

Congruences in Pilosity between Three Species of *Ophrys* (Orchidaceae) and their Hymenopteran Pollinators

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ABSTRACT

Ågren, L., B. Kullenberg & T. Sensenbaugh (Ecological Station of Uppsala University, S-386 00 Färjestaden, Sweden, and Zoological Institute, Uppsala University, Box 561, S-751 22 Uppsala, Sweden.) *Congruences in pilosity between three species of Ophrys (Orchidaceae) and their hymenopteran pollinators.*

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Congruences in pilosity between two verified Hymenoptera/orchid associations: *Campsoscolia ciliata*/*Ophrys speculum* and *Argogorytes* sp./*O. insectifera*, and the suggested association *Eucera nigrilabris*/*O. scolopax* were investigated using the scanning electron microscope. Morphological evidence suggests that *Ophrys* flowers mimic the hair patterns of hymenopteran females, offering males copulatory stimuli and positioning them correctly at the labellum for pollination. Males are initially attracted olfactorily and visually at short distances. It is not believed to be the visual appearance of the hairs that is mimicked, but their ability to stimulate males tactilely at appropriate mechano/proprioceptive sites and by being distributed in optimal patterns on the flowers.

Key words: *Argogorytes*, *Campsoscolia*, copulatory behavior, *Eucera*, mimesis, SEM, tactile stimuli.

INTRODUCTION

In the orchid genus *Ophrys*, an unusual dependence upon males of certain species of wasps and bees as pollinators has evolved. A co-evolutionary association between plant and insect species seems apparent in a number of cases. The *Ophrys* flower offers hymenopteran males a set of sensations, that act at varying distances, and that simulate sensations produced by females.

Comprehensive studies (Borg-Karlson, in press) have shown that a wide spectrum of volatile components are emitted by *Ophrys* species. Specific, motivated hymenopteran males, respond to these odors at varying ranges (Kullenberg, 1956, 1961, 1973). It is believed that certain unidentified glandular cells in the labellum produce these complex secretions.

Visual cues have been shown to be active in a general way (Kullenberg, 1961) in attracting males at shorter distances. Photographic data (Kullenberg, 1957, 1961) indi-

cates that a centrally located patch on the orchid labellum reflects ultraviolet (UV) light. Similar UV reflections have been obtained from wings of the investigated hymenopterans.

Attracted olfactorily and perhaps visually, the male alights on the orchid labellum and attempts copulation. The male is further stimulated tactilely by fine hairs arranged in patterns on the labellum surface in a manner similar to those found on females and is thus correctly positioned for pollen transfer (Kullenberg, 1950b). The overall shape, hair pattern, and turgor of the labellum can also stimulate male mechano/proprioceptors (Kullenberg, 1961). Some *Ophrys* species even have a distal appendix on the labellum that is palpated by the male genital apparatus or abdominal end part.

On the labellum, the male comes in contact with the sticky endplates (viscidia) of the pollinaria. These attach to the anterior side of the head¹ and can be transferred to the next flower as the insect visits it. Flowers pollinated by hymenopteran males do not offer foraging or any other additional rewards than copulation stimuli. Occasionally beetles or other insects can be pollinators, but generally this seems to be insignificant for *Ophrys* reproductive success.

Vegetative propagation is of importance to varying degrees in different species and localities within the *Ophrys* complex. *Ophrys* have a low rate of fertilization, but a high production of seeds per capsule, and depend to a certain degree on vegetative propagation by producing extra tubers. Many *Ophrys* species occur in a number of forms which evidently are in a process of speciation. The present taxa *O. speculum* and *O. insectifera* are distinct species, whereas *O. scolopax* s.l. is less well defined (Kullenberg, 1961; Nelson, 1962; Baumann & Künkele, 1982).

This method of pollination, in which *Ophrys* species utilize hymenopteran males is more or less obligate. Of the investigated species, *Campsoscolia ciliata* is the only pollinator of *O. speculum*, but *O. scolopax* is pollinated by several *Eucera* species (Kullenberg, 1961; Kullenberg, Büel & Tkalcü, 1984).

¹ In the pollination of the species group *Fusci-Luteae* the bee males are guided to take a reverse position on the flower labellum and consequently remove the pollinaries and pollinate with the distal part of the abdomen.

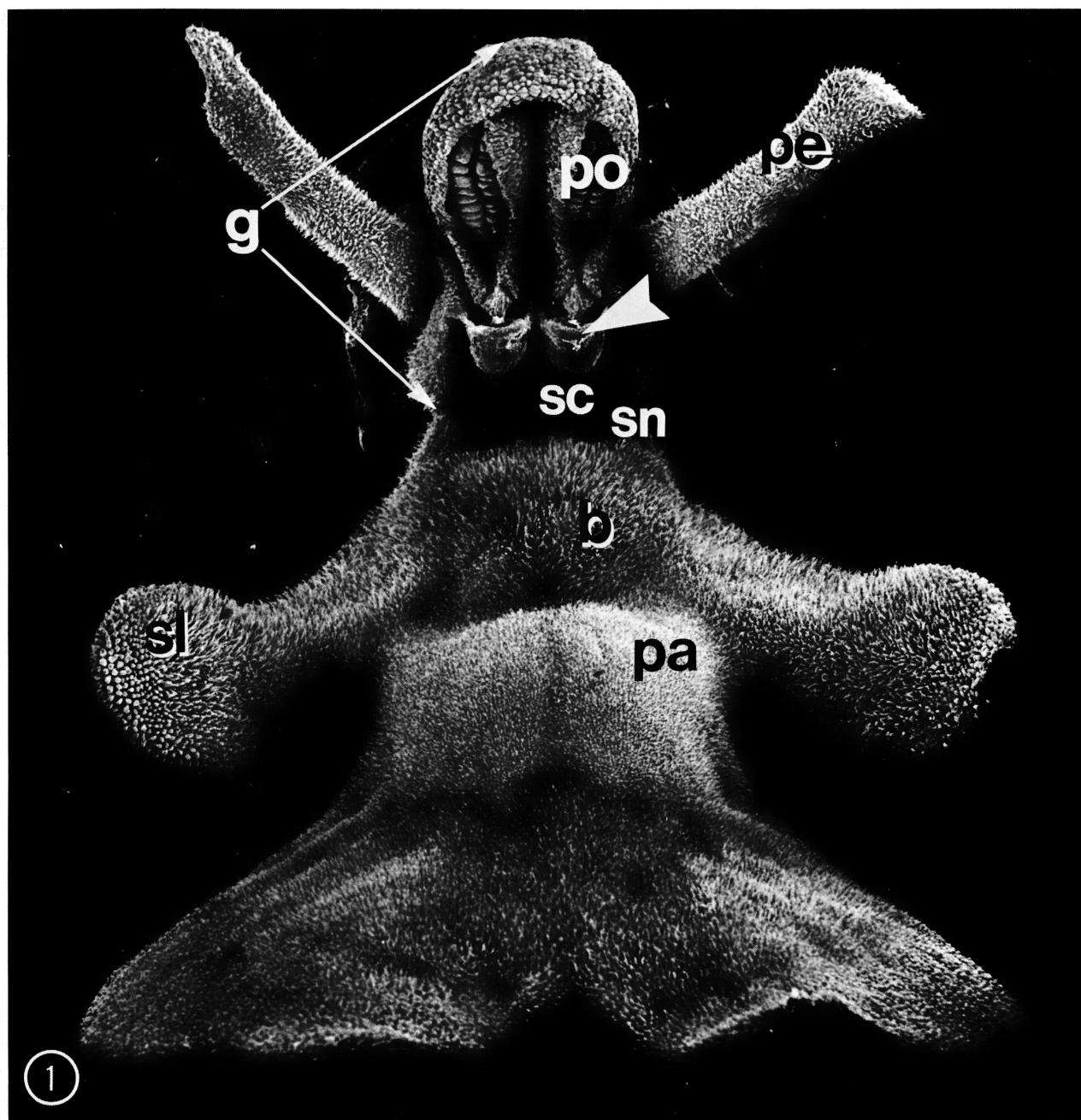


Fig. 1. Labellum of *O. insectifera* as seen obliquely from the distal end. The sepals are removed. Note the dense, even pilosity and the brighter patch, that in life reflects UV more than the other surfaces. Also the gradual transition from typical hairs centrally to rounded protuberances distally or at the side lobes can be seen.
b: boss
g: gynostemium
pa: patch
pe: petal
po: pollinarium with viscidium (arrow) protected by the bursicle
sn: "sham nectary"
sl: side lobe
sc: stigmatic cavity
 × 18.

Eucera nigrilabris has not been previously observed as a pollinator of *O. scolopax* (Kullenberg, Büel & Tkalců, 1984), but is a pollinator of *O. tenthredinifera*, a species belonging to the same section of the genus. Instead, *E. nigrescens continentis* males have been recorded as pollinators of *O. scolopax*. *Eucera nigrilabris* males are, however, strongly excited by volatiles of extracts from flower labella of both *O. scolopax* and *O. tenthredinifera*. It is of interest to compare superficial structures of the *O. scolopax* labellum with integumental structures of the female *E. nigrilabris*. From morphological information it should be possible to prognosticate whether *O. scolopax*

could be pollinated by *E. nigrilabris* if the two organisms were to meet in the same biotope.

Ophrys insectifera utilizes both *Argogorytes mystaceus* and *A. fargei* as pollen vectors. The geographical distributions of orchid species and the present hymenopterans do not completely coincide. The insects are apparently not dependent on the flowers for survival.

For several decades our group has worked with the complex signal logistics between flower and hymenopteran; chemically, ethologically, taxonomically, physiologically, ecologically and morphologically (Kullenberg, 1948, 1950a, 1950b, 1950c, 1951, 1952, 1953, 1956, 1961, 1973, 1977; Kullenberg & Bergström, 1973, 1975, 1976a, 1976b; Kullenberg & Guinochet, 1978; Kullenberg, Büel & Tkalců, 1984).

The present study is an attempt to more completely understand the morphological similarities of orchid labellar superficial structures and female hymenopterans within several of the numerous orchid/hymenopteran pollination associations.

In earlier papers Kullenberg (1960b, 1961) and Kullenberg & Bergström (1976) studied pilosities and other superficial structures of the labella and also those of the bee and wasp bodies using the light microscope. Since then the scanning electron microscope (SEM) has become a standard instrument for detailed morphological investigations.

MATERIALS AND METHODS

Up to three individuals from both sexes of the hymenopteran species *Campsoscolia ciliata* (Fabricius, 1787) (Scoliidae), *Argogorytes fargei* (Schuckard, 1837) or *A. mystaceus* (L., 1761) (Sphecidae, Nyssoninae), *Eucera nigrilabris* Lepelletier, 1841 (Anthophoridae) plus one single female specimen of *E. nigrescens continentis* Tkalců, 1984 (= *E. tuberculata* auct.) were investigated. Of the orchids, labella were investigated from at least three individual plants of *Ophrys insectifera* L., 1753, *O. speculum* Link, 1800, and *O. scolopax* Cavanilles, 1793. Insects were air-dried on pins (Ågren, 1975). Flowers were fixed in 4 % glutaraldehyde in a 0.2 M cacodylate buffer at pH 7.4 for several days, and postfixed with 2 % OsO₄ in a phosphate buffer for about one hour at 4°C. After dehydration through a graded ethanol series, orchids were transferred through a graded series of Freon TF for one hour, then critical point dried in liquid CO₂. Insects and flowers were mounted on stubs and Au/Pd-sputtered to a metal thickness of 20–40 nm. Microscope used was a Jeol JSM-35 at voltages of 15–25 kV.

Insects were captured on Mallorca, Spain (*C. ciliata* and *E. nigrilabris*), in Languedoc, France (*E. nigrescens continentis*), and on Öland, Sweden (*A. fargei* and *A. mystaceus*). *Ophrys speculum* were obtained from Montferrier, Languedoc, France, *O. scolopax* from Montbazin, Languedoc, France, and *O. insectifera* from Öland, Sweden.

Designation of morphological details follows that of Richards (1977), the first gastral segment is counted as abdominal segment 2.

RESULTS

Hymenoptera

Hair and bristle measurements for investigated Hymenoptera are found in Table I.

Campsoscolia ciliata, female. The abdomen has long tufts or bands of hairs of relatively constant length along the posterior borders of the segments, but few elsewhere (Fig. 3, Table I). Since the segments become gradually thinner posteriorly, the bands cover the hind segments more completely than the anterior ones. All hairs are directed posteriorly. On the thorax, hairs are relative sparse and less regularly directed, and placed in formations that leave the dorsalmost areas of the segments relatively free (Fig. 11). Tegulae and wings have few hairs (Fig. 2), except for the anteriormost region around the costal vein, and at the medial vein. Seen at higher magnification, all hairs are needle-like with a faint spiralled pattern, and never branched (Fig. 21).

Campsoscolia ciliata, male. Compared with female abdomina, those of the males are much hairier and have no bald surfaces (Fig. 17). The thorax is bushier. Proximally on the costal vein of the wing, there is a somewhat denser hair pattern than on the female and there are also a few hairs on the wing cells. Individual hairs are similar to those of the female. Seen at higher magnification, their bandedness or spiralled appearance arises from a scale-like construction.

Eucera nigrilabris, female. The abdomen has a less obvious banding of hairs than in *C. ciliata* females (Fig. 6). The hairs of the fur are directed slightly upwards and are zoned on the segments. The pygidial plate has about 25 rows of 30 µm scales (Fig. 25). Thoracic hairs are long, dense, and plume-like (Figs. 13, 23). Wing hairs are needle-like and are found more densely on the veins than in the cells of the wings (Fig. 5).

Eucera nigrilabris, male. As in *C. ciliata*, the male is hairier than the female and has no zonation of hair bundles on the abdomen. Otherwise as the female.

Eucera nigrescens continentis, female. Superficial body structures are not incongruent to those of *E. nigrilabris* females, although some minor differences in hair pattern and hair lengths are found.

Argogorytes fargei/mystaceus, female. Hairs are short and directed posteriorly on the abdomen (Fig. 9). Those on the proximal second tergite are somewhat longer, as are those dorsally on the seventh tergite. The sides of the latter are quite bald. Thoracic hairs also vary in length and

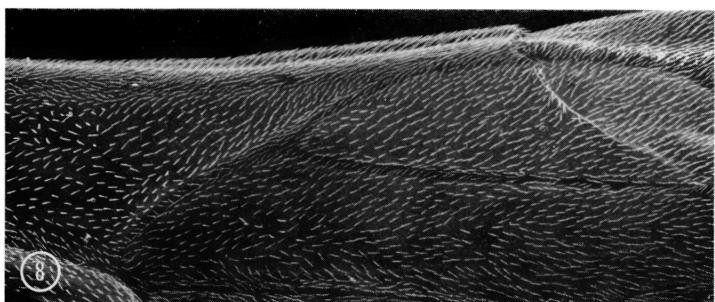
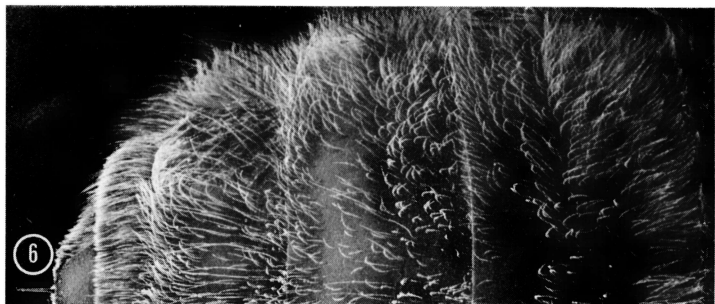
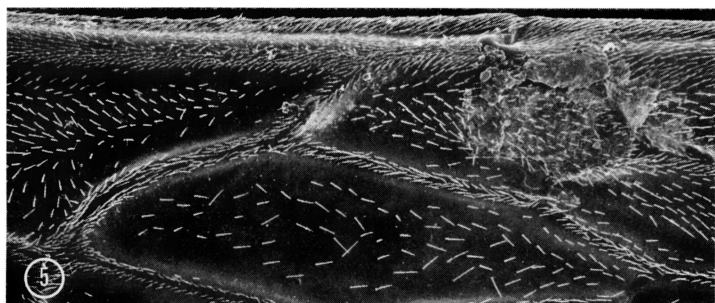
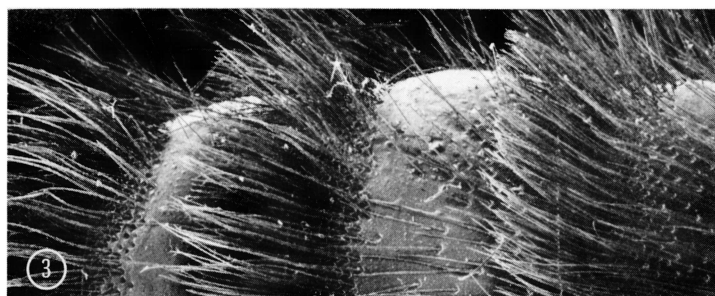
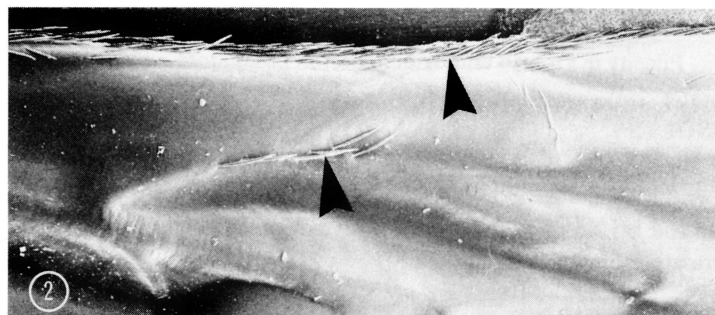


Table 1 Comparison between hair and bristle size of proposed mimicking *Ophrys* species and their models, females of the pollinators (males in parentheses).

| Plant mimic | μm | Hymenopteran model | μm |
|-----------------------|---------------|-----------------------------|-------------------|
| <i>O. speculum</i> | | <i>Campsoscolia ciliata</i> | |
| labellar fringe | 1,000 | female abdomen | 800–1,000 (1,200) |
| labellar base | 150 | female thorax | 1,100 (1,100) |
| labellar center | no hairs | female wings | 200 (120) |
| <i>O. scolopax</i> | | <i>Eucera nigrilabris</i> | |
| labellum distally | 250 } | female abdomen | 975 (900) |
| labellar rims | 450 } | female thorax | 1,500 (1,000) |
| sham nectaries | 90 | female wings | 60–100 (30–100) |
| labellum medially | 30 | | |
| <i>O. insectifera</i> | | <i>Argogorytes</i> sp. | |
| labellum acentrally | 70 | female abdomen | 40–100 (75) |
| boss | 150 | female thorax | 75–300 (75–300) |
| labellar patch | 40 | female wings | 50 (50) |

Fig. 2. Middle part of *C. ciliata* female wing as seen dorsally. Hairs only on the costal and medial veins (arrows). $\times 30$.

Fig. 3. *C. ciliata* female abdomen dorsally. The hair pattern is banded on the tergites. Compare to male in Fig. 17. $\times 20$.

Fig. 4. *O. speculum* labellum. The central area is bald and the hairs form a peripheral fringe. The crack is an artifact. The left side-lobe is broken to show the cell layers. Area at white arrow is shown in higher magnification in Fig. 12. Black arrow shows the distal hairy wedge. $\times 12$.

Fig. 5. *E. nigrilabris* female. Central part of the wing, dorsally. Much more hairs compared to Fig. 2, but only on the cells and very few on the veins, only among them. $\times 30$.

Fig. 6. *E. nigrilabris* female. Abdomen dorsal view. A more even hair distribution than in Fig. 3. Male in Fig. 18. $\times 12$.

Fig. 7. *O. scolopax* labellum. Note the convex surface with the patch (single arrows), the velvet-like pilosity and the longer hairs distally (double arrow). The bald distal appendix is seen in higher magnification in Fig. 26. $\times 12$.

Fig. 8. *A. mystaceus* female. Central part of the wing, dorsally. The pilosity is more even than in *E. nigrilabris* (Fig. 5), the hairs are shorter and also situated on the very veins. See also Fig. 27. $\times 30$.

Fig. 9. *A. fargei* female, abdomen dorsal view. A completely different pilosity pattern than in the former two species (Figs. 3, 6). Shorter and more evenly distributed hairs. Male in Fig. 19. $\times 16$.

Fig. 10. *O. insectifera* labellum. For explanations, see Fig. 1. $\times 12$.

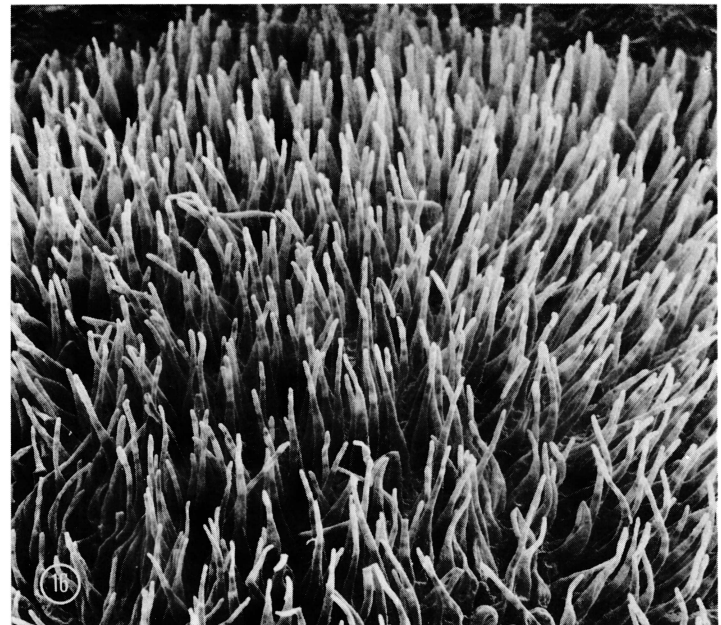
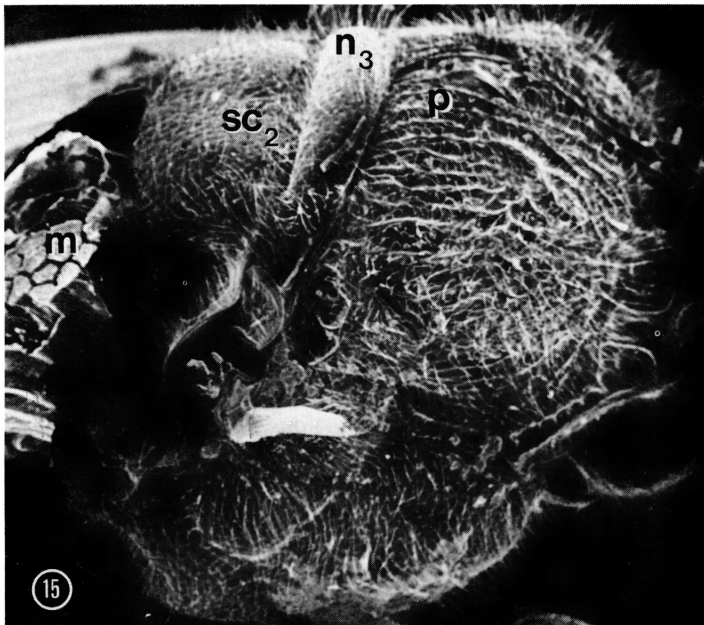
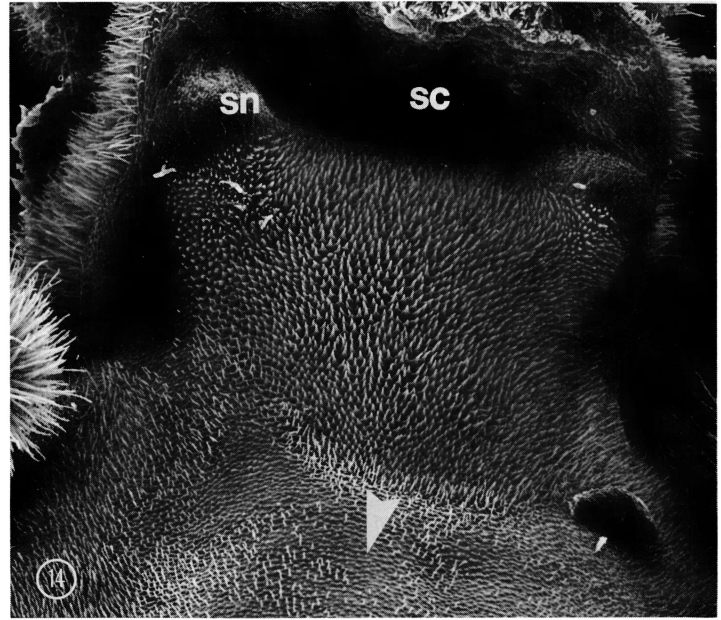
are nondirectional, following furrows and crevices (Fig. 15). On notum 3 and in some whorls at the axillae, hairs are directed anteriorly. Centroposteriorly on the scutellum there is a 100 μm tuft of hairs. Tegulae are hairy. The wings are evenly bristled (Figs. 8, 27). All hairs and bristles are situated in small depressions and are needle-like.

Argogorytes fargei, male. The hairs of the abdomen are similar to those of the female, but are not as dense on the anterior parts of the segments (Fig. 19). The posteriormost tergite has the same pattern as the female; on segment two the male has comparatively few hairs. On the sternites, there are longer, (100 μm) coarser hairs scattered amongst the others. Pilosities of the thorax and wings are similar to those of the female. On the cuticle at the hairy tuft of the scutellum there are clusters of fine pores that could be glandular openings.

Orchids

For reading ease, the morphological structures described below are shown in Fig. 1. Hair lengths are given in Table 1.

Ophrys speculum. The most conspicuous feature of the flower is the large, hairless area in the center of the labellum. Surrounding this area and the side-lobes is a dense fringe of hairs (Fig. 4). On the basal part of the labellum there is a small patch of hair (Fig. 12). Additionally, at the distal edge of the labellum, there is a protruding triangular wedge of hairs (Fig. 4). The petals are hairy. The fringe hairs on the labellar rim are slightly spiralled (Fig. 22). Cells at the bottom of the stigmatic cavity are hairless and have an undulated surface. The labellum is 6–8 cell layers thick.



Ophrys scolopax. The labellum is convex, ending distally in a trilobular hairless appendix (Figs. 7, 26). The pilosity over the surface is quite fine; shorter medially and longer towards the appendix and between the sham nectaries (Fig. 14). At the labellar base the hairs gradually shorten, as followed centripetally, until disappearing at the opening of the stigmatic cavity. The rims and outer edges of the side lobes are densely covered with spiralled hairs (Fig. 24). The patch or design on the labellum has the shortest hairs, in the center of it there is a tuft of around 70 μm . The underside of the labellum has only protuberances, no hairs. The inner areas (facing inwards) of the side lobes and the sham nectaries are hairless. The thickness of the labellum is similar to that of *O. speculum*, the walls of the stigmatic cavity are thicker than the labellum. The labellar hairs emerge from a wide base, as if they originated from the protuberances. Petal hairs are thin and spiralled.

Ophrys insectifera. The pilosity is uniformly short; at the backside and towards the distal margins the hairs shorten to become more like protuberances (Figs. 1, 10, 20). At the boss, hairs are longer than at the patch and denser (Figs. 16, 28). The petals are hairy. Centrally, and on the backside of the labellum, some of the protuberances show a slight knobiness.

Fig. 11. *C. ciliata* female thorax dorsally. Anterior is upwards. Tufty long hairs in irregular directions and bald tegulae. $\times 20$.

Fig. 12. *O. speculum* basal part of the labellum ("hypochile", cf. Fig. 4). Note the restricted area with coarse hairs between labellum and gynostemium (arrow). $\times 65$.

Fig. 13. *E. nigrilabris* female thorax dorsally. Anterior is upwards. Compared to Fig. 11, longer and more plume-like hairs. $\times 22$.

Fig. 14. *O. scolopax* basal part of the labellum. The hairs are gradually longer towards the gynostemial base, shorter again towards the stigmatic cavity.
 sc: stigmatic cavity
 sn: "sham nectary"
 arrow: part of patch
 $\times 25$.

Fig. 15. *A. fargei* female thorax dorsoposteriorly from the left side. Longer hairs than on abdomen (Fig. 9) and also less uniformly directed.
 m: cut muscles
 sc₂: scutellum
 n₃: notum 3
 p: propodium or median segment
 $\times 35$.

Fig. 16. *O. insectifera* boss of labellum seen towards the stigmatic cavity. The hairs are longer than in the surrounding areas. $\times 125$

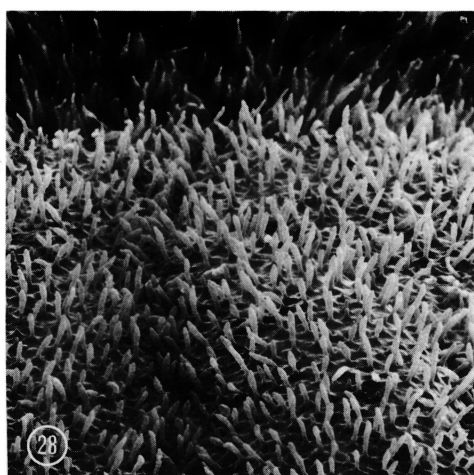
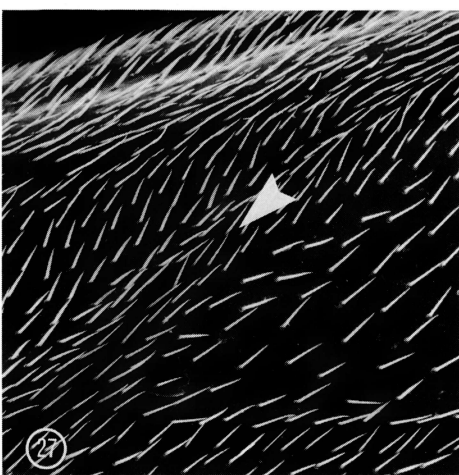
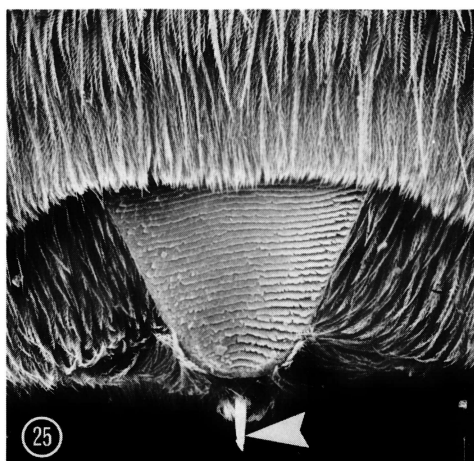
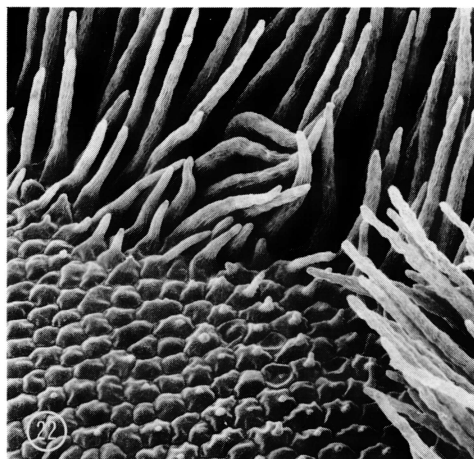
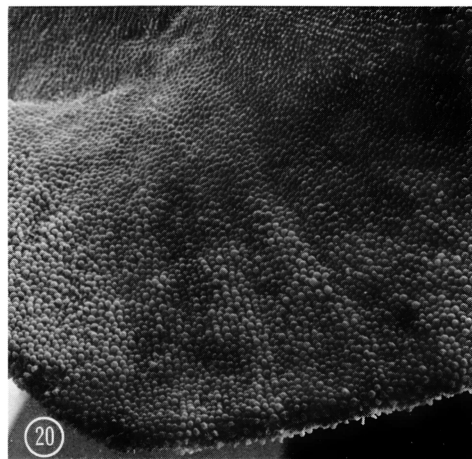
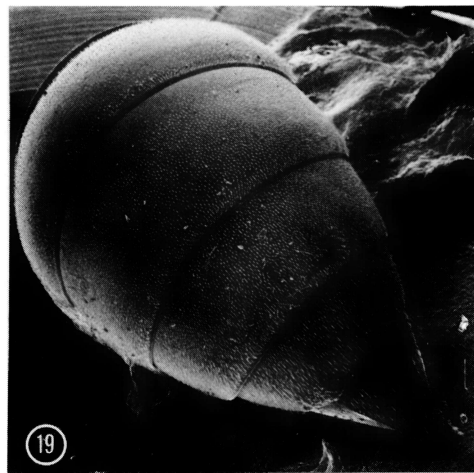
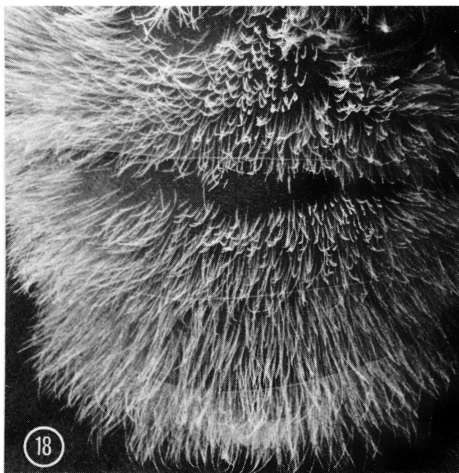
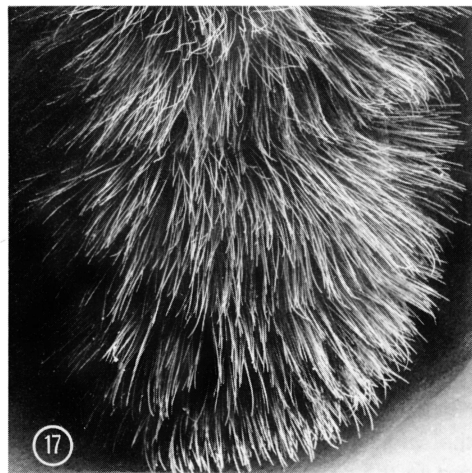
DISCUSSION

We suggest that congruences in pilosity and hair patterns of the investigated orchids and female insects are too similar to be purely accidental, and represent a set of adaptations to improve the pollination probabilities of the plants. Other selection pressures on *Ophrys* hair structures are believed to have been of minor importance in this adaptive process.

Morphological evidence for a co-evolution involving an exploitation of a pollinator behavior, other than for food-seeking is supported by ethological field studies (Kullenberg, 1961, 1973). Of interest in the orchid/insect association is the utilization of a vector for pollen transfer and that the sexual behavior of the pollinator is exploited, not the insects foraging behavior as most commonly occurs. Instead of providing nectar the flowers apparently only present triggers or stimuli leading to a copulation attempt by the male insect.

If the cost of producing a specific scent mixture is not considered, one might suggest that instead of offering a product for the male insect, the flowers obtain a cost-free service. The plant appears then to have achieved a reduction in terms of energy expenditure, although accepting a lowered pollination rate. An adaptation of this type suggests that the *Ophrys* species have become quite specialized and dependent on a limited number of pollinator species. It is presumed that the production of a specific odor combination or scent does not require a great amount of energy, which is quite probable, since many flowers produce both nectar and scent. *Ophrys* has evolved from orchid types producing only nectar (Kullenberg, 1961). A plant utilizing food-seeking pollinators is able to exploit a broader spectrum of vectors, since foraging behaviour of insects is more uniform than sexual behavior. Thus, an efficient sexually attracted pollinator must be specially adapted for by the plants.

As we suggest, the arrangement, size, stroking direction and stiffness of hairs and superficial structures on the labella of these three *Ophrys* species have evolved to utilize the sexual behavior of hymenopteran males. There are three examples of specificity demonstrated by the three investigated associations of which one is hypothesized. In order to position their insect pollinators correctly on the labellum, enhance their excitation, and retain them for a sufficiently long time on the labellum, the hairs stimulate mechano/proprioceptors at proper positions on the insect males. The hairs do not imitate precisely those of the females, but give appropriate sensations by their distributional patterns and cumulative stimulatory effects. Since it is difficult to measure stiffness of such small, velvet-like hairs and to quantify their capability to imitate female hairs, a scanning electron microscope was used to indirectly demonstrate distributional patterns, the approximate sizes of the hairs, and morphological similarities.



1. The *Ophrys speculum*—*Campsocolia ciliata* association

This association was the first of the *Ophrys*—insect associations to be described (Correvon & Pouyanne, 1916; Pouyanne, 1917). The long hairs of *O. speculum* seem to mimic those on the body of the *C. ciliata* female. A large, hairless area is seen both on the female wings and on the labellum of the flower. Both probably reflect UV in a similar manner. During legitimate copulation the female crosses her wings directly over the abdomen. Seen from above, the target for a male is then a hairless area surrounded by a fringe of abdominal hairs and a tuft of hair on the mesonotum or scutellum. A tuft similar to that of the scutellum is found on the basal part of the labellum, and there is also a long-haired triangle of hairs distally, as

Fig. 17. *C. ciliata* male abdomen dorsally. Compared to the female (Fig. 3), the fur is denser and thicker. $\times 11$.

Fig. 18. *E. nigrilabris* male abdomen dorsally. Also in this species, the male has denser fur than the female (Fig. 6). $\times 12$.

Fig. 19. *A. fargei* male abdomen dorsoposteriorly. Similar to the female (Fig. 9). $\times 16$.

Fig. 20. *O. insectifera* backside of the labellum. There are no hairs, only protuberances. $\times 18$.

Fig. 21. *C. ciliata* female thorax obliquely. Dense hairs, but none branched. Note the very fine spiral groove on the individual hairs. $\times 110$.

Fig. 22. *O. speculum* at the margin of the bald area of the side lobe. The hairs are spiralled and long. $\times 90$.

Fig. 23. *E. nigrilabris* female. Thoracic hairs, pair-wise branched. $\times 110$.

Fig. 24. *O. scolopax*, apex of side lobe. Hairs are long and spiralled. $\times 50$.

Fig. 25. *E. nigrilabris* female. Abdominal distal end with pygidial plate. Dense rows of scales on the latter, under it the sting (arrow). $\times 40$.

Fig. 26. *O. scolopax* labellar apex with appendix. The hairs are gradually longer towards the appendix. $\times 20$.

Fig. 27. *A. mystaceus* female wing, centrodorsally. Note the even hair pattern, both on the veins (arrow) and on the cells. $\times 110$.

Fig. 28. *O. insectifera* labellum at the patch area, distally of Fig. 16. Hairs are less densely packed here. $\times 115$.



Fig. 29. *E. nigrescens continentis*, female abdomen as seen dorsally. The hair pattern is similar to that of *E. nigrilabris* females. $\times 12$.

seen on the area of the female abdomen not covered by the wings. Additionally, the size of the flower is similar to that of the female and lends appropriate stimuli to the proprioceptors.

2. The hypothesised *Ophrys scolopax*—*Eucera nigrilabris* association

The labellar hairs of *O. scolopax* are believed to tactilely stimulate a male in a similar manner as bristles on the wings of the *Eucera* female. In this association, the similarity of the uneven pilosity of the orchid medial patch and the insect wing is of interest. However, *E. nigrilabris* is not an established pollinator of *O. scolopax* and the status of *O. scolopax* s.l. as a valid species can be questioned.

Referring to the presence of only minor differences observed in the hair pattern of the two investigated *Eucera* species, it would seem to us quite natural if also *E. nigrilabris* males could act as pollinators of *O. scolopax*.

The increasingly longer hairs distally on the labellum could be a mimic of the hair coat on the dorsal surface of the abdomen (distally between the wings). The labellar appendix is also similar in appearance to the last visible abdominal segment; the pygidial plate of the female. Even here, the convexity of the labellum gives an overall abdomen-like shape. The hairs of the lateral lobes fringe could correspond to the longer hairs of the hind legs, abdomen and thorax of the female.

3. The *Ophrys insectifera*—*Argogorytes fargei/mystaceus* association

Linnaeus recognized the labellum as looking like a fly by sometimes calling the flower "*muscifera*", and at a glance, the dark flower really looks like an insect sitting on a stem. The overall pilosity of the labellum and that of the female wings are quite similar. The central patch of the flowers has short hairs; the boss has longer. The boss then seems to mimic the female thorax.

The question arises whether the pilosity of the flower labella could serve any other purpose, such as raising and preserving temperature in connection with heating by solar radiation. Such a property could be of positive value in both scent evaporation and the activity of pollinators (Kullenberg, 1961). This aspect has not been investigated in other orchid species which are known to have hair structures on the labella. Seen from an evolutionary/taxonomical point of view, the hairs of *Ophrys* might have evolved from hairs of the type found on the flowers of *Orchis* and *Serapias* (Kullenberg, 1961). It is suggested by Correvon and Pouyanne (1916) that *O. fusca* and *O. lutea* retain a remnant of the spur in the structure of the stigmatic cavity at the base of the labellum.

A waxy hydrocarbon coat on the hairs could function in tactilely stimulating and positioning the male correctly on *Ophrys*. This waxy coat can play an active role in positioning bees for natural copulation. It is also believed that the waxy coat could, at short distances, or at contact, chemically stimulate male Hymenoptera.

Why is the pilosity of the hymenopterans variable both between species and sexes? It seems to be common in Hymenoptera Aculeata that males are more fully equipped with hairs than females. In a study of the scent marking behavior of bumblebees, Kullenberg *et al.* (1973) compared the hairy bodies of the male bumblebees with "veritable perfume-brushes".

It must be kept in mind that the proprioceptive and tactile stimuli should not be looked upon as separate phenomena, but are integrated as mechanical stimuli in the whole stimulus situation in which both chemical and perhaps visual stimuli have excited the males to a high level of sexual motivation. The non-directional orientation movements of the female-searching flight becomes a telotaxis by a "cross-fiber" triggering to nearly all sense modalities. It was earlier stated by Kullenberg (1956) that tactile stimuli *per se* are inadequate to release an effectful copulation attempt. There must always be a chemical stimulation in coordination with the mechanical. On the other hand, a chemical stimulus without the proper tactile stimulation only results in undirected crawling and fluttering of the wings of the males.

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