanulaceae (rarely Asteraceae, as in the case of *C. wheeleri* Brauns, 1905). A few species are polylectic, such as *C. capensis* Brauns, 1905, visiting flowers of at least seven plant families (Gess & Gess, 1989, 2010; Gess *et al.*, 1997). In general, trophic preferences are better known for the Afrotropical and the Mediterranean species of *Celonites*, while flower-visiting records for the Central Asian representatives are scarce (Fateryga *et al.*, 2023).

The purpose of the present contribution is to report preliminary data on the foraging behavior of two species of *Celonites* from Central Asia: *C. tristiculus* Kostylev, 1935 and *C. montanus* Mocsáry, 1906. For *C. tristiculus*, flower visiting records are presented for the first time, while *C. montanus* was previously recorded at flowers of *Lagochilus platyacanthus* Rupr. (Lamiaceae) (Fateryga & Fadeev, 2023), but the flower visiting behavior of the wasps at the flowers was not observed.

MATERIAL AND METHODS

The research was carried out in Kazakhstan in 2024. Imagines of *Celonites tristiculus* were observed at three localities of the Altyn-Emel National Park, Jetisu Province: Shylbyr (43.9582°N, 78.1869°E) on 5 May, Taygak-1 (43.9163°N, 77.8626°E) on 7 May (Fig. 1), and Taygak-2 (43.8999°N, 77.8626°E) on 8 and 9 May. All three localities were situated on the Sholak Range, the most south-western end of the Dzungarian Alatau Mountains. Imagines of *C. montanus* were present at one of the localities in the Altyn-Emel National Park (Taygak-1) but most observations on this species were made in the Valley of Castles, Charyn National Park, Almaty Province (43.3496°N, 79.0811°E) on 13, 14, and 16 May (Fig. 2). This locality was a part of the Toraygyr Mountains, the north-eastern spurs of the Trans-Ili Alatau Range of the Northern Tian Shan Mountains. An additional brief observation of *C. montanus* was made in the vicinity of the Kokpek Pass, 6 km to the nort-nort-west of Kokpek, Almaty Province (43.5017°N, 78.6225°E) on 19 May. This locality was situated in the Boguty Mountains, other north-eastern spurs of the Trans-Ili Alatau Range.

At most localities, except the vicinity of the Kokpek Pass, all plant species in flower were photographed and voucher specimens were collected and preserved dried, regardless whether they were visited by the wasps or not. Plant specimens were deposited in the herbarium PHEO; the photographs were uploaded to the Plantarium website (Plantarium, 2007–2025) and identified there. Taxonomy of plants follows POWO (2025) except that *Allium caricifolium* Kar. & Kir. is considered here a separate species according to Friesen *et al.* (2022), not a synonym of *A. pallasii* Murray, and the genus *Phelipanche* Pomel is not a synonym of *Orobanche* L. according to Sánchez Pedraja *et al.* (2016–2025).

Flower preferences of imagines of *C. tristiculus* and *C. montanus* were studied by counting the number of independent sightings of flower-visiting individuals at the flowering plant species. A sighting was defined as the first observation of a flower-visiting individual on a flower during a single observed foraging incident, as opposed to the numerous, non-independent observations performed when following an individual during a foraging trip, which is likely to include many non-independent visits to the same host plant owing to floral constancy. At the study sites, sightings were recorded during non-systematic random observations and focal observations (total investigation time 17 h in the Altyn-Emel National Park and 5 h in the Charyn National Park). Wasp activity at flowers was photographically documented with a Canon EOS RP digital camera with a Sigma AF 105 mm f/2.8 macro lens (scale up to 1:1).

An additional flower record for *C. montanus* was taken from label data in the entomological collection of the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia (ISEN).

RESULTS

A total of 22 species of plants in flower from 12 families were recorded at three localities in the Altyn-Emel National Park and 18 species from 14 families at the locality in the Charyn

National Park. Of them, nine species were present in both territories. Plant species whose flowers were visited by *Celonites tristiculus* and *C. montanus* are listed in Table 1, while flowering species that were not visited by the wasps are summarized in the footnote of Table 1. Three species of the family Asteraceae were not counted: *Centaurea pulchella* Ledeb., *Lactuca undulata* Ledeb., and *Tragopogon ruber* S.G. Gmel. They were in flower during the observation period but their capitula had closed rather early in the morning, before the activity of the studied species of *Celonites* started.

Altogether, 73 sightings (= first observations) at flowers were made, 26 of *C. tristiculus* and 47 of *C. montanus*. *Celonites tristiculus* was observed at flowers of three plant species from two families; most visits were to flowers of *Allium caricifolium* Kar. & Kir. (Amaryllidaceae) and *Ziziphora tenuior* L. (Lamiaceae); just one female visited *Nepeta micrantha* Bunge (Lamiaceae). *Celonites montanus* was observed at flowers of three plant species from three families but females visited only *Lagochilus diacanthophyllus* (Pall.) Benth. (Lamiaceae).

Figs 1–2. Habitats of *Celonites tristiculus* Kostylev, 1935 and *C. montanus* Mocsáry, 1906 in Kazakhstan: 1 – habitat of both species in the Altyn-Emel National Park (Taygak-1); 2 – habitat of *C. montanus* in the Charyn National Park (Valley of Castles).

Males visited mostly either *L. diacanthophyllus* or *Convolvulus fruticosus* Pall. (Convolvulaceae); just one male visited *Z. tenuior*. It is of note, that most observations of *C. montanus* were made in the Valley of Castles, from where the latter plant species was absent (Table 1). At the Taygak-1 locality, where *Z. tenuior* was abundant and visited by both species of *Celonites*, there were plants of *Lagochilus* sp. as well, but they were still in bud.

Table 1. Flower-visiting records of *Celonites tristiculus* Kostylev, 1935 and *C. montanus* Mocsáry, 1906 during 17 h of observations in the Altyn-Emel National Park ([A]) and 5 h of observations in the Charyn National Park ([C])

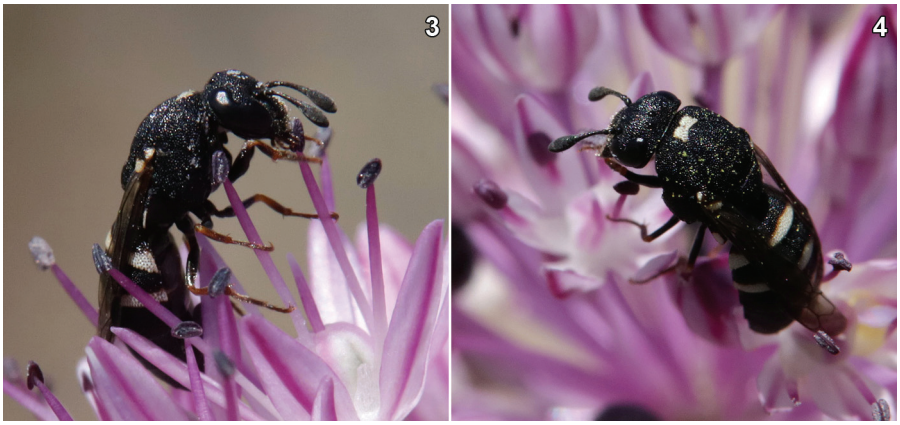
Plant taxon	Σ sightings of flower-visiting individuals			
	C. tristiculus		*C. montanus*	
	♀	♂	♀	♂
Amaryllidaceae *Allium caricifolium* Kar. & Kir. [A, C]	11	–	–	–
Convolvulaceae *Convolvulus fruticosus* Pall. [C]	–	–	–	6
Lamiaceae *Lagochilus diacanthophyllus* (Pall.) Benth. [C]	–	–	36	4
Nepeta micrantha Bunge [A]	1	–	–	–
Ziziphora tenuior L. [A]	13	1	–	1
Other plant taxa*	–	–	–	–

* – other plant taxa in flower: Asteraceae: *Cancrinia discoidea* (Ledeb.) Poljakov ex Tzvelev [A]; Berberidaceae: *Berberis integerrima* Bunge [C]; Boraginaceae: *Arnebia guttata* Bunge [A, C], *Lappula microcarpa* (Ledeb.) Gürke [A], *Nonea caspica* (Willd.) G. Don [A]; Brassicaceae: *Leiospora beketovii* (Krasn.) D.A. German & Al-Shehbaz [C], *Rudolf-kamelinia korolkowii* (Regel & Schmalh.) Al-Shehbaz & D.A. German [C]; Cistaceae: *Helianthemum songaricum* Schrenk ex Fisch. & C.A. Mey. [A]; Fabaceae: *Caragana balchaschensis* (Kasn. ex Kom.) Pojark. [A, C], *Chesneya dshungarica* Golosk. [A], *Medicago medicaginoides* (Retz.) E. Small [A]; Geraniaceae: *Erodium oxyrhinchum* M. Bieb. [A]; Lamiaceae: *Phlomoides isochila* (Pazij & Vved.) Salmaki [C], *Scutellaria sieversii* Bunge [A, C]; Nitrariaceae: *Peganum harmala* L. [C]; Orobanchaceae: *Orobanche amoena* C.A. Mey. [A], *Phelipanche* sp. [A]; Papaveraceae: *Glaucium elegans* Fisch. & C.A. Mey. [A, C], *G. squamigerum* Kar. & Kir. [A, C]; *Papaver laevigatum* M. Bieb. [A], *Roemeria pavonina* (Schrenk) Banfi, Bartolucci, J.-M. Tison & Galasso [A]; Phyllanthaceae: *Andrachne telephioides* L. [A, C]; Plantaginaceae: *Linaria popovii* Kuprian. [A, C]; Polygonacae: *Calligonum* sp. (probably *C. junceum* (Fisch. & C.A. Mey.) Litv.) [C]; Scrophulariaceae: *Scrophularia incisa* Weinm. [A, C]; Zygophyllaceae: *Zygophyllum rosowii* Bunge [C].

In the vicinity of the Kokpek Pass, females of *C. montanus* were recorded at flowers of *Lagochilus platyacanthus*, a species very similar to *L. diacanthophyllus*. Sightings were not counted at this locality, as was the total number of plants in flower. Examination of the ISEN collection revealed three females of *C. montanus* collected in Kyrgyzstan on 17.VII.2003 by V.V. Dubatolov and D.A. Milko and labeled as collected at *Othostegia* (sic). The genus *Otostegia* Benth. (Lamiaceae), in its current treatment, is not distributed in Central Asia at all (POWO, 2025). Some species previously considered members of this genus are currently treated within the genus *Moluccella* L. (also Lamiaceae) and the only species of this genus

known from Kyrgyzstan is *Moluccella olgae* (Regel) Ryding (POWO, 2025). Thus, this flower record for *C. montanus* obviously refers to *M. olgae* and a total number of plants known as flower records for this wasp species is five species from three familes.

Females of *C. tristiculus* visiting flowers of *A. caricifolium*, alighted on an inflorescence and held on to filaments and tepals with their mid and hind legs. Then, they started to consume pollen directly from the anthers with their mouthparts (Fig. 3), or they removed pollen from the anthers with their foretarsi, from which it was finally also consumed with the mouthparts (Fig. 4). Usually, a female visited one flower within about 3–5 s; after that she visited other flowers of the same inflorescence, moving on foot from flower to flower. After visits to several flowers, which usually took about 0.5 min or more, the female left the inflorescence and flew to another inflorescence or disappeared. Females were never observed to collect nectar at flowers of *A. caricifolium*, although some other insects did this. On four occasions, a female was observed to alternate between pollen uptake from flowers of *A. caricifolium* and nectar uptake from flowers of *Z. tenuior*.



Figs 3–4. Females of *Celonites tristiculus* Kostylev, 1935 collecting pollen from flowers of *Allium caricifolium* Kar. & Kir.: 3 – pollen consumption directly from an anther with the mouthparts; 4 – pollen consumption from the foretarsi.

During visits to flowers of *Z. tenuior*, females of *C. tristiculus* alighted on the lower lip and usually held on to it with all pairs of legs. Afterwards, a female usually protracted her proboscis into the corolla tube to reach the nectar. The whole visit to a flower lasted about 1 s or even less. Just in one case, a female remained for a moment at the entrance of the bilabiate flower with her head raised up, indicating that she probably tried to collect pollen from the nototribic anthers. Examination of the anthers of several flowers of *Z. tenuior* at the study sites revealed that all of them were nearly empty, since the pollen grains had already been removed by other flower visitors. The only flower visiting male of *C. tristiculus*, that was observed at a flower of *Z. tenuior*, also collected nectar only. The wasps always moved between the flowers of *Z. tenuior* in flight, even within the same inflorescence.

Females of *C. montanus* collected both pollen and nectar at flowers of *L. diacantho-phyllus* but most observed visits were only for nectar uptake. A typical nectar-collecting visit to a flower lasted about 1–2 s. A female alighted on a flower and held on to its lower lip with all pairs of her legs. Then, she touched the lower anthers with her frons for a moment (apparently actively), and after that she moved deep into the corolla tube, where she protracted the

proboscis to reach the nectar. After nectar uptake, she moved backwards out of the corolla tube, and before she flew away, her vertex came into contact with the lower anthers and her scutellum with the upper anthers for a moment (apparently not actively). Thus, even during nectar-collecting visits, some pollen accumulates on the frontal surface of the head of the female and the dorsal surface of her mesosoma. The wasps moved between flowers only in flight, even within the same inflorescence. After several flower visits, the females alighted on the ground (or rarely small stones or dry twigs) where they brushed pollen, which had accumulated on the head and the mesosoma, from the cuticula with the foretarsi, and then consumed it from the foretarsi with their mouthparts. Females were not observed to come into contact with the stigma; therefore, they are questionable pollinators of *L. diacanthophyllus*.

Active pollen collection was observed in some females, but only on 16 May, not on the days before (perhaps it was the first day of the flight season, where the females started with brood cell provisioning). The pollen-collecting visits to flowers lasted about 5–15 s and they were performed only to freshly opened (male-phase) flowers. Females never collected pollen directly from the anthers with the mouthparts and/or the forelegs. A female, holding on to the lower lip of the flower with all pairs of legs, performed rapid movements of her head, rubbing its anterior parts over the upper anthers (Fig. 5). Rubbing movements of the head alternated with pollen brushing from its anterior surface with the foretarsi, from which the pollen was finally consumed with the mouthparts, while mid and hind legs were still used to hold on to the flower (Fig. 6). After several alternating cycles of rubbing movements over both upper anthers and pollen-brushing over the surface of the head, the female moved somewhat deeper into the flower and repeated the behavior described above with the lower anthers. She also performed several cycles of rubbing movements over both lower anthers (Fig. 7) that alternated with brushing movements of the foretarsi. In this way, the pollen that accumulated on the frontal surface of the female's head, and even the dorsal surface of her mesosoma, was completely transferred with the foretarsi to the mouthparts and finally consumed (Fig. 8). After that, the female moved her head into the corolla tube and protracted her proboscis to reach the nectar, as in the case of a nectar-collecting visit (Fig. 9). Rarely, visits to flowers without nectar uptake were also observed.

Males of *C. montanus* collected only nectar actively during visits to flowers of *L. diacanthophyllus*. Males visiting flowers of *C. fruticosus* actively collected also only nectar but during the visit some pollen grains were deposited on the frons (Fig. 10). In this case, the males were observed to brush the pollen with the foretarsi from the frons and to consume it from the foretarsi with the mouthparts. Pollen of *L. diacanthophyllus* that occasionally accumulated on the frons as well, was probably also consumed. One male was observed to alternate between visits to flowers of *L. diacanthophyllus* and those to flowers of *C. fruticosus*. Sometimes males were also observed perching on the ground near patches of *L. diacanthophyllus*.

DISCUSSION

Females of both *Celonites tristiculus* and *C. montanus* visit several species and genera of Lamiaceae with nototribic flowers. However, these two wasp species demonstrate two different foraging strategies. *Celonites tristiculus* uses flowers of *Allium caricifolium* (Amaryllidaceae) as the main source of pollen, while flowers of *Ziziphora tenuior* (Lamiaceae) are mainly used as a source of nectar. However, pollen is apparently collected from flowers of *Z. tenuior* as well, at least in some cases. Therefore, the foraging strategy of *C. tristiculus* can be treated as an eclectic oligolecty sensu Müller & Kuhlmann (2008) ("pollen collection from two to four plant genera belonging to two or three plant families"). However, the present

Figs 5–10. Females of *Celonites montanus* Mocsáry, 1906 at flowers of *Lagochilus diacanthophyllus* (Pall.) Benth. (5–9) and a male at a flower of *Convolvulus fruticosus* Pall. (10): 5, 7 – pollen uptake by rubbing the head over an upper (5) and a lower (7) anther; 6, 8 – pollen brushing from the head (6) and the mesosoma (8); 9, 10 – nectar uptake.

observations on *C. tristiculus* are rather brief and it is unknown how many other plant taxa can be visited by this species, especially in other parts of its distribution range that is larger (Fateryga, in preparation) than that of *A. caricifolium* (Friesen *et al.*, 2022). It cannot be excluded that it is actually a polylectic species, as was confirmed for *C. kozlovi* (Fateryga *et al.*, 2023). Both *C. tristiculus* and *C. kozlovi* take up pollen directly from the anthers only with their mouthparts and foretarsi. Pollen uptake from the anthers with the forelegs is a plesiomorphic character of the ground pattern of the Masarini (Richards, 1962; Mauss, 2007; Mauss *et al.*, 2019).

Females of *C. montanus* use nototribic flowers of Lamiaceae (*Lagochilus* spp. and apparently also *Moluccella olgae*) as the only source of pollen and nectar; plants of other genera (such as *Convolvulus* L., Convolvulaceae) are only used as a source of nectar and only by males. Therefore, the foraging strategy of this wasp species is probably broad oligolecty sensu Müller & Kuhlmann (2008) ("pollen collection from two to several genera belonging to one plant tribe, subfamily or family"). Females of *C. montanus* remove pollen from the nototribic anthers indirectly with pollen-collecting setae on the anterior side of their head. A similar behavior is known for the members of the *C. abbreviatus*-complex and *C. sibiricus*, which are also broadly oligolectic on Lamiaceae with nototribic flowers (Schremmer, 1959; Müller, 1996; Mauss, 2006; Mauss *et al.*, 2016; Fateryga, 2020; Fateryga *et al.*, 2022, 2023).

The genus *Allium* L. and the family Amaryllidaceae as a whole has been apparently not previously reported as a pollen or nectar host of any species of the genus *Celonites* and the subfamily Masarinae as a whole (see Gess, 1996; Gess & Gess, 2010). Flowers of plants of the genus *Convolvulus* have been already reported as a source of nectar for *C. kozlovi*. Plants of the family Lamiaceae are a very common pollen source for the genus *Celonites* in the Palaearctic region (but not in the Afrotropical region, where no species of this genus has been recorded at any plant of this family, see Gess & Gess, 1989, 2010). It is noteworthy, that in the present study both species of *Celonites* visited plants of Lamiaceae with bluish (*Z. tenuior* and *Nepeta micrantha*), pale pink (*Lagochilus* spp.), or whitish flowers (*M. olgae*). Moreover, the flowers of the two other visited plant species belonging to other families (*A. caricifolium* and *Convolvulus fruticosus*) were also purple or pale pink. At the same time, neither *C. tristiculus* nor *C. montanus* visited yellow flowers, not even yellow notoribic flowers of the Lamiaceae that were also flowering at the study sites (*Scutellaria sieversii* Bunge and *Phlomoides isochila* (Pazij & Vved.) Salmaki). Other species of the genus *Celonites* that are oligolectic on Lamiaceae also usually visit purple, bluish, or pale pink flowers (Schremmer, 1959; Müller, 1996; Mauss, 2006; Mauss *et al.*, 2016; Fateryga, 2020; Fateryga *et al.*, 2022, 2023) or rarely whitish ones (such as *Teucrium montanum* L., see Bellmann, 1984) but never yellow. However, *C. sibiricus* visits yellow flowers of other plant families for nectar uptake and the polylectic *C. kozlovi* collects pollen from yellow flowers of several plant families (Fateryga *et al.*, 2023).

It should be noted that *C. tristiculus* did not collect nectar from the flowers of its main pollen host, *A. caricifolium*, using flowers of *Z. tenuior* for nectar uptake instead. Most species of the pollen wasps usually collect pollen and nectar from the flowers of their pollen hosts, but some of them can also use flowers of other plant taxa for additional nectar uptake. This is the case in females of the Afrotropical *Ceramius braunsi* Turner, 1935 that collect pollen only from flowers of Asteraceae, while they visit flowers of *Aspalathus* L. (Fabaceae) for additional nectar uptake (Gess & Gess, 1989, 1990). However, in the Palaearctic region, the polylectic *Quartinia tenerifina* Richards, 1969 is known to collect only pollen from flowers of *Zygophyllum creticum* (L.) Christenh. & Byng (Zygophyllaceae), while it takes up both pollen and nectar from flowers of *Aizoon canariense* L. (Aizoaceae) and probably also from flowers of two other plant families (Mauss & Mauss, 2016). *Celonites tristiculus* apparently demonstrates a similar foraging strategy.

As was stated above, females of *C. montanus* use pollen-collecting setae on the frontal surface of the head to take up pollen from nototribic anthers of Lamiaceae. Schremmer (1959) was apparently the first, who described a similar behavior for the European species *C. abbreviatus* (Villers, 1789). This species has specialized morphological structures of the females for pollen-uptake from the nototribic anthers and pollen-transfer from the exoskeleton to the mouthparts (see also Müller, 1996; Fateryga *et al.*, 2022; Fateryga & Fadeev, 2023). They consist of specialized stiff "knobbed" pollen-collecting setae covering the anterior surface of the head, particularly the frons and the clypeus, as well as comb-like rows of specialized, particularly strong pollen-brushing setae along the anterior margins of the inner surface of the first and the second segments of the foretarsi. A female performs rubbing movements of her head over the nototribic anthers and in this manner pollen grains are removed from the pollen sacs and accumulate on frons and clypeus. Periodically, the pollen grains are transferred from the frons and the clypeus to the mouthparts by alternating brushing movements of the forelegs and the pollen is ingested. Gess & Gess (1989) did not cite Schremmer (1959) directly, but questioned the observations made by that author, citing a book reproducing Schremmer's drawings (Barth, 1985). Gess & Gess (1989) did not find "button-ended collecting bristles on the front surface" of the head of *C. abbreviatus* and considered that all species of the genus *Celonites* simply draw pollen from the anthers (or from the "floor" of the horizontal corolla tube in some cases) towards the mouthparts with the forelegs. However, specialized stiff "knobbed" pollen-collecting setae were then confirmed for *C. abbreviatus* by Müller (1996) and found in other species of the *C. abbreviatus*-complex as well (Mauss, 2013; Mauss *et al.*, 2016; Fateryga *et al.*, 2022).

Females of *C. sibiricus* demonstrate a similar behavior at nototribic flowers of Lamiaceae as the members of the *C. abbreviatus*-complex but their frons is covered with stiff, thick, flattened setae that are spatula-like with a roundly pointed distal tip; their foretarsi are less specialized (Fateryga *et al.*, 2023). Anyway, the specialized pollen-collecting setae of *C. sibiricus* are relatively short (about as long as the diameter of the median ocellus) and thick, similarly to those in the members of the *C. abbreviatus*-complex. Females of *C. montanus* have distinctly longer and much thinner setae on the frons (see Fateryga & Fadeev, 2023). Due to the delicate structure of the setae, the latter authors hypothesized that *C. montanus* was not able to use them for pollen uptake and consumed pollen directly from the anthers with its mouthparts. However, the present observations suggest that the hypothesis by Fateryga & Fadeev (2023) was incorrect. Interestingly, there is a species of *Celonites* with even longer (but denser) setae on the frons, *C. laetus* Panfilov, 1968 (Fateryga, 2025a), and the type series of its synonym (*C. phlomis* Gusenleitner, 1973) was collected at flowers of the genus *Phlomis* L. (Lamiaceae) (Gusenleitner, 1973), which are also nototribic.

Pollen uptake with specialized pollen-collecting setae occurs in the subfamily Masarinae not only in the genus *Celonites*. Panfilov (1968) reported that the type series of *Masaris tianshanicus* Panfilov, 1968 was collected at *Thymus* sp. (Lamiaceae) and this wasp species has specialized stiff pollen-collecting setae covering the anterior surface of the head, as well as the closely related *M. longicornis* (Kuznetzov, 1923) (Fateryga, 2025b). An Australian pollen wasp *Metaparagia maculata* (Meade-Waldo, 1910) has specialized stiff pollen-collecting setae on the propleura, forecoxae, foretrochanters, and mesepisternum used to uptake pollen from sternotribic flowers of the genus *Jacksonia* R. Br. ex Sm. (Fabaceae) (Houston, 1995). Mauss (1996) also reported a European masarine *Ceramius tuberculifer* de Saussure, 1854 using setae on the frons to collect pollen from nototribic flowers of *Teucrium montanum*; however, the setae of this wasp species are apparently not specialized, as are those of *C. montanus*.

Pollen collection, contrary to nectar collection, is a specific and stereotypic behavior that often requires morphological and behavioral adaptations (Mauss *et al.*, 2024). Pollen uptake from the anthers with specialized pollen-collecting setae may be evolved from an accidental consumption of pollen adhering to the body during nectar uptake. Many pollen wasp species from various genera regularly receive pollen on either frontal surface of the head and anterior part of the dorsal surface of the mesosoma or the ventral surface of the mesosoma during nectar uptake (Gess & Gess, 1989; Gess *et al.*, 1995) and many of them subsequently brush and consume this pollen (Mauss & Müller, 2016; Mauss *et al.*, 2006, 2018), as in the observed case of the males of *C. montanus* at *Convolvulus fruticosus*. Therefore, not specialized setae are available in many species of pollen wasps for pollen uptake as a pre-adaptation. Further development of the behavioral adaptations to active pollen uptake with these setae, like in the cases of *C. montanus* or *Ceramius tuberculifer*, may be followed by morphological adaptations of the setae themselves, like in the cases of the members of the *C. abbreviatus*-complex and *C. sibiricus*. It is interesting that pollen removal from the anthers and nectar uptake take place separately from each other in temporal succession in both *C. montanus* and *C. sibiricus* (Fateryga, 2020). Females of *C. abbreviatus* and the closely related *C. tauricus* Kostylev, 1935 can take up pollen and nectar either also separately (Schremmer, 1959; Fateryga *et al.*, 2022) or simultaneously (Mauss, 2006; Mauss *et al.*, 2016), depending on the flower morphology of the forage plant species.

The trophic relationships of the genus *Celonites* with the angiosperm plants are still insufficiently studied in Central Asia and more field data are necessary to improve our knowledge on the ethology of these wasps.

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