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NEW RECORDS OF *CELONITES KOZLOVI* KOSTYLEV, 1935 AND *C. SIBIRICUS* GUSENLEITNER, 2007 (HYMENOPTERA: VESPIDAE: MASARINAE), WITH OBSERVATIONS ON THEIR BEHAVIOR AT FLOWERS

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Summary. The distribution of *Celonites kozlovi* Kostylev, 1935 and *C. sibiricus* Gusenleitner, 2007 is summarized. *Celonites kozlovi* is firstly reported from Russia and *C. sibiricus* is firstly reported from Kazakhstan. The lectotype of *C. kozlovi* is designated and its type locality in Mongolia is specified in detail (to the south of Mt. Dund Saikhany Nuruu, Ömnögovi Prov.). Both species were observed in Kosh-Agach District of the Altai Republic, Russia. Females of *C. kozlovi* collected pollen at flowers of *Dracocephalum peregrinum* L. (Lamiaceae). They consumed pollen directly from the anthers and then penetrated deeply into the corolla tube to collect nectar. Females of *C. sibiricus* used flowers of *D. peregrinum* and *D. nutans* L. but collected pollen by a different way. They used specialized pollen-collecting setae on the frons by rubbing them over the anthers so that pollen grains accumulated on them; afterwards, pollen was transferred from the head to the mouthparts by brushing movements of the fore legs. After that, they also collected nectar from the same flowers of *Dracocephalum* spp. Both wasp species occasionally visited flowers of some other plant species for nectar collecting only. Males of *C. sibiricus* were observed at the forage sites while males of *C. kozlovi* are still unknown.

Key words: pollen wasps, lectotype, distribution, trophic relations, Lamiaceae, *Dracocephalum*, Altai, Russia, Kazakhstan, Mongolia, Palaearctic region.

А. В. Фатерыга. Новые находки *Celonites kozlovi* Kostylev, 1935 и *C. sibiricus* Gusenleitner, 2007 (Hymenoptera: Vespidae: Masarinae) с наблюдениями за их поведением на цветках // Дальневосточный энтомолог. 2020. N 405. С. 20-32.

Резюме. Обобщено распространение *Celonites kozlovi* Kostylev, 1935 и *C. sibiricus* Gusenleitner, 2007. *Celonites kozlovi* впервые приводится для России, а *C. sibiricus* – для Казахстана. Обозначен лектотип *C. kozlovi* и уточнена его типовая местность в Монголии (аймак Умнеговь, к югу от горы Дунд-Сайханы-Нуру). Проведены наблюдения за обоими видами в Кош-Агачском районе Республики Алтай (Россия). Самки *C. kozlovi* отмечены собирающими пыльцу на цветках *Dracocephalum peregrinum* L. (Lamiaceae). Они потребляли пыльцу напрямую из пыльников, а затем проникали глубоко внутрь трубки венчика для сбора нектара. Самки *C. sibiricus* посещали цветки *D. peregrinum* и

D. nutans L., но собирали с них пыльцу иным способом, используя для этого специализированные волоски на лбу. Они терлись этими волосками о пыльники так, что пыльца накапливалась в них, а затем перемещали ее с головы к ротовым органам с помощью передних ног. После этого самки собирали нектар с этих же цветков *Dracocephalum* spp. Оба вида ос также эпизодически посещали цветки некоторых других видов растений, но только для сбора нектара. Самцы *C. sibiricus* наблюдались на участках фуражировки, в то время как самцы *C. kozlovi* остаются неизвестными.

INTRODUCTION

Celonites Latreille, 1802 is the second largest genus of pollen wasps (Hymenoptera: Vespidae: Masarinae) after *Quartinia* André, 1884 (Richards, 1962; Carpenter, 2001). The genus is distributed in the Palaearctic and Afrotropical regions. Sixty two species of *Celonites* are recognized in the World; of them 40 species with six additional subspecies are known in the Palaearctic region (Carpenter, 2001, combined with newly described or synonymized species by Gusenleitner, 2002, 2007, 2012, 2018; Mauss, 2013; Mauss *et al.*, 2016; Mauss & Prosi, 2018). Most species of *Celonites* are poorly known and rarely collected. Data on bionomics of the genus are also scarce. Nesting has been studied just for three Palaearctic (Bellmann, 1984; Mauss & Müller, 2014; Mauss *et al.*, 2016) and seven Afrotropical species (Gess, 1996; Gess & Gess, 2010). Females of most species (including all studied Palaearctic taxa) build aerial mud nests consisting of cylindrical cells usually covered with an additional mud layer; nests are usually attached to stones or twigs. Some Afrotropical species place their nest cells within excavated or preexisting holes in an earthen substrate. Palaearctic species are known to collect pollen from plants of the families Lamiaceae and Boraginaceae while Afrotropical taxa usually use Scrophulariaceae, Campanulaceae, and less often also Asteraceae, Boraginaceae, and Aizoaceae (Gess, 1996; Gess & Gess, 2010; Mauss & Müller, 2014).

Celonites kozlovi Kostylev, 1935 was described on the base of a female or females from Gobi Desert, Mongolia; the sex and the number of specimens examined, however, were not indicated in the original description (Kostylev, 1935). Together with five other species, *C. kozlovi* was placed into a new subgenus *Paracelonites* Kostylev, 1935 (unavailable name, no type species was designated), which was later synonymized with the subgenus *Celonites* s. str. (Richards, 1962; Carpenter, 2001). Then, an additional female of *C. kozlovi* was reported from the Khovd Prov. of Mongolia (Gusenleitner, 1991). *Celonites sibiricus* Gusenleitner, 2007 was described on the base of a series of one female and seven males from the environs of Aktru Glacier (Severo-Chuyskiy Range) in Altai Mountains, Russia (Gusenleitner, 2007). Just two additional females collected near to the type locality were reported (Fateryga *et al.*, 2017). Nothing has been hitherto known on the bionomics of these rarely collected species.

The purpose of the present paper is to designate the lectotype of *C. kozlovi*, report new records of *C. kozlovi* and *C. sibiricus*, and provide the data on their forage plants and behavior at flowers in Altai.

MATERIAL AND METHODS

Field observations were carried out at two localities in Kosh-Agach District of the Altai Republic, Russia on July 6–10, 2019. The first locality was the Chuya River valley in 24 km NWW of Aktash, 50°21′31″N 87°16′15″E. Wasps were observed there at a roadside slope covered with sparse herbaceous vegetation. Several plant species were in flower; among them, the most abundant were *Dracocephalum nutans* L., *D. peregrinum* L., *Nepeta sibirica* L., *Ziziphora clinopodioides* Lam. (Lamiaceae), and *Polygala sibirica* L. (Polygalaceae). Up the slope, this vegetation was changed to sparse trees of *Picea obovata* Ledeb. and *Larix sibirica* Ledeb. (Pinaceae) and shrubs of *Spiraea* sp. (Rosaceae), *Ribes* sp. (Grossulariaceae), *Lonicera* sp. (Caprifoliaceae), and *Berberis* sp. (Berberidaceae).

The second locality was the Tydtuyaryk River valley in 5 km SE of Chagan-Uzun, 50°04′25″N 88°25′12″E. The wasps were observed there mainly at a plot of steppe vegetation with abundant flowering specimens of *D. peregrinum*, as well as *Vicia costata* Ledeb. (Fabaceae). The plot was surrounded by mountain semidesert with sparse herbaceous vegetation of very rich species composition. The most abundant species were *Psathyrostachys juncea* (Fisch.) Nevski, *Agropyron kazachstanicum* (Tzvelev) Peschkova (Poaceae), *Chenopodium frutescens* C.A. Mey., *Anabasis brevifolia* C.A. Mey., *Krascheninnikovia ceratoides* (L.) Gueldenst. (Chenopodiaceae), *Zygophyllum pinnatum* Cham. (Zygophyllaceae), *Ephedra dahurica* Turcz. (Ephedraceae), *Atraphaxis pungens* (M. Bieb.) Jaub. & Spachs (Polygonaceae), *Saussurea pricei* N.D. Simpson, *Artemisia frigida* Willd. (Asteraceae), *Convolvulus ammannii* Desr. (Convolvulaceae), and *Gypsophila patrinii* Ser. (Caryophyllaceae). Some shrubs of *Caragana bungei* Ledeb. and *C. pygmaea* (L.) DC. (Fabaceae) were also present around the plot.

Wasp activity was observed visually during the whole day, except during bad weather, and documented with a Canon PowerShot SX160 IS camera. Two days were spent at the Chuya River valley and three ones at the Tydtuyaryk River valley. Wasps' forage plants were collected, preserved dried, and deposited in the Moscow University Herbarium, Moscow, Russia (MW). They were identified following Krasnoborov & Artemov (2012). Flower preferences of the wasps were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the locality.

The studied specimens of both species of *Celonites* are deposited in the collection of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia [ZISP], the Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far East Branch of the Russian Academy of Sciences, Vladivostok, Russia [FSCV], the Institute of Systematics and Ecology of Animals of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia [ISEN], the Altai State University, Barnaul, Russia [ASUB], the collection of the author stored in T.I. Vyazemsky Karadag Scientific Station – Nature Reserve of RAS – Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Feodosia, Russia [CAFK], and the collection of Volker Mauss, Michelfeld, Germany [CVMM].

Photographs of the lectotype of *C. kozlovi* were taken in ZISP with a Canon EOS 70D digital camera attached to an Olympus SZX10 stereomicroscope. Multifocus-images were created from stacks of photographs using Helicon Focus 6 Pro software. Final illustrations were post-processed for sharpness, contrast, and brightness using Adobe Photoshop CS2 software. SEM micrographs of the wasp heads were taken using a Hitachi SE3500 Scanning Electron Microscope. The heads of dried specimens were not critical-point dried; they were simply mounted on stubs and coated with gold and palladium.

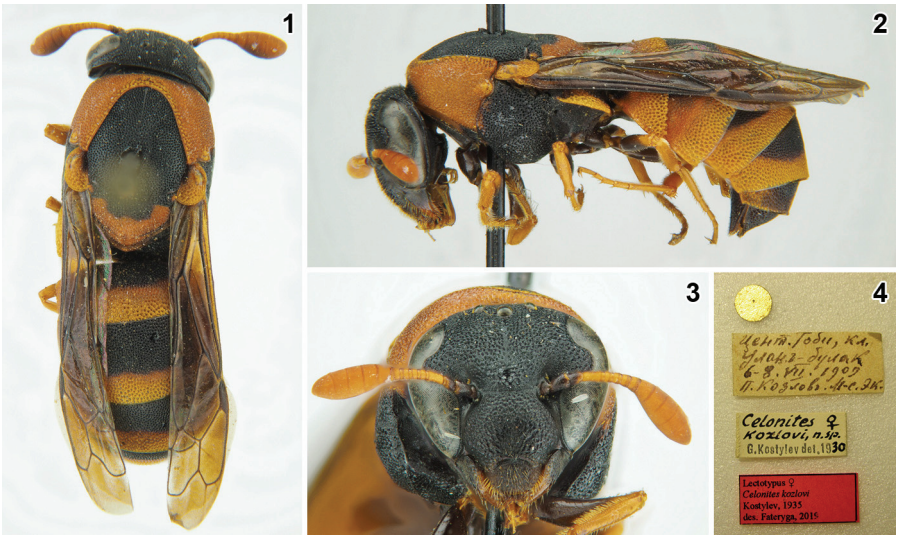
RESULTS

***Celonites kozlovi* Kostylev, 1935**
Figs 1–4, 7, 8, 19–21

Celonites kozlovi Kostylev, 1935: 110, [♀] (type locality: "Пустыня Гоби (Монголия)" [Gobi Desert, Mongolia]), **lectotype (designated here):** ♀, <golden disc> // Центр.[альная] Гоби, кл.[юч] Улан-булак [Central Gobi, Ulan-Bulak Spring] 6–8.VII.1909 П.[К.] Козлов [P.K. Kozlov]. М.[онголо]-С.[ычуанская] эк.[спедиция] [Mongolia-Sichuan expedition] // *Celonites* ♀ *kozlovi*, n. sp. G. Kostylev det. 1930 // Lectotypus ♀ *Celonites kozlovi* Kostylev, 1935 des. Fateryga, 2019 <red label> [ZISP] (Figs 1–4); Gusenleitner, 1991: 640, Mongolia (Khovd Prov.); Carpenter, 2001: 10, Mongolia.

REMARKS. According to Kerzhner (1972), P.K. Kozlov collected in those days in South-Gobi aimak [Ömnögovi Prov.] on the south slope of Mt. Dund Saikhany Nuruu (middle mountain of the Gurvan Saikhan Mountains). Kozlov spent those days in a camp at some "red" hills (Kozlov, 2015). Thus, the type locality of *C. kozlovi* was located at approximately 43°33′N 103°43′E (the rightmost point on Fig. 5), where a relatively large area of red-colored ground is visible via Google Earth (https://www.google.com/earth/).

Males of this species are still unknown.



Figs 1–4. *Celonites kozlovi* Kostylev, ♀, lectotype: 1 – habitus, dorsal view; 2 – habitus, lateral view; 3 – head, frontal view; 4 – labels.

Fig. 5. Distribution of *Celonites kozlovi* Kostylev and *C. sibiricus* Gusenleitner (background map was taken from https://www.openstreetmap.org/).

ADDITIONAL MATERIAL EXAMINED. **Russia:** *Altai*: 2 km SE Chagan-Uzun, Balkhash River valley (50°05′35″N 88°23′22″E), 9.VII 2016, 3 ♀, leg. M.Yu. Proshchalykin, V.M. Loktionov [FSCV]; 5 km SE Chagan-Uzun, Tydtuyaryk River valley (50°04′25″N 88°25′12″E), 8.VII 2019, 8 ♀, 9.VII 2019, 1 ♀, leg. A.V. Fateryga [CAFK, CVMM]; ibid., 8.VII 2019, 2 ♀, 9.VII 2019, 1 ♀, leg. V.O. Dorofeev [ASUB]; ibid., 8–9.VII 2019, 1 ♀, leg. Yu.N. Danilov [ISEN].

DISTRIBUTION. Russia (new record) (Altai), Mongolia (Khovd Prov., Ömnögovi Prov.) (Fig. 5).

BIONOMICS. In the field *C. kozlovi* was observed in the Tydtuyaryk River valley only (Fig. 6); it was absent from the Chuya River valley. Females of this species visited flowers of five plant species of the families Lamiaceae and Asteraceae (Table 1). The only pollen source, however, was flowers of *Dracocephalum peregrinum*. During pollen uptake from these flowers, females stood on the lower lip of the corolla and consumed pollen directly from the anthers. They did this with their mouthparts supported by movements of the fore legs; mid and hind legs were used to hold onto the corolla (Fig. 7). The duration of pollen collecting per flower was approximately 40–45 sec. After that, females went deeply inside the corolla to take up nectar. During nectar collecting they were not visible from outside due to the deep and broad corolla tube which completely hid the wasps. The duration of nectar collecting was significantly less (about 5 sec.) than that of pollen collecting.

Table 1. Flower-visiting records of *Celonites kozlovi* Kostylev and *C. sibiricus* Gusenleitner

Plant taxon	Σ sightings of flower-visiting individuals			
	C. kozlovi		*C. sibiricus*	
	♀	♂	♀	♂
Lamiaceae				
Dracocephalum nutans L.			77*	4
Dracocephalum peregrinum L.	19*		46*	
Ziziphora clinopodioides Lam.	7			
Asteraceae				
Aster alpinus L.	1			
Saussurea pricei N.D. Simpson	1			
Youngia tenuifolia subsp. *altaica* Babc. & Stebbins	1			
Geraniaceae				
Geranium sibiricum L.			1	1

* – collecting of both pollen and nectar (other cases are nectar collecting only).

Only nectar collecting was observed at flowers of *Ziziphora clinopodioides*. Flowers of this species are significantly smaller than those of *D. peregrinum*; the corolla tube is even shorter than the proboscis of the wasp. Thus, during flower visits females alighted on the lower lip, hold onto it with all their legs and simply inserted the proboscis into the flower (Fig. 8). Duration of nectar collecting on *Z. clinopodioides* was also about 5 sec. One female was observed to collect earth after visiting several flowers of *Z. clinopodioides*. She did this on a slope with quite loose ground between plants of this species.

It must be specified that there were no plants of *Dracocephalum nutans* in the Tydtuyaryk River valley. Other species of Lamiaceae were represented in this habitat by *Panzerina canescens* (Bunge) Soják and *P. lanata* (L.) Soják, but they were not visited by *C. kozlovi*.

Visiting plants of the family Asteraceae, females landed directly on the center of the capitulum and inserted the proboscis into one of the florets for a very short time. Then, they flew away in all three observed cases.

First activity of the wasps was recorded in the morning at 9.35 (solar time). In the late afternoon, the activity finished at various times depending on the weather.

No males of *C. kozlovi* were observed despite thorough searching.

Figs 6–8. Bionomics of *Celonites kozlovi* Kostylev: 6 – habitat in the Tydtuyaryk River valley; 7 – female collecting pollen on a flower of *Dracocephalum peregrinum* L. by consuming pollen directly from the anthers; 8 – female collecting nectar on a flower of *Ziziphora clinopodioides* Lam.

***Celonites sibiricus* Gusenleitner, 2007**
Figs 10–14, 22–24

Celonites sibiricus Gusenleitner, 2007: 133–134, ♀ ♂ (type locality: "Russia, Sibiria, Altaya, Cevero-Chuyskiy"), holotype, ♂, in the collection of J.T. Smit, Duiven, The Netherlands; Fateryga *et al.*, 2017: 32, Russia (Altai); Antropov & Fateryga, 2017: 178, Russia (Altai).

MATERIAL EXAMINED. **Russia:** *Altai*: 15 km SE Kuray, Chuya River valley (50°11′10″N 88°07′04″E), 5.VII 2016, 1 ♀, leg. M.Yu. Proshchalykin, V.M. Loktionov; 2 km SE Chagan-Uzun, Balkhash River valley (50°05′35″N 88°23′22″E), 9.VII 2016, 7 ♀, leg. M.Yu. Proshchalykin, V.M. Loktionov; 5 km SE Chagan-Uzun, Tydtuyaryk River valley (50°04′25″N 88°25′12″E), 11.VII 2016, 5 ♀, leg. M.Yu. Proshchalykin, V.M. Loktionov [FSCV]; ibid., 8.VII 2019, 4 ♀, 4 ♂, 9.VII 2019, 1 ♀, 1 ♂, 10.VII 2019, 1 ♂, leg. A.V. Fateryga [CAFK, CVMM, ZISP]; ibid., 8–9.VII 2019, 4 ♀, leg. Yu.N. Danilov [ISEN]; ibid., 9.VII 2019, 3 ♀, leg. V.O. Dorofeev [ASUB]; 12 km SE Aktash, Chuya River valley (50°13′51″N 87°42′59″E), 13.VII 2016, 1 ♀, leg. M.Yu. Proshchalykin, V.M. Loktionov [FSCV]; 24 km NWW Aktash, Chuya River valley (50°21′31″N 87°16′15″E), 6.VII 2019, 3 ♀, 4 ♂, 7.VII 2019, 2 ♀, 1 ♂, leg. A.V. Fateryga [CAFK, CVMM]; ibid., 6.VII 2019, 1 ♂, 7.VII 2019, 1 ♀, leg. V.O. Dorofeev [ASUB]. **Kazakhstan:** *East Kazakhstan Prov.*: Central Tarbagatay, 80 km S Aksuat, 13.VII 1986, 9 ♀, 1 ♂, leg. V.L. Kazenas [FSCV].

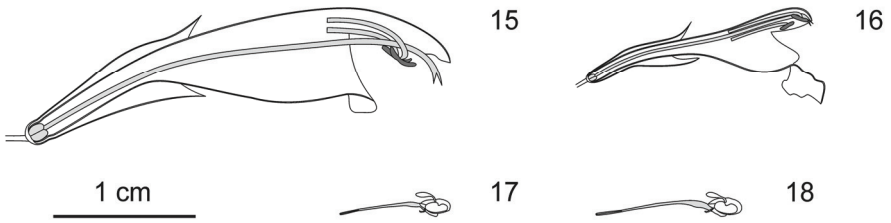
DISTRIBUTION. Russia (Altai), Kazakhstan (new record) (East Kazakhstan Prov.), (Fig. 5).

BIONOMICS. *Celonites sibiricus* was observed in both field study areas that were the Tydtuyaryk River valley and the Chuya River valley (Figs 6 and 9). Females of this species visited flowers of both species of *Dracocephalum* and occasionally *Geranium sibiricum* (Table 1). At the same time, they did not visit *Nepeta sibirica* in the Chuya River valley, two species of *Panzerina* in the Tydtuyaryk River valley, and *Ziziphora clinopodioides* in both habitats. Pollen collecting was observed only at flowers of *Dracocephalum* spp. During visits to *D. peregrinum* flowers, females alighted on the lower lip of the corolla and started pollen uptake by rubbing the head over the anthers which was accompanied by alternating movements of the fore legs brushing pollen from the frons towards the mouthparts. Mid and hind legs were used to hold onto the corolla (Fig. 10). The duration of pollen uptake was significantly shorter (about 5–10 sec.) than in *C. kozlovi*. After that, females moved deeply inside the corolla tube to take up nectar, which was similar to nectar-collecting behavior in *C. kozlovi* (the duration of nectar uptake was also about 5 sec.). While visiting several flowers on the same inflorescence, the females moved upwards along the inflorescence flying from flower to flower from its base towards the top.

Pollen-collecting behavior of the females at flowers of *D. nutans* (Fig. 11) was similar to that on *D. peregrinum*. Nectar collecting, however, was different: females did not move deeply inside the corolla tube; instead, the posterior half of their mesosoma and the whole metasoma remained visible from outside (Fig. 12). The difference was caused by the different shape and size of the corolla in these two plant species. *Dracocephalum peregrinum* has a broad corolla (Fig. 15) and both *Celonites* species can move deeply inside it. The corolla of *D. nutans* is much narrower in its basal half (Fig. 16). The proboscis of *C. sibiricus*, however, is long enough (Fig. 18) to reach nectar in the flower of *D. nutans* without inserting the head into the basal half of the corolla tube, while the proboscis of *C. kozlovi* is shorter due to the smaller size of that species (Fig. 17).

Figs 9–14. Bionomics of *Celonites sibiricus* Gusenleitner: 9 – habitat in the Chuya River valley; 10 – female collecting pollen on a flower of *Dracocephalum peregrinum* L. by rubbing her head over the anthers combined with alternating movements of her fore legs brushing pollen from the frons towards the mouthparts; 11 – female collecting pollen on a flower of *D. nutans* L. in the same way; 12 – female collecting nectar on a flower of *D. nutans*; 13 – female standing on a stone and brushing pollen from the frons towards the mouthparts by alternating movements of the fore legs subsequent to visit of several flowers; 14 – male perching on a stone.

Pollen and nectar collecting at flowers of *Dracocephalum* spp. was periodically interrupted by alighting on the ground, small stones, or fragments of horse dung, where the females remained on the surface for up to a minute. During the first half of such a stay, females performed rapid movements of their metasoma: they alternately pulled it out and drew it back. After that, they brushed pollen from the frons towards the mouthparts by alternating movements of the fore legs (Fig. 13). Often they also partially extended the proboscis and brushed over it as well. Then, they usually returned to flower visiting.



Figs 15–18. Schematic plans of dissected flowers of *Dracocephalum* spp. (15–16) and extended proboscises of *Celonites* spp. (17–18), lateral view: 15 – *D. peregrinum* L.; 16 – *D. nutans* L.; 17 – *C. kozlovi* Kostylev; 18 – *C. sibiricus* Gusenleitner.

During the single observed flower visit of a female at *Geranium sibiricum*, the female landed on a petal holding onto it with all her legs and simply inserted the proboscis into the flower. The duration of the visit was about 10 sec.

Flight activity started in the morning at 7.40–9.05 (solar time) and finished in the late afternoon at various times depending on the weather.

Males of *C. sibiricus* were observed mainly perching on the ground and small stones (Fig. 14) among patches of *Dracocephalum* spp. They also visited flowers of *D. nutans* and *G. sibiricum* for nectar feeding (Table 1). Courtship and copulation were not observed.

DISCUSSION

The present study substantively enlarges the knowledge on distribution of *C. kozlovi* and *C. sibiricus*. *Celonites kozlovi* is reported from Russia for the first time; its type locality in Mongolia is also specified in detail due to designation of the lectotype. *Celonites sibiricus* is reported from Kazakhstan for the first time.

It is well known that wasps of the subfamily Masarinae are distributed over arid areas of the World, except the Oriental region (Gess, 1996; Gess & Gess, 2010). Just two species of the genus *Celonites* were previously known from Russia (Antropov & Fateryga, 2017). The first one was *C. tauricus* Kostylev, 1935 distributed in the Crimea, Greece (Island Kos), Armenia, Azerbaijan, Turkey, Cyprus, Syria, and Northern Iran (Mauss *et al.*, 2016; Fateryga, 2017). Discovering of the second species, *C. sibiricus* in Altai (Gusenleitner, 2007) was very surprising, since it was collected from the environs of Aktru Glacier (Severo-Chuyskiy Range). Such a habitat at the elevation of 2550–3245 m above see level (according to the coordinates published by Gusenleitner, 2007 and Fateryga *et al.*, 2017) is very unusual for pollen wasps because it is alpine tundra close to the snow line. The present records of *C. sibiricus* are situated significantly lower (1040–1785 m above see level) and come from habitats that are more typical for Masarinae (Figs 6 and 9). It is very likely, that the species is very abundant and spread in Altai Mountains. Thus, it could be episodically found even in such extreme habitats as its type locality.

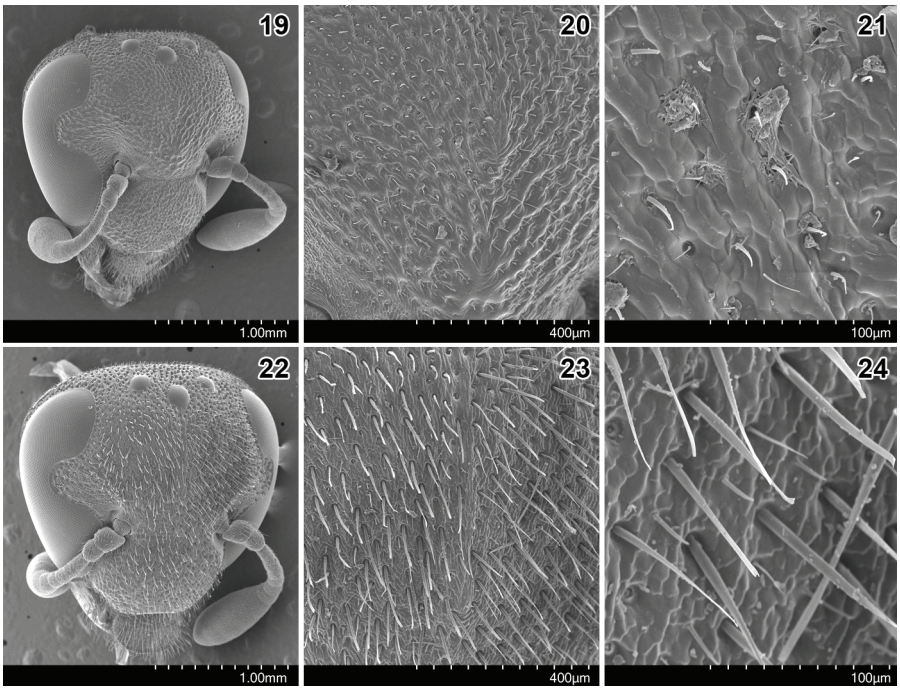
Celonites kozlovi is the third species of pollen wasps known from Russia. Its known distribution in Altai, however, is restricted to the vicinity of Chagan-Uzun (1745–1785 m above see level). This area is characterized by changing of typical Altaian vegetation (Fig. 9) to a mountain semidesert (Fig. 6) extending to the southeast and then occupying vast areas in Mongolia. Thus, the present records of *C. kozlovi* are probably made at the northwest edge of its distributional range. Kozlov (2015) described the vegetation of the environs of Mt. Dund Saikhany Nuruu (type locality of the species). At least four plant species (but in fact probably more) from that place are also present in the Tydtuyaryk River valley: *Aster alpinus*, *Convolvulus ammannii*, *Panzerina lanata*, and *Vicia costata*.

Species of the genus *Celonites*, previously known collecting pollen from nototribic flowers of Lamiaceae, belong to the *C. abbreviatus*-complex which includes *C. abbreviatus* (Villers, 1789), *C. andreasmuelleri* Mauss, 2013, *C. hermon* Gusenleitner, 2002, *C. mayeti* Richards, 1962, *C. persicus* Richards, 1962, and *C. tauricus* (Mauss, 2013; Mauss *et al.*, 2016; Mauss & Prosi, 2018). All of them have a specialized pollen-collecting apparatus in the form of knobbed setae densely covering the frons (Schremmer, 1959; Müller, 1996; Mauss, 2013). Females of *C. abbreviatus* and *C. tauricus* collect pollen from nototribic flowers of Lamiaceae species by rubbing these knobbed setae over the anthers so that pollen grains accumulate on the frons; afterwards, pollen is transferred from the head to the mouthparts by brushing movements of the fore legs (Schremmer, 1959; Mauss, 2006; Mauss *et al.*, 2016). It is important that both *C. abbreviatus* and *C. tauricus* usually take up nectar simultaneously with pollen collecting. This feature probably increases the rate of their forage activity. The *C. abbreviatus*-complex belongs to the *C. abbreviatus*-group (*sensu* Richards, 1962) which includes also the *C. fischeri*-complex with two species: *C. afer* Lepeletier de Saint-Fargeau, 1841 and *C. fischeri* Spinola, 1838. These species collect pollen from sternotribic flowers of *Echium* spp. (Boraginaceae) and they are lacking specialized knobbed setae on the frons. Thus, females of *C. fischeri* consume pollen directly from the anthers, even from flowers which have just started to open. Furthermore, they collect nectar separately from pollen, even from different flowers (Mauss & Müller, 2014).

Celonites kozlovi and *C. sibiricus* do not belong to *C. abbreviatus*-group. Both species seem to be rather closely related to each other but they have strong differences in pollen-collecting behavior. *Celonites kozlovi* is lacking specialized pollen-collecting setae on the frons (Figs 19–21) and it acts similarly to *C. fischeri* in consuming pollen directly from the anthers, however, always from opened flowers. On the other hand, *C. kozlovi* collects nectar from the same flowers after pollen collecting while *C. fischeri* often uses different flowers for pollen and nectar collecting (Mauss & Müller, 2014).

Pollen-collecting behavior of *C. sibiricus* resembles that of *C. abbreviatus* and *C. tauricus* in that pollen is removed from the nototribic anthers by rubbing movements of the frons, while the female is standing on the lower lip of the zygomorphic flower. But it differs distinctly in that pollen removal from the anthers is simultaneously accompanied by alternating brushing movements of the fore legs in *C. sibiricus*, whereas in members of the *C. abbreviatus*-complex pollen uptake from the anthers by rubbing movements of the frons and pollen removal from the frons towards the mouthparts by brushing movements of the fore legs take always place separately from each other in temporal succession (Schremmer, 1959; Mauss, 2006; Mauss *et al.*, 2016). Therefore, pollen-collecting behavior of *C. sibiricus* and members of the *C. abbreviatus*-complex are probably not homogenous. Another important difference in the behavioral pattern is that *C. sibiricus*, like *C. kozlovi*, collects nectar after pollen uptake while members of the *C. abbreviatus*-complex are able to take up nectar and pollen simultaneously.

In *C. sibiricus* and in the members of the *C. abbreviatus*-complex the frons is covered by specialized pollen-collecting setae which allow pollen uptake by rubbing them over the anthers. However, the pollen-collecting setae covering the frons of *C. sibiricus* (Figs 22–24) differ from those of *C. abbreviatus* and *C. tauricus* in that they are not knobbed, i.e., they lack a spherical enlargement at the distal end. Instead, the setae of *C. sibiricus* are rather pointed apically (Fig. 24). Thus, they are not homogenous with the pollen-collecting setae of *C. abbreviatus*-complex.



Figs 19–24. SEM micrographs of *Celonites* spp. structures: 19 – head of *C. kozlovi* Kostylev; 20 – its frons covered with short setae not suitable for pollen collecting; 21 – the same, close up; 22 – head of *C. sibiricus* Gusenleitner; 23 – its frons covered with long pollen-collecting setae; 24 – the same, close up.

In conclusion, the observed similarities in the morphological structures and behavioral patterns in not closely related lineages of the genus *Celonites* can be regarded as an example of homoplasy (*sensu* Pavlinov, 2005). The use of specialized pollen-collecting setae increases the rate of pollen collecting from nototribic flowers and thus can facilitate the general rate of the wasp forage activity.

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