Lindleyana 10(2): 109–114. 1995.

POLLINATION OF *STEVENIELLA SATYRIOIDES* (ORCHIDACEAE) BY WASPS (HYMENOPTERA, VESPOIDEA) IN THE CRIMEA[1]

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ABSTRACT: Pollinators of the *Steveniella satyrioides* were studied in the Crimea. The nectarless orchid is pollinated by two species of wasps: *Paravespula vulgaris* and *Dolichovespula sylvestris*. At the end of the flowering period pollinators had visited about 93% of all flowers in the population. *S. satyrioides* attracts wasps with the help of reddish-brown papillae on the base of the lip, at the spur entrance; the wasps may take them as food. The inner cavity of the spur in *S. satyrioides* may resemble a customary feeding site that is also reddish colored. Scratches from the mandibles were discovered on the inner surface of the spur in 78% of the examined flowers. The wasps press the hemipollinarium on the stigma with great force while attempting to tear off a section of the tissue. As a result, a significant portion of the massulae remain on the stigma. In *Steveniella* the number of ovules per ovary is distinctly geater than in *Orchis* and *Dactylorhiza*: this behavior of the wasps was reflected in the potential seed productivity of *S. satyrioides*.

STEVENIELLA SATYRIOIDES (Stev.) Schltr. is currently the only species described in the genus. Its natural habitat covers Anatolia, Northern Iran, Caucasus and Crimea (Nevski, 1935; Baumann and Künkele, 1988). In the Crimea this orchid is represented only in the mountainous parts of the peninsula. Here it grows in forests among thickets and in forest glades on primarily sothern facing grassy and mossy slopes (Vulyf, 1930). In the past *S. satyrioides* grew in relatively large colonies in places with a well-developed moss cover and high surface moisture (Vanykov, 1914). Only recently it was entered as a rare species in the Red Book of the Ukraine SSR (1980) and USSR (1988).

The flower of *Stevenialla satyrioides* are similar to that of *Orchis*. *Steveniella*, however, is distinguished from *Orchis* by the union of the sepals into a three-pronged hood, the characteristic "T" shape of the three-lobed lip covered at the base by fine papillae and a short dichotomous spur (Senghas, 1973). Few flowers of this type are capable of auto-pollination, and are only pollinated by insects, and then only by those whose morphology corresponds to that of the flower (Darwin, 1862). Furthermore, it is well known that the length of the pollinator's proboscis must not be longer than the length of spur and the width of the facial parts of the head in the central area of the clypeus must correspond closely to the width of the spur-opening in the orchid (Nilsson, 1980, 1983, 1984; Fritz, 1990).

The pollinators and pollination mechanism of *S. satyrioides* had not been investigated. This lack of information induced us to conduct the present research, as it is beyond doubt that pollination data about any plant are relevant in organizing projects to restore the species in areas where it has disappeared.

MATERIAL AND METHODS

The research was carried out in 1992 at two points on the northern incline of the interior ridge of the Crimean mountains. The first sample group of plants was located in the vicinity of Skalistoye Bachchisaraisko district (A). The second sample group was situated in the central basin of the Crimean reserve (B). Sample group A was inspected regularly during the entire flowering season. In sample B the observations were made sporadically. All insects seen visiting the orchid's flowers were captured for subsequent identification. At the end of the flowering period the number of

[1] I am grateful to Dr. Guenter Gerlach, Botanischer Garten, München, Germany who has made encouraging and constructive comments and the correction of the English translation. Field assistance was provided by my friend A.A. Alekseev, Nikitskij Botanical Garden, Jalta (Crimea). Mrs. S. Werner, München, Germany, I thank for the translation of this article into English.
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visited flowers was determined by changes caused by pollinators in the flowers. The flowers were defined as visited when the hemipollinaria had been removed or massulae had been deposited on the stigma.

Ovules were counted following Nazarov (1989). The morphological measurement of the flowers and insect-pollinators was carried out by using the measuring scale of the MBC-9 binocular microscope and sliding callipers down to an accuracy of 0.1 mm.

RESULTS AND DISCUSSION

Plants of *Steveniella satyrioides* in samples groups A and B flowered from the end of April to the second/third week in May 1992. During this period they were visited by ten individual wasps, nine of them going to sample A. All were identified as workers of *Paravespula vulgaris* L. Plants in sample B attracted only one specimen, a worker of *Dolichovespula sylvestris* (Scop.). Two hemipollinaria of *S. satyrioides* were found in the center of the clypeus of one *D. sylvestris* and six *P. vulgaris* wasps. Another individual of *P. vulgaris* wasp had four hemipollinaria on its clypeus.

The clypeus of both species of wasp is well suited to the distribution of pollen. Sparse and small hair on ist surface permit close contact of the viscidium with the chitin of the head (Fig. 1). The viscidium of *S. satyrioides* in the studied samples adhered reliably to the pollinators. Intact hemipollinaria on the stigma of the flowers were not seen. Viscidia with caudicles remained on the pollinators even after all the massulae of the hemipollinaria were removed by visits to many flowers.

An investigation of the major parameters of the *S. satyrioides* flower and the heads of the worker wasps revealed excellent morphological agreement between them. The width of the throat of the spur in *S. satyrioides* in the samples studied averaged 3.2 mm (n=50). The width of the wasp heads measured through the center of the clypeus exceeded the width of the orchid's spur-mouth. With *P. vulgaris* it came to 3.9 mm (n=9) whereas with *D. sylvestris* it was 3.4 mm (n=1) (Fig. 2 A). However, while visiting the flower the center of the clypeus of both wasp species was exactly opposite to the bursicula, which in *S. satyrioides* is located slightly higher than the edge of

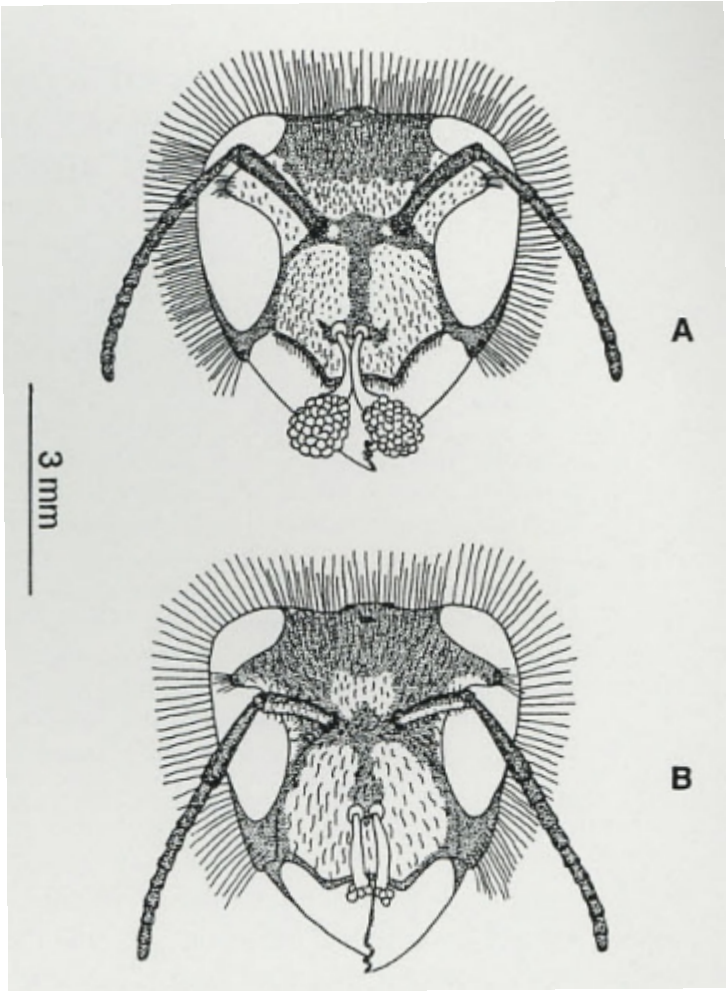
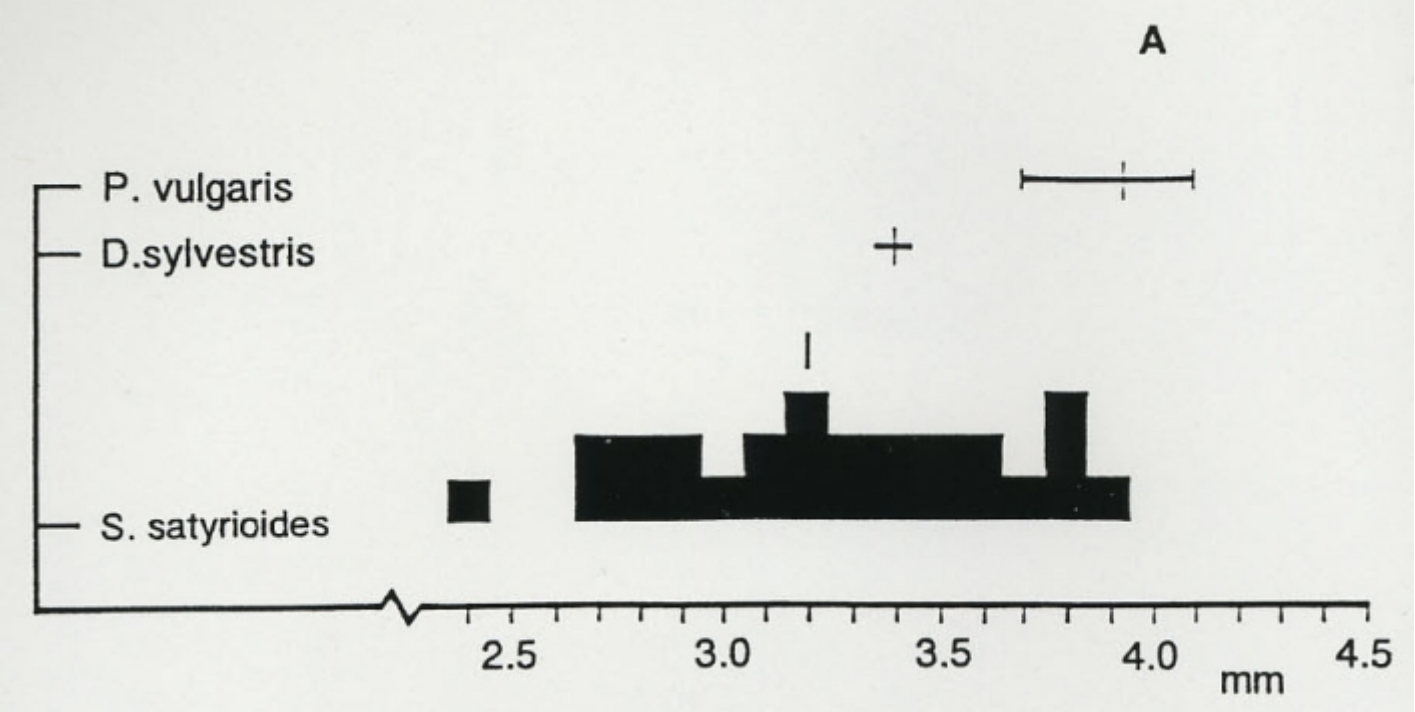


Fig. 1. Deposited hemipollinaria of *Steveniella satyrioides* on the heads: **A.** *Paravespula vulgaris*; **B.** *Dolichovespula sylvestris* (after various flower visits, most massulae removed).

the spur (Fig. 3 B). The spur of *S. satyrioides* reached, on avarage, 3.7 mm in length (n=50). The proboscis of both wasps hardly reached beyond the border of the mandible. Therefore the length of the spur of *S. satyrioides* is slightly greater than the distance from the center of the clypeus to the edges of mandible: the distance reached 2.9 mm in *P. vulgaris* and 2.8 mm in *D. sylvestris* (Fig. 2 B). A similar relationship between the length of the spur and the mouth parts of the pollinator was repeatedly recorded in species of *Dactylorhiza* and *Orchis*. In these cases the insects had to press their head into the throat of the flower with great strength, which led to closer contact of the facial parts of the head with the viscidia (Nilsson, 1980, 1981a, 1983, 1984).

It is known that wasps prefer visiting brownish-green colored flowers (Faegri and van der Pijl, 1982). This type of flower coloring is often encountered within the Orchidaceae. For example, it is characteristic for the *Epipactis* species that are pollinated by solitary and social wasps (Dar-



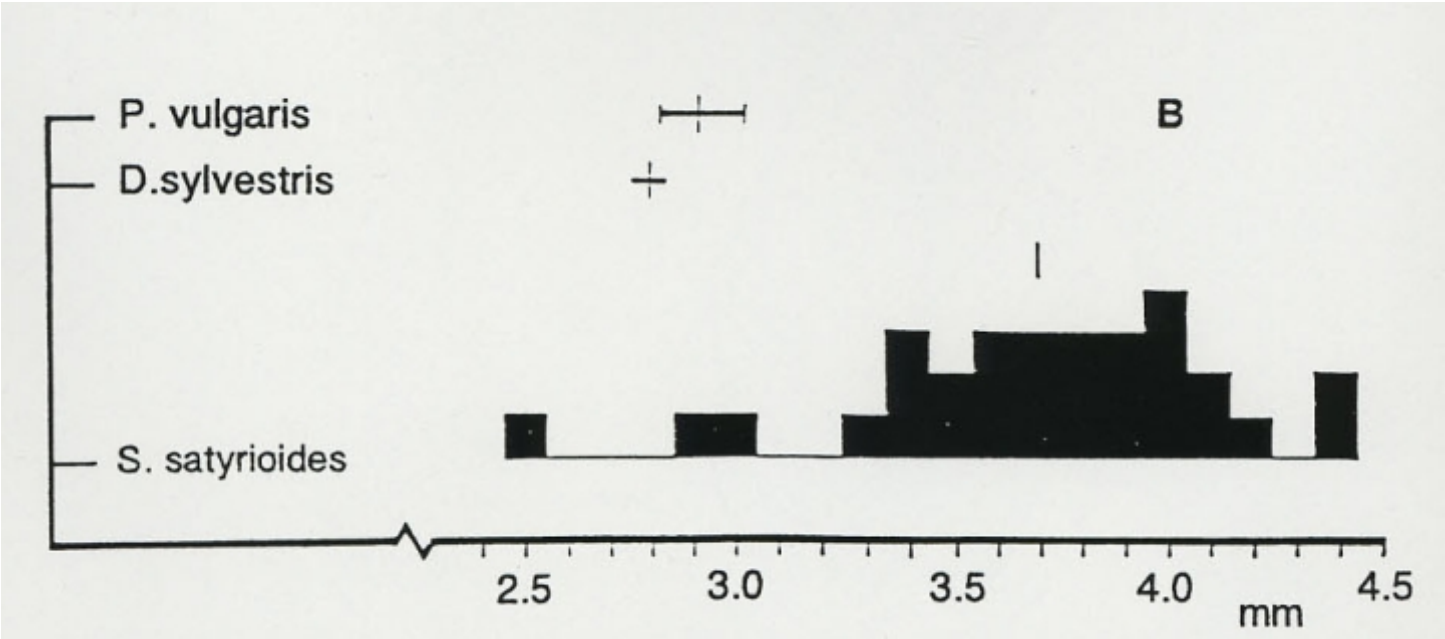


Fig. 2. Comparison between: **A.** Width of spur in flowers of *Steveniella satyrioides* and width of face (across the center of clypeus in ist pollen vectors); **B.** Length of spur in flower of *Steveniella satyrioides* and distance from center of clypeus to top of mandible in pollen vector species.

win, 1862; Nilsson, 1978, 1981a; Judd, 1971). Within orchids pollinated by wasps, a different type of flower coloring also occurs, e.g. *Herminium monorchis* has the yellow-green flowers that are, pollinated by primitive wasps of the genus *Tetrastichus* (Nilsson, 1979). Well documented is the role of the parasitic Ichneumonidae in the pollination of greenish flowers of *Listera ovata*. The

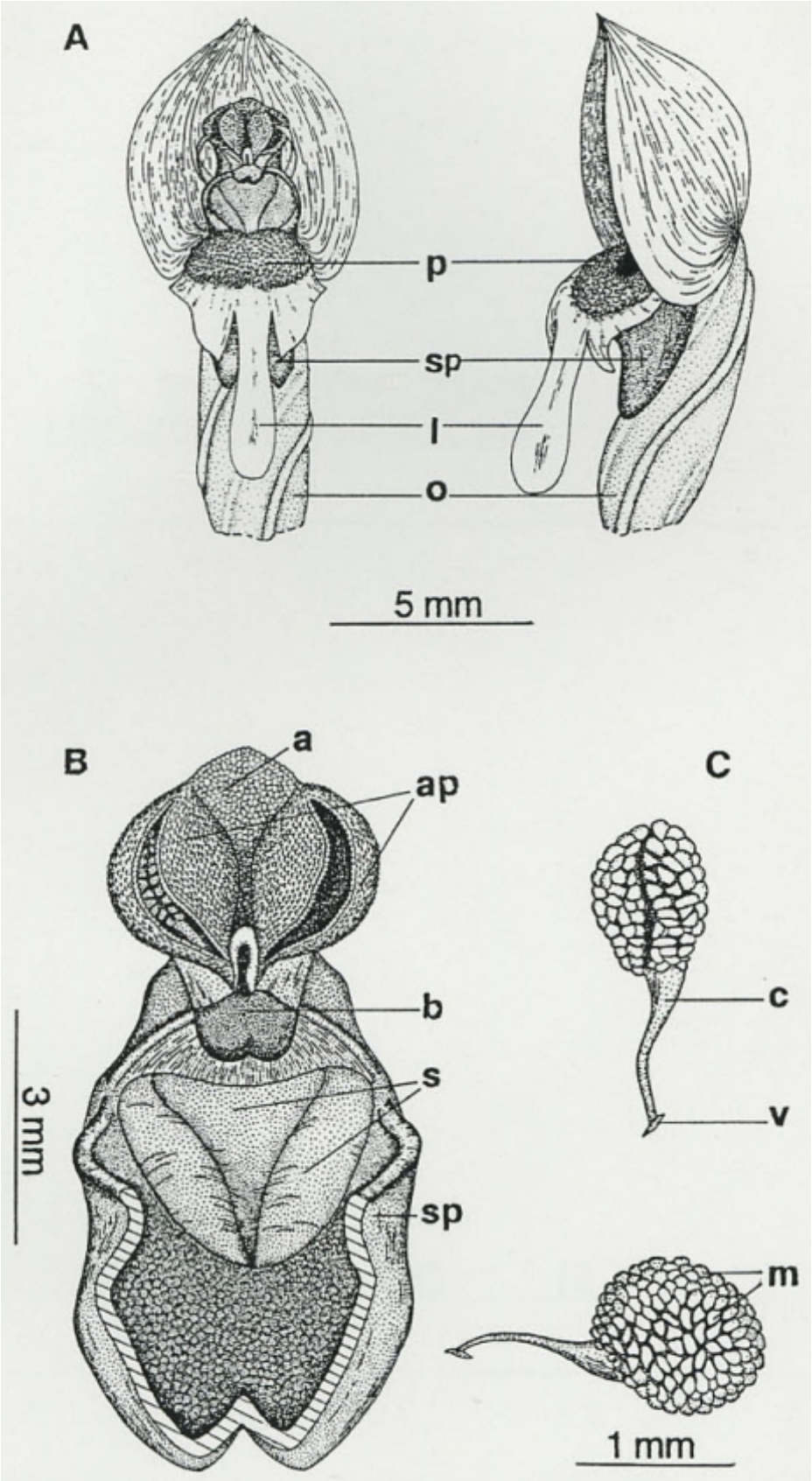


Fig. 3. Floral morphology in *Steveniella satyrioides*. **A:** Flower and ovary, front (left) and lateral (right) view; **B:** Column and spur (lip and part of spur removed), front view; **C:** Hemipollinaria, front (above) and lateral (below) view.

Abbreviations: anther (**a**), anther-pockets with one removed hemipollinarium (**ap**), bursicula (**b**), caudicule (**c**), labellum (**l**), massulae (**m**), ovary (**o**), stigma (**s**), spur (**sp**), papillae (**p**), viscidia (**v**).

wasps are guided to the orchid flowers by their fragrance (Nilsson, 1981b). The orchid species mentioned above reward their pollinators with nectar. They produce nectar in open nectaries that are easily accessible for wasps with a short proboscis.

Non-nectar producing species are uncommon among orchids pollinated by wasps. These orchids attract wasps to their flowers by deceit. It is known that several Australian species of *Caladenia*, for example, are pollinated by *Thynninae* males as a result of pseudo-copulation (Stoutamire, 1983). In other species of the *Caladenia* and *Diuris* a "false prey"-syndrome has been described: when the *Scoliidae* wasps produce stinging movements at the part of the lip that resembles the insects, they take it as prey (van der Pijl, 1966). In these cases investigators may easily confuse the stinging movements with copulative movements.

The spurs of *Steveniella satyrioides* do not contain free nectar. However, worker *Paravespula vulgaris* and *Dolichovespula sylvestris* wasps actively visit the flowers. At the end of the flowering period, 93 % of all flowers had been visited by pollinators in population A; 69% of the flowers bore fruits. Such high percentages of visits and pollination are not characteristic for non-nectar producing orchids. In non-nectar producing species that attract pollinators to their flowers by mimicking “reward giving” plants, the percentage of fruit set is almost half (Dafni, Ivri, 1981a, b).

The observations have shown that the wasps are interested not only in the spur but also in the special lip of *S. satyrioides*. After landing on the orchid flower, the workers of *P. vulgaris* wasps generally first inspect the papillae at the base of the lip. Only after a few seconds do they plunge their mandibles into the spur. Direct sighting makes it reasonable to assume that in doing so the wasp is attempting to tear off a section of the tissue. An inspection of the inner surface of the spur of 60 pollinated flowers showed that in 78 % of the flowers were there scratches made by the wasp’s mandibles. The morphology of the spurs are adapted to the wasps' behavior. The profile of the spurs repeats exactly the profile of the lower parts of the wasps' heads with expanded mandibles (Fig. 3 B).

P. vulgaris and *D. sylvestris*, like other specimens of *Vespidae*, are predatory insects. The food given to the larvae of these wasps consists chiefly of pulped animal food (Tobias, 1978). The flowering period of *S. satyrioides* starts at the beginning of the establishment of the wasp colony when the workers were actively preparing food for their larvae.

The general model of flower coloring in *S. satyrioides* is excellently suited to flowers visited by wasps. In its coloring it has yellowish-green and reddish-brown tones. The peripheral part of the perianth including the distal part of the lip creates an olive or yellowish-green background. The reddish-brown center clearly stands out against this. It forms the upper part of the column and the base of the lip. The reddish-brown flower is strongly colored on the part of the lip covered with flattened papillae (Fig. 3 A). The worker wasps probably take the reddish-brown centre of the *S. satyrioides* flower to be a piece of animal food. Apart from the similarity in coloring, the imitation could be reinforced by the flat papillae at the base of the lip. Above all they imitate the texture of a fleshy substratum. The inner cavity of the spur, also coloured in a reddish tone, possibly resembles a customary feeding site of other wasps.

The morphology of the *S. satyrioides* flower is also well adapted to the “aggressive” behavior of the pollinating wasps. The sepals of its flower are united to form a rigid hood, and it is joined from behind to the upper part of the column. A relatively tight but heavy lip is directed almost vertically downward which considerably reduces the force of the shoulder of the lever. At the same time the “T”-shaped form of the lip and the small broadening at the end of its central lobe probably create favorable conditions on the lip for retaining the wasps while they attempt to eat in the spur (Fig. 3 A).

“Aggressive” behaviour of the worker *Vespidae* wasps on the flowers of *S. satyrioides* is also reflected in the basic reproductive characteristics of this orchid. In the species of *Dactylorhiza* and *Orchis* that are pollinated by such powerful pollinators as *Bombus* and *Psithyrus* (Nilsson, 1980, 1983, 1984), one often finds as many massulae remaining on the hemipollinaria (on a pollinator) as have been deposited on stigmas. Such a phenomenon is not typical for *S. satyrioides*. Its massulae are positioned on the stigma of the pollen-

producing flowers in one layer so that worker *Paravespula* and *Dolichovespula* wasps press the hemipollinarium on the stigma with great force. As a result, in *S. satyrioides* a significant portion of the massulae of the pollinators remain on the stigma; from 21 to 94 massulae were observed (x=57.2, n=15) on the stigmas. In contrast, this figure fluctuated from 8 to 54 in several species of *Dactylorhiza* and *Orchis*. The large amount of pollen on the stigma was also reflected in the potential seed productivity of the *S. satyrioides* flower. From 2432 to 10570 (x = 6128, n =18) ovules were counted in the developing ovary, whereas in *Orchis* and *Dactylorhiza* species there were 5436 and 4674, respectively.

Color and morphology of the flowers in *Steveniella* are adapted to the pollination of wasps with a short proboscis. These orchids are non-rewarding—nevertheless wasps visit them often. The wasps are attracted by the reddish-brown centre of the flower. It is possible that the wasps confuse the base of the lips with a piece of animal food. This method of attraction can be defined as "false prey"-syndrome. It results in high reproductive success in *S. satyrioides*. and it is much more effective than the syndrome of nectarless *Orchis* and *Dactylorhiza* that imitate the flowers of rewarding plants.

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