A.V. FATERYGA[1,2], S.P. IVANOV[1,2], V.V. FATERYGA[1]
[1] Karadag Nature Reserve, National Academy of Sciences of Ukraine
24, Nauki Str., Kurortnoye, Feodosiya, 98188, Ukraine
fater_84@list.ru
[2] V.I. Vernadsky Taurida National University
4, Academician Vernadsky Ave., Simferopol, 95007, Ukraine
spi2006@list.ru

POLLINATION ECOLOGY OF *STEVENIELLA SATYRIOIDES* (SPRENG.) SCHLTR. (*ORCHIDACEAE*) IN AYAN NATURAL LANDMARK (THE CRIMEA)

Key words: Steveniella satyrioides, *distribution, pollination, pollinators, Vespidae, Crimea*

Abstract. The nectarless orchid, *Steveniella satyrioides* (Spreng.) Schltr., occurs in the mountain part of the Crimean Peninsula; it is known from 26 localities 10 of which were found during the last 50 years. Pollination ecology of the species was studied in Ayan Natural Landmark (Simferopol District). From 1 to 55 individuals of this species flowered here in different years; one year there was no flowering plants. The pollination rate of *S. satyrioides* varies from 16 % to 79 % and positively correlates with the density of specialized pollinators — females of diplopterous wasps of genera *Vespula* Thomson, 1869, and *Dolichovespula* Rohwer, 1916. A probable mechanism of attraction of wasps by flowers of *S. satyrioides* and its evolution are discussed.

Introduction

The genus *Steveniella* Schltr. has one species, *Steveniella satyrioides* (Spreng.) Schltr., distributed in the Crimean Mountains, Caucasus, Asia Minor (eastern part) [1—3, 12] and particularly in West Asia, where *Steveniella satyrioides* var. *iranica* Kreutz has been described [19]. According to the molecular phylogenetic data, *S. satyrioides* (together with the genus *Comperia* K. Koch) may be included in the genus *Himantoglossum* Spreng., under the name *Himantoglossum satyrioides* Spreng. [8], but morphological studies of these taxa suggested this view to be not advisable [7].

Steveniella satyrioides is distributed sparcely throughout its area and studied insufficiently. Its pollination ecology was first described by V.V. Nazarov [20]. Flowers of *S. satyrioides* are visited only by social species of diplopterous wasps (Hymenoptera, Vespidae); four species have been recorded among them until now: *Vespula* (*Paravespula*) *germanica* (Fabricius, 1793), *Vespula* (*Paravespula*) *vulgaris* (Linnaeus, 1758), *Dolichovespula sylvestris* (Scopoli, 1763), and *Polistes* (*Polistes*) *nimpha* (Christ, 1791) [6, 9, 11, 20]. The species is nectarless and wasps are obviously attracted to its flowers by the special food-deceptive mechanism.

The purpose of this study was to ascertain the distribution of *S. satyrioides* in the Crimea and to describe its growth conditions, population dynamics, pollinators and pollination effectiveness in one of the discovered localities.

Materials and methods

Pollination ecology of *S. satyrioides* was studied in 2004—2011 in Ayan Natural Landmark (vicinity of the Ayan Reservoir near the village of Perevalnoye, Simferopol District, Crimean Foothills), 44°49'56" N, 34°18'05" E, 470 m above sea level. Each year we counted the number of flowering specimens of *S. satyrioides* growing in this territory and estimated the comparative density of potential pollinators — social wasps of the family Vespidae. The wasp density was studied by the itinerary method; we recorded all wasp specimens discovered in the studied area during several hours once a week in sunny weather. At the end of the blossoming period of *S. satyrioides* we calculated the average density of wasps per hour.

At the end of the blossoming period we also checked all the flowers from all plants found in the sample and recorded 9 conditions of them: «0» — both hemipollinaria present, stigma without massulae; «1» — both hemipollinaria absent, stigma without massulae; «2» — both hemipollinaria absent, stigma with massulae in both right and left sides; «3» — only one hemipollinarium present, stigma with massulae in both right and left sides; «4» — both hemipollinaria present, stigma with massulae in both right and left sides; «5» — only one hemipollinarium present, stigma without massulae; «6» — both hemipollinaria absent, stigma with massulae only in one side; «7» — only one hemipollinarium present, stigma with massulae only in one side and «8» — both hemipollinaria present, stigma with massulae only in one side. The first condition, «0» corresponds to non-visited flowers and conditions «1» and «5» cor-

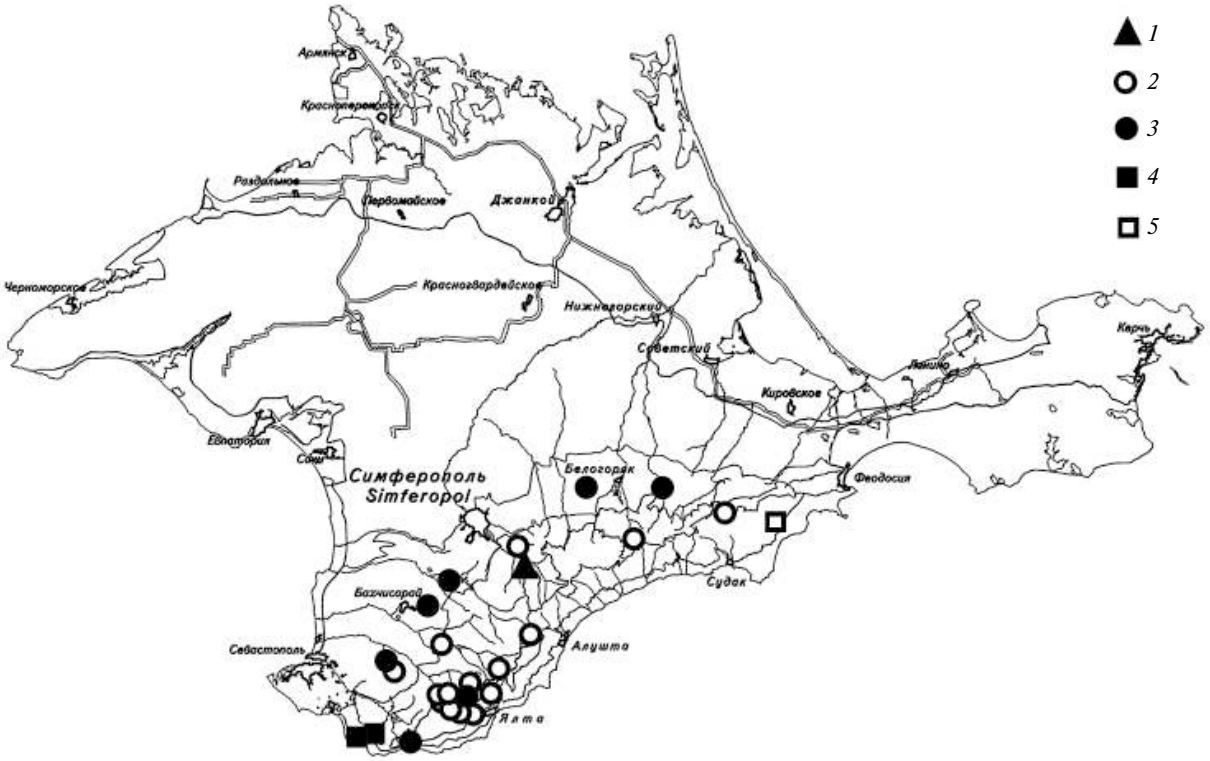

Fig. 1. Distribution of *Steveniella satyrioides* in the Crimea: *1* — Ayan Natural Landmark, where the species was studied; *2* — points where the species was collected earlier than 50 years ago (according to herbaria); *3* — points where the species was collected during the last 50 years (according to herbaria); *4* — points where the species was recorded according to the photos on "Plantarium"; *5* — point where the species is known only from the article of I.V. Vankov [1]

respond to the flowers visited once (first flowers visited by a pollinator in certain site). Other conditions («2»—«4» and «6»—«8») correspond to the pollinated flowers. Pollinated flowers without hemipollinaria («2» and «6») demonstrate persistent behavior of the pollinator during the flower visits, and pollinated flowers with both hemipollinaria («4» and «8») indicate that the visits were not persistent [5].

On the base of the obtained data we counted the rate of the pollinated flowers and the rate of the flowers visited by pollinators once. Then we estimated the index of the flower visit repetition by means of dividing the amount rate of pollinated flowers by the amount of the flowers visited once [4, 16]. This index is approximately equal to the mean number of the flowers visited by a pollinator after its visit of the first flower.

Distribution of *S. satyrioides* in the Crimea was studied on the base of data from 5 herbaria (55 specimens): National Herbarium of Ukraine, Kiev (*KW*) — 3 specimens; Herbarium of Nikita Botanical Garden — National Science Center, Yalta (*YALT*) — 33 specimens; Herbarium of V.I. Vernadsky Tavrida National University, Simferopol (*SIMF*) — 4 specimens; Herbarium of National University of Life and Environmental Sciences of Ukraine, Southern Branch «Crimean Agrotechnological University», Simferopol (*CSAU*) — 2 specimens, and Herbarium of V.L. Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg (*LE*) — 13 specimens. We also examined the photos of this species deposited on the website «Plantarium» (http://www.plantarium.ru/).

Distribution of *Steveniella satyrioides* in the Crimea

The points where *S. satyrioides* has been recorded in the Crimea are represented on the map (fig. 1). The species grows only in the mountain part of the peninsula where it is known from 26 localities. Among them, there are 16 points where plants of *S. satyrioides* were recorded more than 50 years ago; 10 records are made during the last 50 years, including 7 points confirmed by herbarium specimens; 2 points are added on the base of the photos from «Plantarium», and 1 point (Ayan Natural Landmark) — according to our investigations. Predomination of all

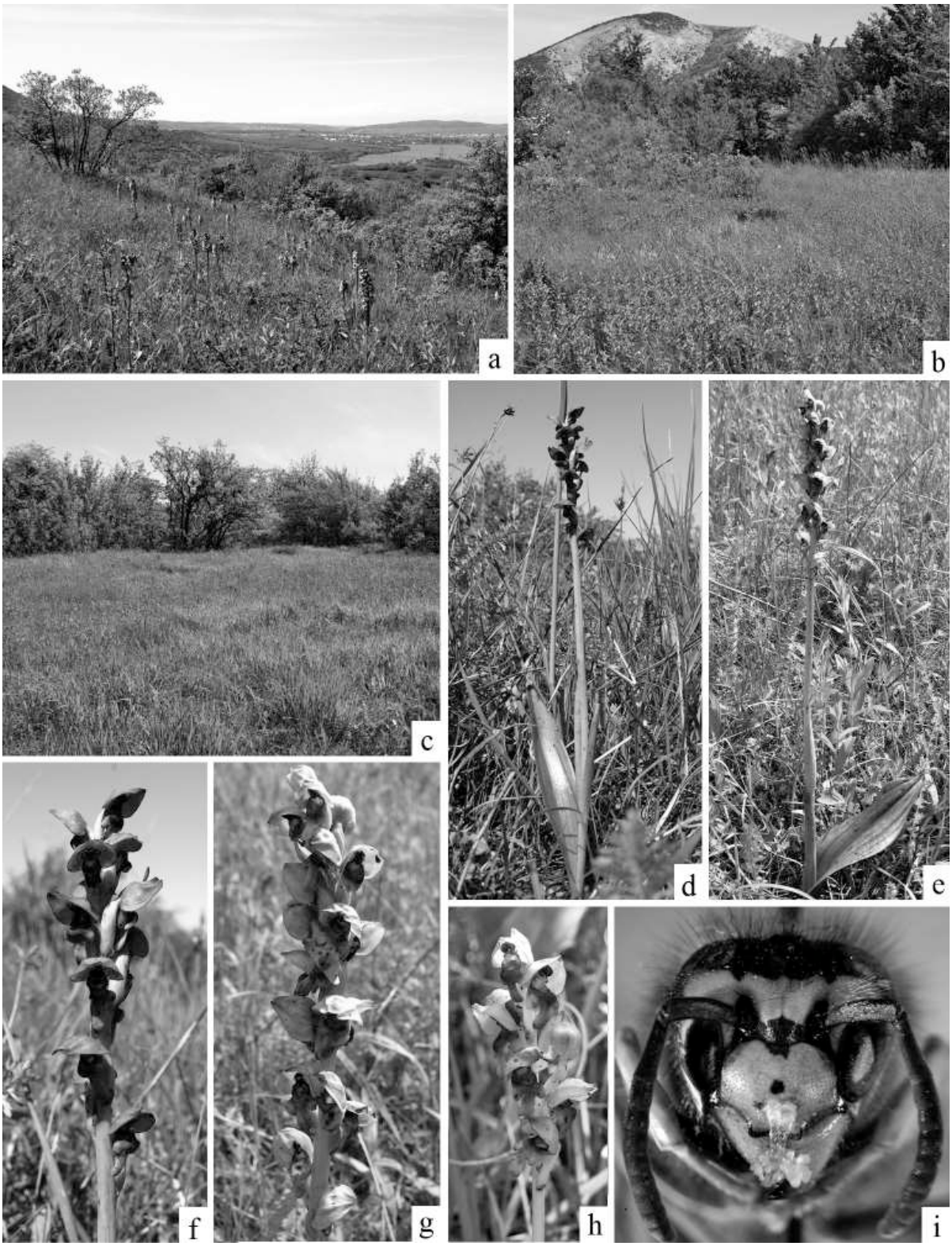

Fig. 2. *Steveniella satyrioides* in Ayan Natural Landmark: *a—c* — habitat sites; *d—e* — flowering plants; *f—h* — inflorescences; *i* — head of the female of *Vespula germanica* (Fabricius, 1793) with two hemipollinaria, frontal view

records of *S. satyrioides* made more than 50 years ago makes an impression of decreasing of the species abundance here. More probably there was more intensive collecting in the first half of the 20th century. Thus, the changes in the population abundance of *S. satyrioides* require further investigations.

Description of the population in Ayan Natural Landmark

Steveniella satyrioides grows in Ayan Natural Landmark on the area about 0.75 hectares in 3 localities, each of 100—200 square meters. In the localities studied, three associations were revealed: *Filipenduleto* (*vulgaris*) — *Primuletum* (*acaulis*) *caricosum* (*michelii*) with flowering *Orchis purpurea* Huds. (coverage — 60—70 %, grass height — 10—20 cm) (fig. 2, *a*); *Inuleto* (*asperi*) — *Galietum* (*rubioidis*) *festucosum* (*rupicolae*) (projective cover — 90—100 %, grass height — 20—30 cm) (fig. 2, *b*), and *Brachypodieto* (*pinnati*) — *Inuletum* (*asperi*) *filipendulosum* (*vulgaris*) (coverage — 100%, grass height — 15—25 cm) (fig. 2, *c*).

Number of the flowering plants of *S. satyrioides* varied greatly on the studied territory in different years. In 2006 we did not find any plant, in 2008 there was only 1 plant, and in other years the number of plants was 12 to 55 (tab. 1). These data show that the population dynamics of the species is not simple and requires continuing monitoring. In addition, plants of *S. satyrioides* vary in helmet's coloration, from limy green to reddish brown (fig. 2, *d—h*).

Flower visitors

Four species of the social wasps from the family Vespidae, subfamily Vespinae was recorded in the territory studied in 2004—2011; among them, 3 species were recorded as flower visitors and pollinators of *S. satyrioides*: *V. germanica*, *V. vulgaris* and *D. sylvestris*. The fourth species, *Vespula* (*Vespula*) *rufa* (Linnaeus, 1758), has not been recorded on the flowers but it is obvious that it also can take part in the pollination process. The flowering period of *S. satyrioides* in Ayan Natural Landmark continues from the beginning of May to the middle of June [4]. At this time only «queens» (overwintered females) of the social wasps can occur [10]. Thus, only females of the listed species were visiting flowers of *S. satyrioides*, not workers as it was reported by V.V. Nazarov [20].

The density of wasp females also varied considerably in different years (tab. 1). During four seasons (2004, 2006, 2008 and 2011) the populations of wasps were abundant but in the other four ones (2005, 2007, 2009, 2010) the wasps occurred very rarely. The density of pollinators does not correlate with the abundance of flowering plants of *S. satyrioides*: in 4 years when wasps were abundant, the number of orchids could be both high and very low (tab. 1). Fifty-eight wasp females were collected: 3 *V. germanica*, 33 *V. vulgaris*, 17 *V. rufa*, and 5 *D. sylvestis*; among them, 6 specimens were collected directly on flowers and 52 — in flight. Only 1 female of *V. germanica* collected in flight carried the orchid hemipollinaria on its clypeus (fig. 2, *i*).

Pollination effectiveness

There were 16 % to 79 % pollinated flowers of *S. satyrioides* in different years (tab. 1). According to data from the table, two pollination effectiveness indexes (rate of the pollinated flowers and repetition of the flower visits) strongly correlate positively with the density of po-

Table 1. **Number of discovered flowering specimens of *Steveniella satyrioides*, their pollination effectiveness and the density of wasps in Ayan Natural Landmark in different years**

Year	Number of flowering plants in the studied area	Number of plants / flowers in the sample	Rate of the flowers visited once, %	Repetition of flower visits by pollinators	Rate of the pollinated flowers, %	Average density of social wasps per hour
2004	17	17 / 172	19.2	4.05	77.8	6.6 ± 2.3
2005	12	12 / 123	43.9	0.80	35.0	<0.1
2006	0	—	—	—	—	3.0 ± 1.1
2007	55	20 /265	30.6	0.53	16.2	<0.1
2008	1	—	—	—	—	0.8 ± 1.2
2009	32	28 / 310	37.1	1.13	41.9	<0.1
2010	20	20 / 262	29.4	1.04	30.5	<0.1
2011	52	37 / 443	26.0	2.37	61.6	1.2 ± 0.6

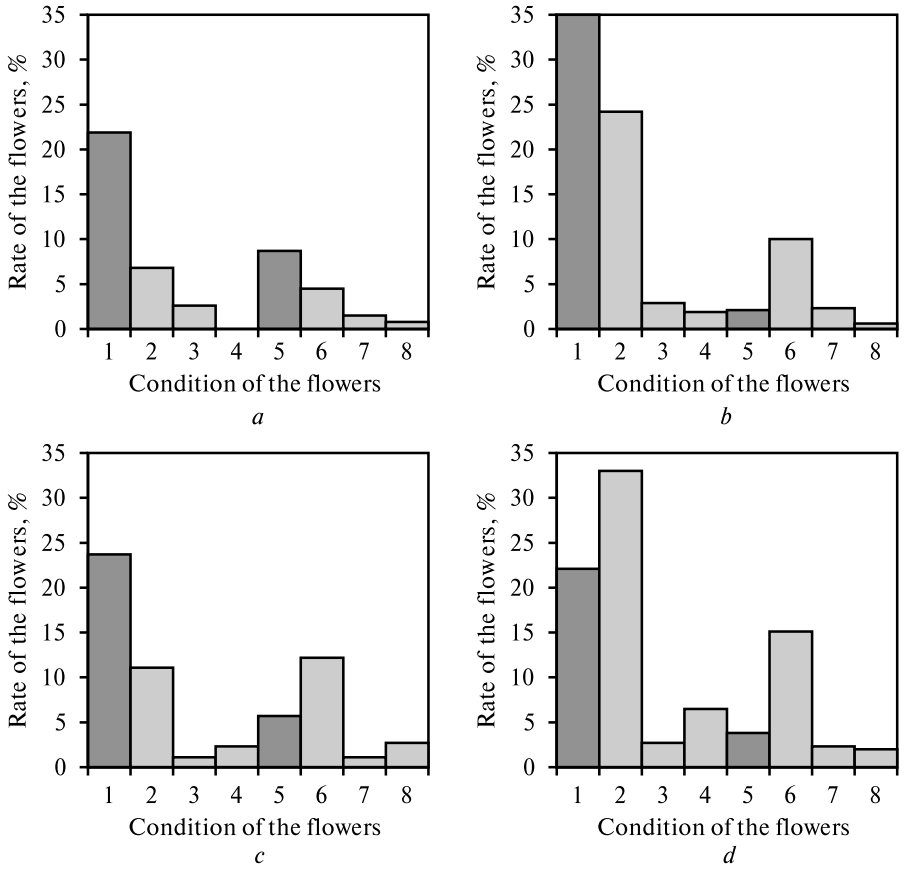

Fig. 3. Rate of flowers of *Steveniella satyrioides* of different conditions visited by pollinators in Ayan Natural Landmark in different years: *a* — 2007; *b* — 2009; *c* — 2010; *d* — 2011

tential pollinators — wasp females. The third index (rate of the flowers visited once) negatively correlates with the wasp density. These data confirm that the wasp females are specialized pollinators of *S. satyrioides*. Additional confirmation of this conclusion can be obtained from the diagrams where the rates of flowers with different conditions are represented (fig. 3). Independently of the rate of pollinated flowers, the flowers with condition «1» predominate among non-pollinated flowers, and the flowers with condition «2» and «6» — among pollinated ones. These facts allow to suppose that the visits of flowers by pollinators were persistent and tended to the retrieving both hemipollinaria. When the density of wasps is abundant, most of flowers lose their hemipollinaria very early. This hypothesis can explain the fact that most wasps that visited the flowers left them without hemipollinaria.

Each year from 1/5 to 1/3 of the plants were wound by the spider's web of *Dictyna arundinacea* (Linnaeus, 1758) (Aranei, Dictynidae). These plants had low pollination rate and have not been included in the analysis of pollination effectiveness.

Thus, females of the social wasps of the family Vespidae, subfamily Vespinae are effective and obviously the only possible pollinators of *S. satyrioides* in our area. The main determinant of the pollination effectiveness of the species is wasp abundance, which greatly varies in different years but in general is not very low as compared to specialized pollinators of other orchids because of high ecological flexibility of these wasps and synanthropic character of most species.

Discussion

Wasps of the family Vespidae are not usual pollinators of orchids (especially nectarless ones). Among their six subfamilies, Eumeninae (potter wasps), Polistinae (paper wasps) and Vespinae (hornets and yellowjackets) are most common in the Northern Hemisphere. Potter wasps of the genus *Eumenes* Laterille, 1802 were recorded as the specialized pollinators of nectar-rewarding

species *Epipactis palustris* (L.) Crantz (section *Arthrochilium* Irmisch) [21]. Yellowjackets (the genera *Vespula* Thomson, 1869 and *Dolichovespula* Rohwer, 1916) were recorded as specialized pollinators of nectar-rewarding species of the genus *Epipactis* Zinn, section *Epipactis* [17, 18] and nectar-rewarding orchid *Coelogyne fimbriata* Lindl. [15]. Only one known nectarless orchid, except *S. satyrioides*, *Dendrobium sinense* Tang & F.T. Wang, is pollinated by a wasp of the family Vespidae, the hornet species *Vespa bicolor* Fabricius, 1787 [14]. Flowers of these orchids attract the hornet foragers by the imitation of the scent of their preys — honeybee workers (*Apis mellifera* Linnaeus, 1758 and *Apis cerana* Fabricius, 1793). However, imitation of the scent of wasp preys also occurs in nectar-rewarding species, *Epipactis helleborine* (L.) Crantz [13]. All listed species are pollinated by the wasp workers, thus the pollination of *S. satyrioides* by overwintered females of the wasps is unique among all wasp-pollinating orchids.

The wasp females are very effective pollinators of *S. satyrioides*: this species has significantly higher reproductive success values in comparison to other orchids studied in the Crimea [20]. So, the low number of wasp-pollinating species in orchids is not provided by morphology or behaviour of these insects but by other factors, probably connected with their abundance in certain ecosystems. Only social species of wasps are abundant in the forest landscapes but the terms of their mass flight usually fall on July — September [10] when most species of orchids have already finished their flowering. The flowering terms of *S. satyrioides* fall on May—June [4] and its pollination by wasps is possible only via the overwintered females, which are not abundant in comparison with the workers flying later.

The wasps that visit the flowers of *S. satyrioides* demonstrate an aggressive food behaviour which is expressed by scratching of the inner surface of the spur [20]. We can suppose that the most possible factor of the wasp attraction is the specific scent that is similar to wasp preys: flies or honeybees. Wasp-pollinating syndrome could have evolved via nectar attraction confirmed by scent mimicry (like in *E. helleborine*) with loosing nectar reward in the consequence (like in *D. sinense*). Pollination by wasp females (not by workers) evolved via the early period of *S. satyrioides* flowering in contrast to *D. sinense*, which grows in significantly more wet climate and therefore can blossom later, when wasp workers are already abundant. It is also interesting, that like *S. satyrioides*, *Himantoglossum caprinum* (M. Bieb.) Spreng. is also pollinated by a few closely related species of insects, in this case by bees of the genus *Megachile* Latreille, 1802 (Hymenoptera, Megachilidae) [16]. We can suppose that it also have a special olfactory attractant which can attract only several morphologically and ethologically suitable pollinators.

Thus, *S. satyrioides* is a highly specialized orchid species in respect of its pollination ecology. The measures intended for its conservation must also include conservation of its pollinators; however, the actual situation with them in the Crimea gives no reason for concern.

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О.В. Фатерига[1, 2], С.П. Іванов[1, 2], В.В. Фатерига[1]

[1] Карадазький природний заповідник НАН України, м. Феодосія, Україна

[2] Таврійський національний університет імені В.І. Вернадського, м. Сімферополь, Україна

ЕКОЛОГІЯ ЗАПИЛЕННЯ *STEVENIELLA SATYRIOIDES* (SPRENG.) SCHLTR. (*ORCHIDACEAE*) В УРОЧИЩІ АЯН (КРИМ)

Безнектарна орхідея *Steveniella satyrioides* (Spreng.) Schltr. поширена в Криму в межах гірської частини півострова та відома з 26 локалітетів, 10 з яких представлено знахідками, зробленими в останні 50 років. Вивчено екологію запилення виду в урочищі Аян (Сімферопольський р-н). У різні роки тут цвіло від 1 до 55 екземплярів даного виду, в один із років — жоден. Рівень запилення *S. satyrioides* коливається від 16 до 79 % і позитивно корелює зі щільністю спеціалізованих запилювачів — самок складчастокрилих ос родів *Vespula* Thomson, 1869 і *Dolichovespula* Rohwer, 1916. Обговорюється можливий механізм залучення ос на квітки та його еволюційне становлення.

Ключові слова: Steveniella satyrioides*, поширення, запилення, запилювачі, Vespidae, Крим.*

А.В. Фатерыга[1, 2], С.П. Иванов[1, 2], В.В. Фатерыга[1]

[1] Карадагский природный заповедник НАН Украины, г. Феодосия, Украина

[2] Таврический национальный университет имени В.И. Вернадского, г. Симферополь, Украина

ЭКОЛОГИЯ ОПЫЛЕНИЯ *STEVENIELLA SATYRIOIDES* (SPRENG.) SCHLTR. (*ORCHIDACEAE*) В УРОЧИЩЕ АЯН (КРЫМ)

Безнектарная орхидея *Steveniella satyrioides* (Spreng.) Schltr. распространена в Крыму в пределах горной части полуострова и известна из 26 локалитетов, 10 из которых представлены находками, сделанными в последние 50 лет. Изучена экология опыления вида в урочище Аян (Симферопольский р-н). В разные годы здесь цвело от 1 до 55 экземпляров данного вида, в один год — ни один. Уровень опыления *S. satyrioides* колеблется от 16 до 79 % и положительно коррелирует с плотностью специализированных опылителей — самок складчатокрылых ос родов *Vespula* Thomson, 1869 и *Dolichovespula* Rohwer, 1916. Обсуждается возможный механизм привлечения ос на цветки и его эволюционное становление.

Ключевые слова: Steveniella satyrioides*, распространение, опыление, опылители, Vespidae, Крым.*