Entomofauna carpathica, 2021, **33**(2): 73-88

NOTES ON *STRUMIGENYS ARGIOLA* (EMERY, 1869) (HYMENOPTERA: FORMICIDAE) WITH EMPHASIS ON ITS DISTRIBUTION, ECOLOGY AND BEHAVIOUR

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PURKART, A., REPTA, F., SELNEKOVIČ, D., JANCÍK, L. & HOLECOVÁ, M. 2021. Notes on *Strumigenys argiola* (Emery, 1869) (Hymenoptera: Formicidae) with emphasis on its distribution, ecology and behaviour. *Entomofauna carpathica*, **33**(2): 73-88.

Abstract: The knowledge on the distribution of *Strumigenys argiola* (Emery, 1869) has been summarized. Four new localities in Slovakia are presented and the northern limit of distribution was moved to 49°N. A total of nine observations of nuptial flights were associated with meteorological data and the weather conditions under which this phenomenon occurs were described. A single ant queen was successfully bred in captivity in an artificial setup and crucial milestones were set for the establishment of a colony. Several remarkable observations related to the bionomy of this cryptic ant species were added.

Key words: nuptial flight, Dacetini, Attini, Slovakia, faunistics, colony founding

INTRODUCTION

Strumigenys F. Smith, 1860 is a genus of tiny Attini ants (most < 4 mm) that live mainly in the tropics and subtropics and currently comprise 853 described species. They are characterised by their small size and cryptic lifestyle, mostly nesting and foraging on the ground, in ground litter or in burrows in rotting wood (WILSON 1953, WETTERER 2011, BOLTON 2021). They are specialised predators of Collembola (springtails) and other tiny soft-bodied arthropods, which has led them to evolve special forms of mandibles designed for hunting fast-moving prey (BROWN & WILSON 1995, BOOHER et al. 2021). In addition, some species have unusual spongy tissue below the waist segments, the role of which is still unknown (SEIFERT 2018). Although *Strumigenys* is the third most speciose ant genus, only ten species are currently known from the western Palaearctic: *S. argiola* (Emery, 1869), *S. baudueri* (Emery, 1875), *S. emmae* (Forel, 1909), *S. lewisi* Cameron, 1886, *S. membranifera* Emery, 1869, *S. perplexa* (Smith, 1876), *S. rogeri* Emery, 1890, *S. silvestrii* Emery, 1906, *S. tenuipilis* Emery, 1915 and *S. tenuissima* (Brown, 1953), with only *S. argiola*, *S. baudueri*, *S. lewisi*, *S. tenuipilis*, and *S. tenuissima* being native (MacGown et al. 2012, Borowiec 2014, Wetterer 2011, Hamer et al. 2021).

There is only one species in Central Europe whose native populations are distributed north to 48°N – *S. argiola.* Due to its small size (workers < 2 mm) and cryptobiotic habits, *S. argiola* is considered to be certainly under-recorded (Seifert 2018). So far, its distribution in Europe has been reported in Portugal (Boieiro et al. 1999), Spain (Tinaut 1988), France (Bondroit 1918), Corsica (Casevitz-Weulersse 1990), Switzerland (Kutter 1973, Borcard et al. 1997), Italy (Emery 1869), Hungary (Gallé et al. 1998), Austria (Fellner et al. 2009), Slovakia (Deván 2008), former Yugoslavia (Petrov & Collingwood 1992), Romania (Tăușan & Pintilioaie 2016), Bulgaria (Lapeva-Gjonova & Ljubomirov 2020), Greece (Bolton 2021), Turkey (Karaman et al. 2014) and the European part of Russia (Yusupov 2009). A single gyne was also found in the Cologne zoo (Buschinger 1997), but it is most likely an artificial introduction (Seifert 2018).

The ecology of this species is even more unknown than what is known about its range. Natural habitats occur in a variety of summer-warm sites, such as rough grasslands, semi-arid grasslands, and dry pine forests (Seifert 2018). It also inhabits rocky structures, even in a synanthropic environment (Fellner et al. 2009, Holecová et al. 2015). For its subterranean lifestyle the most effective method to find this species seems to be the Winkler litter-shifting (all castes) or the Moericke traps (flying alates). According to current knowledge, *S. argiola* disperses by nuptial flights, which mainly take place on August afternoons when air temperatures are at least 23°C (Seifert 2018). Mating itself takes place only on the ground (Fellner et al. 2009), while gynes later spread on the wings (Borovsky 2009). The subsequent fate of the gynes and the process of colony foundation have not yet been studied.

In this study, we summarised the current knowledge on the distribution of *S. argiola* in Slovakia and added new findings. In particular, we have added data on the climatic conditions under which swarming takes place, and we have described the successful establishment of a colony by a single queen under artificial conditions.

MATERIAL AND METHODS

Distribution data

This study summarise all previously published finds of *S. argiola* from the area of Slovakia, including new, previously unpublished data. The individual finds are sorted by date. All newly found specimens were identified using the key in Seifert

(2018) and/or compared with specimens already present in the collection of the first author (see HOLECOVÁ et al. 2015). These dead specimens were preserved in 96% ethanol. Digital photographs of male and female were taken with a Canon EOS 5D Mark II camera connected to a Zeiss Axio Zoom.V16 stereoscope. Image stacks were created manually, combined using Zerene Stacker software, and processed in Adobe Photoshop CC.

Meteorological data

Samples associated with direct observation of ant swarming behaviour were supplemented with weather parameters from the nearest meteorological stations. Following the studies of different authors (e.g. BOOMSMA & LEUSINK 1981, DEPA 2006, STAAB & KLEINEIDAM 2014), we analysed these variables: date, time, precipitation (mm), air temperature (°C), maximum air temperature (°C), average relative humidity (%), wind speed (km/h), sea level pressure (hPa), total cloud cover (%), cloud cover by high-level cloud fraction (%), visibility (km), solar radiation (W/m2) and maximum solar radiation (W/m2) – each measured 2 m above the ground surface. These data were obtained from www.ogimet.com (accessed 31.10.2021) and the Slovak Hydrometeorological Institute (SHMÚ).

Laboratory observations

Observations began on 20 August 2020 with the housing of a single *S. argiola* gyne in an artificial setup (100x80x20mm of aerated concrete block with 74x54x7mm free space in the centre, connected to the outside by an 8mm hole; the central space was filled with pressed fluvisol and artificially created chambers). Transparent covers (glass and red transparent film) of the nest chambers allowed detailed observations. The artificial nest was on a plastic square placed on constantly moist perlite in a closed plastic box of appropriate dimensions (Fig. 1). The ants were fed *ad libidum* with springtails (*Folsomia candida* Willem 1902) twice a week. As this species is considered completely zoophagous, no sugared water or honeydew was offered. The laboratory nest was kept in the dark at a temperature between 20 and 25°C. A Canon EOS 70D body with a Canon EF 100MM F/2.8L Macro is Usm (Canon, Tokyo, Japan) was used to record behaviour of the ant colony. The latest photo documentation of the ant nest was made with uncovered glass, which provided better image quality.

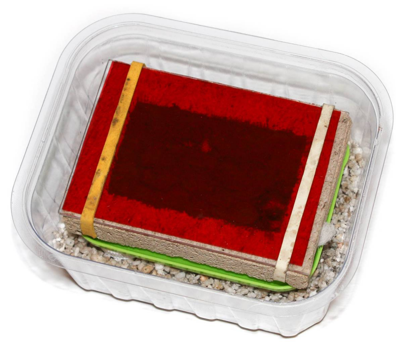

Fig. 1. The artificial nest used for observations consisted of aerated concrete filled with fluvisol, glass, and red transparent foil placed on constantly moist perlite. Photo: Filip Repta.

RESULTS

Material examined

W Slovakia: Omšenská Baba – Ihrište (48°54'38''N, 18°14'08''E), 550 m a. s. l.,1 male, leg. P. Deván, det. et rev. D. Vepřek, G. Alpert, P. Werner, captured in a Moericke trap (DEVÁN 2008)

SW Slovakia: Ivanka pri Dunaji (48°11'35''N, 17°15'45''E), 131 m a. s. l., 30.7.2012, 1 male, leg. F. Repta, det. et coll. A. Purkart, rev. M. Wiezik, captured in a bucket of water in a garden of a family house at 16:00 (HOLECOVÁ et al. 2015 and unpublished data)

SW Slovakia: Bratislava (48°08'35''N, 17°11'26''E), 134 m a. s. l., 5.7.2013, 1 worker, leg. et coll. M. Holecová, det. M. Klesniaková, extracted from litter sample using a Tullgren funnel (HOLECOVÁ et al. 2015)

SW Slovakia: Bratislava (48°08'54''N, 17°05'57''E), 170 m a. s. l., 17.8 – 17.9.2013, 1 gyne, leg. det. et coll. M. Holecová, captured in a formaldehyde pitfall trap (HOLECOVÁ et al. 2015)

SW Slovakia: Bratislava (48°9'24''N, 17°9'29''E), 133 m a. s. l., August 2016, 3 workers, leg. det. et coll. M. Klesniaková, extracted from litter sample using a Tullgren funnel (KLESNIAKOVÁ 2017)

NW Slovakia: Púchov (49°6'57''N, 18°18'19''E), 276 m a. s. l., 30.7.2018 – 30.8.2018, 1 male, leg. det. et coll. L. Jancík, captured in a formaldehyde pitfall trap, new data

SW Slovakia: Bernolákovo (48°11'54''N, 17°17'27''E), 134 m a. s. l., 20.8.2020, 2 males and 1 gyne, leg. det. et coll. F. Repta, captured in a bucket of water in a garden of a family house at 16:00, new data

SW Slovakia: Bernolákovo (48°11'54''N, 17°17'27''E), 134 m a. s. l., 21.8.2020, 1 male, leg. det. et coll. F. Repta, captured in a bucket of water in a garden of a family house at 17:00, new data

SW Slovakia: Bernolákovo (48°11'54''N, 17°17'27''E), 134 m a. s. l., 22.8.2020, 3 males, leg. det. et coll. F. Repta, captured in a bucket of water in a garden of a family house at 16:00, new data

SW Slovakia: Bernolákovo (48°11'54''N, 17°17'27''E), 134 m a. s. l., 23.8.2020, 4 males, leg. det. et coll. F. Repta, captured in a bucket of water in a garden of a family house at 16:00, new data

SE Slovakia: Ruská (48°31'39''N, 22°8’26''E), 102 m a. s. l., 27.8.2020, 1 gyne, leg. det. et coll. F. Repta, captured in a tub filled with water in a garden of a family house at 16:00, new data

SE Slovakia: Ruská (48°31'39''N, 22°8'26''E), 102 m a. s. l., 28.8.2020, 1 male (Fig. 2A, B) and 3 gynes, leg. det. et coll. F. Repta, captured in a tub filled with water in a garden of a family house at 15:00, new data

SE Slovakia: Ruská (48°31'39''N, 22°8'26''E), 102 m a. s. l., 5.9.2020, 1 gyne (Fig. 2C, D), leg. det. et coll. F. Repta, captured in a tub filled with water in a garden of a family house at 16:00, new data

E Slovakia: Soľ (48°55'42''N, 21°36'0''E), 139 m a. s. l., 20.8.2021, 1 male, leg. Radoslav Kopčo, det. et coll. L. Jancík, captured in a tub filled with water in a garden of a family house, new data

SE Slovakia: Ruská (48°31'39''N, 22°8'26''E, Fig. 3), 102 m a. s. l., 11.8.2021, 2 males and 3 gynes, leg. det. et coll. F. Repta, captured in a tub filled with water in a garden of a family house at 17:00, new data

NW Slovakia: Púchov (49°6'57''N, 18°18'19''E, Fig. 4), 276 m a. s. l., 14.6.2021 – 22.8.2021, 2 gynes and 5 males, leg. det. et coll. L. Jancík, captured in a formaldehyde pitfall trap, new data; this locality currently represents the northernmost known distribution of *S. argiola* in Europe (Fig. 5)

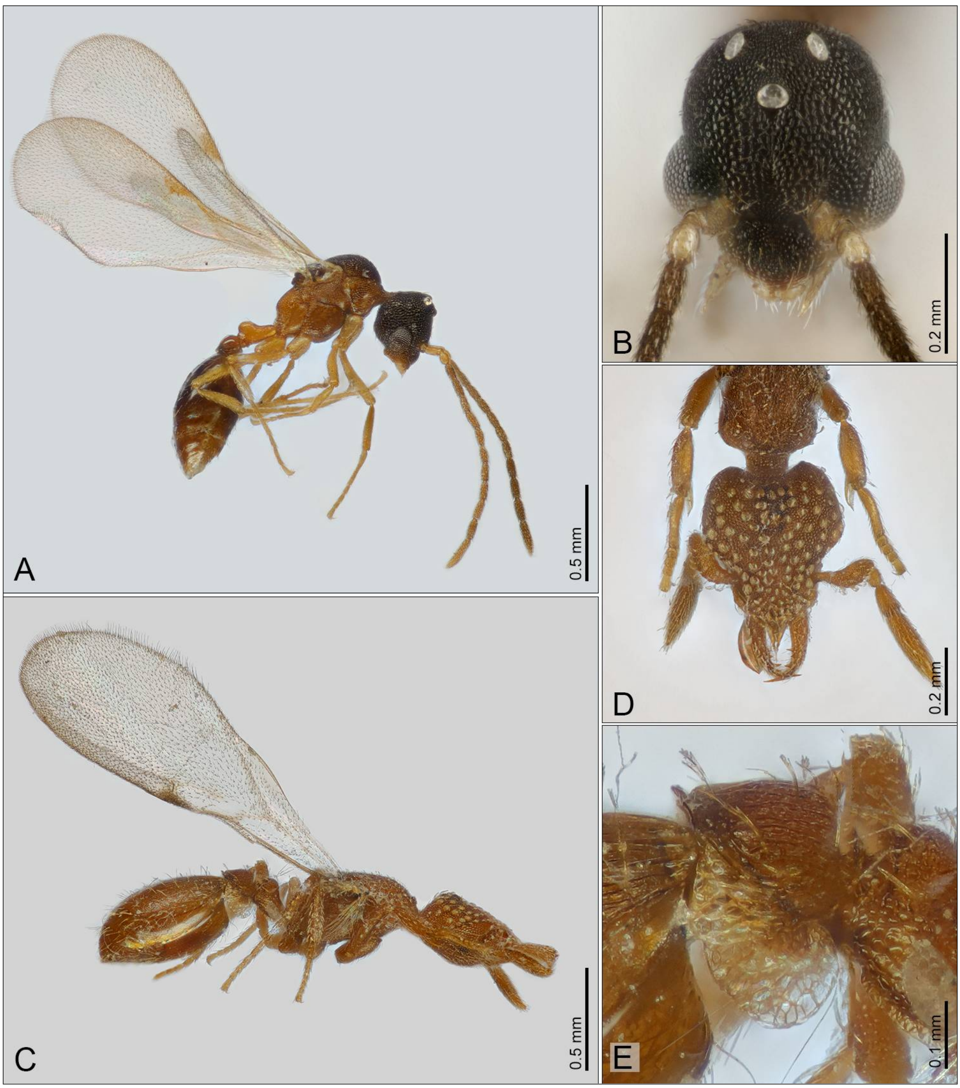

Fig. 2. Habitus of *Strumigenys argiola* alates: **A** – male; **B** – male head, frontal view; **C** – gyne; **D** – gyne head, frontal view, and the astigmatic mite attached on its right mandible; **E** – spongy tissue below the waist segments of gyne. Photo: Dávid Selnekovič.

Fig. 3. Tub filled with rainwater in the garden of a family house in Ruská, SE Slovakia, where alates of *Strumigenys argiola* were collected. Photo: Filip Repta.

Fig. 4. Habitat of *S. argiola* near the vicinity of Púchov, where south-facing slopes are covered with patchy vegetation of sparse stands of scots pine (*Pinus sylvestris*), common hazel (*Corylus avellana*), and black locust (*Robinia pseudoacacia*). Photo: Lukáš Jancík.

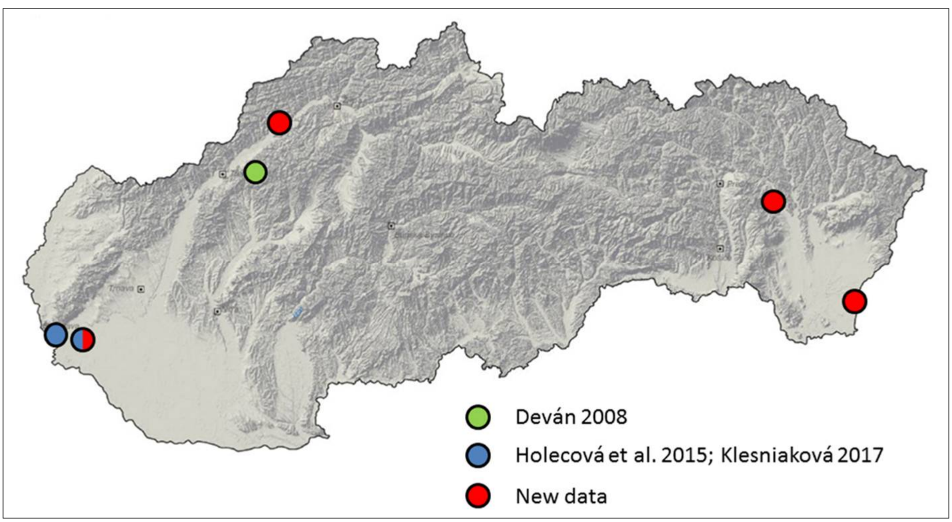

Fig. 5. Distribution of *Strumigenys argiola* in Slovakia.

Nuptial flight ecology

A total of nine observations of nuptial flights were recorded (Tab. 1). All individuals were captured still winged (Fig. 6). Possible phoresy of unidentified astigmatic mite was detected on a single gyne mandible (Fig. 2D). Gynes and males were easily distinguished from each other by sexual dimorphism, including spongy tissue below the gyne waist segments (Fig. 2E). According to the data, this behaviour occurs in Slovakia in the second half of summer, with the earliest record on 30 July and at the latest on 5 September. Both males and females were usually detected in the afternoon between 15:00 and 17:00. The climatic conditions (see Material and methods) under which this phenomenon occurs can be described as follows: air temperature 24.4-30.3 °C; maximum air temperature 25-31.8 °C; average relative humidity 32-58 %; wind speed 7.2-21.6 km/h; precipitation 0 mm; sea level pressure 1010.9-1017.9 hPa; total cloud cover 0-40 %; cloud cover by high-level cloud fraction 0-30 %; visibility 40-50 km; solar radiation 196-548.8 W/m^2 and maximum solar radiation 725.2-859.6 W/m^2.

Tab. 1. Observations of nuptial flights and meteorological data. The time given is UTC+2.

Locality	Day	Time	T	Tmax	Hr	Ws	P	Pr	Nt	Nh	Vis	R	Rmax
Ivanka pri Dunaji	30.7.2012	16:00	24.4	25	32	7.2	1017.9	0	20	10	40	526.4	859.6
Bernolákovo	20.8.2020	16:00	28	28.9	40	10.8	1013.5	0	30	30	50	548.8	840.0
Bernolákovo	21.8.2020	17:00	29.9	30.6	45	21.6	1014.8	0	10	10	50	358.4	806.4
Bernolákovo	22.8.2020	16:00	30.3	31.8	47	14.4	1012.7	0	30	20	50	196	795.2
Bernolákovo	23.8.2020	16:00	26.8	27.5	39	18	1014.9	0	40	30	50	484.4	747.6
Ruská	27.8.2020	16:00	26.2	26.4	41	10.8	1010.9	0	30	30	50	305.2	775.6
Ruská	28.8.2020	15:00	25	25.1	44	10.8	1011.6	0	10	10	50	473.2	750.4
Ruská	5.9.2020	16:00	26.7	27.6	52	10.8	1017	0	20	20	40	299.6	725.2
Ruská	11.8.2021	17:00	26.6	29	58	10.8	1015.9	0	40	10	40	397.6	859.6

Abbreviations: **T** – air temperature (°C), **Tmax** – maximum air temperature (°C), **Hr** – average relative humidity (%), **Ws** – wind speed (km/h), **P** – sea level pressure (hPa), **Pr** – precipitation (mm), **Nt** – total cloud cover (%), **Nh** – cloud cover by high-level cloud fraction (%), **Vis** – visibility (km), **R** – solar radiation (W/m^2), **Rmax** – maximum solar radiation (W/m^2).

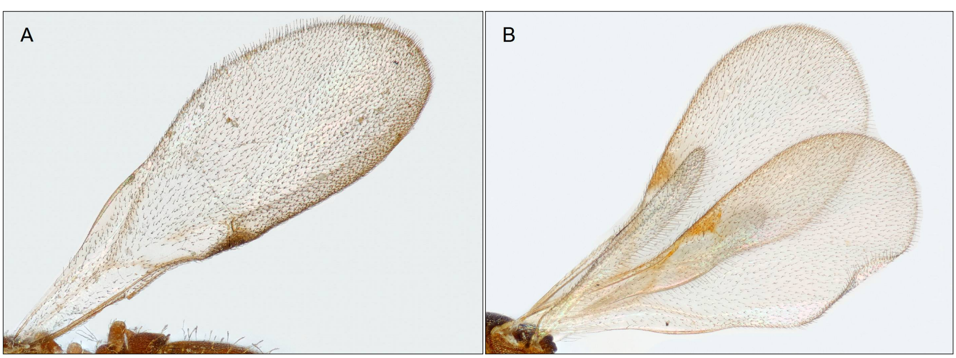

Fig. 6. Details on pilosity and reduced wing veins of *Strumigenys argiola* alate specimens (see Fig 2). **A** – gyne, **B** – male. Photo: Dávid Selnekovič.

Colony founding

The presented gyne was captured 20.8.2020 at 16:00 in Bernolákovo, SW Slovakia (see Material examined). As the gyne drowned in the water, the collector placed it on a napkin in a Petri dish with two males caught at the same place. Within a few minutes, mating took place with at least one male. At about 17:00, the gyne dropped its wings and was transferred to an artificial setup. During transport, the gyne was observed to be able to climb the glass wall of the container. Late in the evening, a dead springtail was placed in the area where the gyne was exploring soil cavities (Fig. 7). Shortly before midnight, a gyne was observed eating the offered springtail (Fig. 8). The next day (August 21, 2020), another springtail was placed in the same place. The gyne spotted it and ate it a few hours later.

Fig. 7. *Strumigenys argiola* gyne exploring soil cavities. Photo: Filip Repta.

Fig. 8. *Strumigenys argiola* gyne and its prey – springtail. Photo: Filip Repta.

The most important milestones for the establishment of the *S. argiola* colony are listed chronologically:

4.11.2020: The first three eggs were found.
11.11.2020: The first two larvae were observed in the nesting chamber, and one of the larvae appeared to be eating the egg.
14.11.2020: At this point, there were only one larger larva and a single egg remained in the nest. The larva was observed eating the springtail that has been brought there by the gyne.
25.11.2020: A larger larva and a single egg were found in the nest. It seemed that not only the larvae were eating the surrounding brood, but also the gyne itself. The gyne moved the brood to different slits in the substrate, so observation was difficult.
13.12.2020: For unknown reasons, the gyne probably ate the largest larva and eggs. From this day on, the second attempt to establish a colony began.
17.1.2021: A new egg was observed. So the gyne has tried again to establish a colony.
13.2.2021: A single larva and two eggs were observed. The gyne built a funnel-shaped entrance into the chamber from the substrate.
27.2.2021: One large larva, two smaller larvae, and three eggs were detected in the nest.
10.3.2021: One prepupa, three smaller larvae, and six eggs were found in the nest.
28.3.2021: Gyne took care of three prepupa, four larvae, and several eggs (Fig. 9). At this stage of colony establishment, the gyne was observed several times a day leaving the chamber in search of springtails, which she then brought back to the nest.
4.4.2021: The first worker hatched (Fig. 10). Its development took about two months. Due to the complexity of observations in this type of setup, it was impossible to estimate how long the development of the brood individuals took. Two pupae, 6 larvae, and several eggs were also found in the nest.
8.4.2021: The worker was observed trying to chase prey from of the nest chamber for the first time.
11.4.2021: The second worker hatched.
19.4.2021: The third worker hatched.
13.5.2021: The colony consisted of 1 queen, 4 workers, 8 larger larvae, 7 small larvae and eggs.
5.8.2021: The colony consisted of 1 queen, 18 workers, 7 pupae, 14 medium-sized larvae, 7 tiny larvae and eggs (Fig. 11). At this time, the colony was fed with about 30 individuals of springtails per feeding.
10.10.2021: The last update of the colony – 1 queen, approximately 50 medium-sized larvae, and 25 workers. The main nest chamber measures about 22x12 mm with a depth of 2-3 mm, and its surface is slightly smoothed with fine soil. The workers enter the nest chamber through two small openings in the soil-seal (Fig. 12).

Fig. 9. Chamber filled with gyne and its brood. Photo: Filip Repta.

Fig. 10. After about two months of development, the first worker (blue dot) appeared in the nest, which consisted of the queen (red dot), mature pupae (green dot), and the remaining brood in various stages of development. Photo: Filip Repta.

Fig. 11. Nest chamber of *Strumigenys argiola* with offspring separated according to developmental stages. Photo: Filip Repta.

Fig. 12. Sealing around the brood chamber made of fine soil. For better image quality, this photo was taken with uncovered glass. Photo: Filip Repta.

DISCUSSION

Almost 20 years after the first discovery by Pavel Deván, new data on the distribution of *S. argiola* in Slovakia were added. Together with other findings, this species is known from the urban environments (Holecová et al. 2015, Klesniaková 2017) and from natural habitats (Deván 2008, this study). The alate specimens (a single male in 2018; 2 gynes and 5 males in 2021) found near the town of Púchov now shift the northern limit of this species' distribution to 49°N. It is not clear from the results of this study whether *S. argiola* has been present in this area for some time or is gradually spreading northwards. However, the geomorphology of the area suggests that the spread could potentially extend to the town of Žilina. Therefore, it is possible that *S. argiola* also inhabits the surroundings of human settlements on the border in the Czech Republic or even in Poland. This idea is supported by the fact that two out of three northernmost finds in Slovakia come from natural habitats that usually have a colder climate than the urban environment all year-round (Robinson 2005). At the same time, it is a new species for the fauna of the Biele Karpaty Mts, and extends the checklist of ants known in this region to 70 species (Bezděčka & Bezděčková 2010). Similarly, specimens collected in the village of Ruská in eastern Slovakia has increased the list of ant species known from the Latorica Protected Landscape Area and its surroundings to 73 (Suvák, unpublished data).

This study also provides interesting insights into the collecting methods of this ant species. While previous studies recommend the use of traditional entomological methods (Winkler litter-sifting, Moericke traps), it should not be overlooked that several new data in this study were obtained by searching for alates in various garden containers filled with water. With a little imagination, it's a sizeable Moericke trap. Most of ant species disperse by nuptial flight, and mated females then depart to found colonies individually or in groups some distance away. While individual mating observations of many species are relatively common in the literature, post-mating recruitment is largely unknown (Hölldobler & Wilson 1990, King & Tschinkel 2016). Due to the very small size, we can assume that gyne pedestrian dispersal is very limited in *S. argiola*. One of the reasons why *S. argiola* mating pairs drop into small water containers could be a deceptive attempt to get closer to the warm and humid microhabitat where its primary food source (springtails) normally also occurs. However, *S. argiola* have not yet been discovered in composting sites. The phenomenon that ant gynes seek out moist sites for nest foundation is known mainly from arid areas (Rissing et al. 1986, Wiernasz & Cole 1995).

Most of the nuptial flights presented in this study were observed on an afternoon in late summer. There are similar observations from this time of year, not even for western Palearctic *S. argiola* (Fellner et al. 2009), but also for the members of Nearctic fauna, i.e. *Strumigenys ananeotes* Longino & Booher, 2019 (BOOHER 2021) or *Strumigenys rostrata* Emery, 1895 (DUFFIELD & ALPERT 2011). This study provides the first detailed information on the climatic conditions under which a nuptial flight occurs in the genus *Strumigenys* and significantly refines the previously known characteristics (see SEIFERT 2018). From the data obtained, it appears that these ants try to avoid high temperatures during midday in summer and fly out of the nests at a time when temperatures drop. At the same time, high wind speeds were not measured during nuptial flights (maximum average wind speed 21.6 km/h). Although in most cases mating took place in sunny weather, the flight of individuals was not affected by the presence of a higher percentage of clouds cover (up to 40 %), nor by a thundercloud near the observation site (Bernolákovo 22.8.2020). Due to the formation of *cumulonimbus* clouds in the Bratislava region, a lower value of solar radiation was also determined by the meteorological station during this observation (196 W/m^2). Therefore, it is more objective to read data on the range of solar radiation when this event occurs, e.g. 299.6-548.8 W/m^2 at a time when it is already more than a third weaker than at noon (up to 859.6 W/m^2). In any case, no precipitation was recorded directly at the observation points during the swarming days. Moreover, other ant species with similar habits, i.e. *Myrmecina graminicola* (Latreille, 1802), *Ponera coarctata* (Latreille, 1802), and *Proceratium melinum* (Roger, 1860) mate around the same time of the year (CZECHOWSKI et al. 2012, SEIFERT 2018), as confirmed by the personal observations of the authors of this study. However, all presented conditions were measured at a height of 2 meters, which is slightly different from the conditions ants encounter on the ground surface before take-off, i.e. conditions that are crucial for the initialisation of nuptial flight and are known in some species (BOOMSMA & LEUSINK 1981).

A single gyne collected in Bernolákovo was successfully bred in captivity, and our observations confirmed the semi-claustral colony establishment in *S. argiola.* In this ancient strategy, which is prevalent in the more socially and morphologically primitive species, the founding queen continues to leave her new nest chamber to forage for food (BROWN & BONHOEFFER 2003). This type of nest foundation is already known in the genus *Strumigenys* (DEJEAN 1987, ITO et al. 2010), as are fully developed trap-jaws of the gynes (OHKAWARA et al. 2017). With them, the gyne was able to hunt springtails that were almost half its own size. In this case, the partially claustral foundation proved to be an evolutionary advantage, as the gyne was able to establish a nest on the second attempt. The observed phenomena, such as cannibalism or chamber wall soil-sealing did not deviate in any way from what is already known from the socially primitive ants of the subfamily Myrmicinae (HÖLLDOBLER & WILSON 1990). The colony is likely to exceed a population of 25 individuals in its first year of existence. As the colony was not bred under climatically correct conditions, and at the same time the winter period was not simulated, these predictions may differ compared to the natural scenario. The other behavioural observations were also difficult to evaluate because the number of colonies observed was too small and the methodology was insufficient.

ACKNOWLEDGEMENT

Dedicated to the memory of Pavel Deván, an outstanding naturalist, who left an unforgettable mark on hymenoptera research in Slovakia. The authors would like to thank B. Csizmárová for her help in collecting material in the field. This work was also prepared thanks to the support of the scientific project VEGA no. 2/0032/19 and 1/0007/21. The authors would also like to thank the Slovak Hydrometeorological Institute (SHMÚ) for providing meteorological data.

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