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Flowers of *Boraginaceae* (*Symphytum, Onosma, Cerinthe*) and Andrena symphyti (Hymenoptera-Andrenidae):

Morphology, Pollen Portioning, Vibratory Pollen Collection, Nectar Robbing

By

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With 52 Figures

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Key words: *Boraginaceae, Cerinthe minor, Onosma* div. spec., *Symphytum officinale, Symphytum tuberosum*. – Anthesis, floral ecology, morphology, scatter-cone-blossoms, streukegel blossoms, pollen portioning, buzzing, vibratory pollen collection, nectar robbing, bite slits, concentrating nectar. – Andrena symphyti, Andrena lathyri, Andrena ovatula, Andrena similis, Andrenidae, Apoidea, Hymenoptera.

Summary

TEPPNER H. 2011. Flowers of *Boraginaceae* (*Symphytum, Onosma, Cerinthe*) and Andrena symphyti (Hymenoptera-Andrenidae): Morphology, pollen portioning, vibratory pollen collection, nectar robbing. – Phyton (Horn, Austria) 50(2): 145–180, with 52 figures.

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Symphytum, Onosma and *Cerinthe* bear streukegel blossoms with nectar. In *Symphytum* and *Cerinthe* a single anther needs 1–4 hours for opening. Pollen portioning results through successive ripening and opening within 1–3 days of the five anthers of a flower. In *Onosma* the anthers of a flower develop synchronously and an individual anther needs 1–3 days to be ripe and open along their whole length. In all the three genera, nectar secretion begins in the late bud stage.

Andrena (Euandrena) symphyti collects pollen in the three mentioned genera by manipulation of anthers and buzzing, nectar by robbing through transversal slits bitten near the base of the corolla-filament-tube. Nectar collection is interrupted by nectar concentrating. Members of Andrena subg. Taeniandrena (A. lathyri, A. ovatula, A. similis) split narrow floral tubes (calyx or corolla) longitudinally for nectar robbing. Other flower- visiting bees of *Symphytum, Onosma* and *Cerinthe* are also mentioned.

Zusammenfassung

Teppner H. 2011. Flowers of *Boraginaceae (Symphytum, Onosma, Cerinthe)* and Andrena symphyti (Hymenoptera-Andrenidae): Morphology, pollen portioning, vibratory pollen collection, nectar robbing. [Blüten von *Boraginaceae (Symphytum, Onosma, Cerinthe)* und Andrena symphyti (Hymenoptera-Andrenidae): Morphologie, Pollenportionierung, Vibrationssammeln, Nektarraub]. – Phyton (Horn, Austria) 50(2): 145–180, mit 52 Abbildungen.

Symphytum, Onosma und *Cerinthe* besitzen Streukegel-Blumen mit Nektar. Bei *Symphytum* und *Cerinthe* benötigt die einzelne Anthere 1–4 Stunden für das Öffnen. Pollenportionierung ergibt sich durch das sukzessive Reifen und Öffnen der fünf Antheren einer Blüte innerhalb von 1–3 Tagen. Bei *Onosma* entwickeln sich die Antheren einer Blüte streng synchron und die einzelne Anthere benötigt 1–3 Tage, bis sie entlang ihrer ganzen Länge reif und offen ist. In allen drei Gattungen beginnt die Nektarsekretion vor dem Öffnen der Knospen bzw. vor der Anthese.

Andrena (Euandrena) symphyti sammelt den Pollen in den drei erwähnten Gattungen durch Manipulation der Antheren und Vibration, den Nektar über Nektarraub durch Querspalten, die nahe der Basis in den Kron-Filament-Tubus gebissen werden. Das Nektarsammeln wird durch Nektareindicken auf den Mundwerkzeugen unterbrochen. Angehörige von Andrena subg. Taeniandrena (A. lathyri, A. ovatula, A. similis) spalten enge Blütenröhren (Kelch oder Krone) für den Nektarraub der Länge nach. Die anderen beobachteten Bienen an *Symphytum, Onosma* und *Cerinthe* sind ebenfalls erwähnt.

1. Introduction

In 1995, I completed a manuscript concerning flower morphology, anthesis and flower visitation in *Onosma* (Teppner 1996); the most important pollinators were the polylectic Anthophora and Bombus species and Megachile parietina, as well as the oligoletic bees on *Onosma* Osmia apicata(Megachilidae-Osmini) and Cubitalia morio (Anthophoridae-Eucerini). At that time, I had made only a single curious observation of the west-palaearctic Andrena symphyti on *Pulmonaria*, the observations on *Symphytum* and *Onosma* of this bee oligolectic on

Boraginaceae, were made not earlier than 1996, after the appearance of the afore-mentioned paper. Thus, this bee remains to be treated. It exploits streukegel blossoms (scatter-cone-blossoms), thus, in this sense, the present study is also a continuation of previous ones (TEPPNER 2005, 2009). In the literature I still haven't found any description of flowers which would have been sufficient for the purposes of floral ecology, thus I abstain from citing all these references. The older literature was extracted by KNUTH 1899 (*Boraginaceae*: p. 97–125).

2. Material and Methods

Observations were made on spontaneously growing *Symphytum tuberosum* L. and *S. officinale* L. in the Botanic Garden of the Institut fuer Pflanzenwissenschaften der Universitaet Graz and suitable natural habitats in the city of Graz as well as in the districts Graz-Umgebung and Deutschlandsberg (all in Styria, Austria, Europe). Furthermore, *Symphytum asperum* LEPECH., *S.* ×*uplandicum* NYMAN and back-crosses with *S. asperum* were grown in the Botanic Garden.

Onosma does not occur in Styria, all observations were made on species grown in the Botanic Garden. The species which were mainly investigated during most of the time and in a number of details are:

O. (Aponosma) isaurica BOISS. & HELDR. from Central Anatolia, Cappadocia, Zelve, 21. 7. 2001, leg. U. BROSCH.

O. erecta SIBTH. & SM. subsp. *erecta* from Greece, Peloponnisos, W. Taygetos, 7.7.1980, leg. H. TEPPNER 80/194.

O. stojanoffii TURRILL (TEPPNER) from N Greece, Menikion and Falakron Mts., June 1994, leg. H. TEPPNER & H. MAYRHOFER.

O. paradoxa JANKA from Greece, Mt. Athos, 19.6.1994, leg. H. TEPPNER 94/90 & H. MAYRHOFER.

O. rigida LEDEB. from Bulgaria, ENE Cap Kaliakra, 6. 6. 2007, leg. R. KARL.

O. heterophylla GRISEB. from N Greece, between Thessaloniki and Serres, 22. 6. 1994, leg. H. TEPPNER & H. MAYRHOFER.

O. mattirolii BALDACCI from Albania, Mali i Tomorit, 10. 8. 1989, leg. E. BALTISBERGER.

O. alborosea FISCH. & MEY. div. origins.

O. gehardica T. POPOVA from Armenia, Sjunik province, 24. 6. 2004, leg. VITEK 04-1453.

Singular observations on flowers or on visitors were made on many other *Onosma* species.

Cerinthe minor L. is cultivated in the Botanic Garden. Origin: Steiermark, Grazer Bergland, Hochlantsch, c. 1500–1700 m, 2002, leg. P. GIGERL. – A small natural population in Graz-Fölling near Sternwirt and between Sternwirt and quarry Kollermichl is the only actually known natural site in Graz.

Flowers were analyzed in the field with the help of a lens or on inflorescences taken in the laboratory with the help of a dissecting microscope Wild M 3B.

Photos were taken with an Exakta VX 1000 with a Steinheil Macro-Quinon objective. The slides were scanned with CanoScan 8800F and the images were edited with Adobe Photoshop CS3. Only in 2010 a small number of photos (especially some close ups of flower details and nectar drops) were made with a Panasonic Lumix DMC-GF1 and a Leica DG Macro-Elmarit objective.

Bees were observed with the naked eye or with the help of a lens. The occurrence of Andrena symphyti SCHMIEDEKNECHT 1883 was proven on the following localities by collecting vouchers (in the collection of the author, later at the Biologiezentrum in Linz) or by the registration of the characteristic bite slits on *Symphytum* corollas.

Graz-Umgebung, Semriach, Rötschgraben, 26. 5. 1996, ♀, *Symphytum tuberosum*.

Graz, Mariatrost, Kirchberg, N-Seite, 1. 6. 1996, ♀, *Symphytum officinale*.

Graz, Geidorf, Botanischer Garten, 18. 5. 1996, 2 ♀, *Symphytum officinale*.

Graz, Geidorf, Botanischer Garten, 18. 5. 1996, ♀, *Onosma stojanoffii*.

Graz, Geidorf, Botanischer Garten, 23. 5. 2006, ♀, *Cerinthe minor.*

Graz, St. Martin, 24. 4. 1993, ♀, *Pulmonaria officinalis*, nectar robbing.

Graz, St. Martin, 4. 5. 1996, ♂ and ♀, *Symphytum tuberosum*.

Graz, Straßgang, Florianiberg, 11. 5. 1996, ♀, *Symphytum tuberosum*.

Deutschlandsberg, Burg, 6. 6. 1996, ♀, *Symphytum officinale*.

Deutschlandsberg, Schloß Hollenegg, Park, 17. 5. 1996, bite slits, *Symphytum tuberosum*.

For the SEM images of *A. symphyt*i air dried material was mounted on aluminium stubs using C-impregnated double sided tape and sputtered with gold. A SEM XL 30 was used (E. STABENTHEINER). The probes are kept in the collection of the Institute of Plant Sciences in Graz.

3. Flower Morphology, Anthesis and Pollen Portioning

In respect of floral ecology *Symphytum, Onosma* and *Cerinthe* possess streukegel blossoms with nectar; this is the *Borago* flower type of FAEGRI 1986: 52 (in contrast to the solanoid flower without nectar).

Pollen portioning, the successive release of pollen of a flower in smaller portions, lengthens the duration of the male phase of a flower: Either by packaging i. e., for e. g., successive opening times of anthers of a flower or by dispensing, i. e. partial release of available pollen (HARDER & THOMSON 1989 and literature cited therein, HARDER 1990: 1121–1122).

3.1. *Symphytum tuberosum* and *S. officinale (Boragineae)*

In *Symphytum officinale* the triangular sepals (6.0–10.0 mm long) are basally connate for c. $^1/_3$ of their length (Fig. 1). The lobes are bent outward, obliquely erect or loosely lying against the corolla, hispid outside, scabrous inside by a dense cover of short, acute hairs, oriented obliquely to the tip. The purple corolla is c. 13–15 mm long (at the end of anthesis or in the last flowers of cincinni often much shorter), tubular with short corolla lobes (petal lobes) reflexed during anthesis (Fig. 1, 2). The corolla is made up of the corolla-filament-tube (see ERBAR 1991 and the comments by TEPPNER 1998) for nearly two thirds of its length (± 8 mm); the lower margin of the insertion of the thick, free parts of the filaments is marked outside by a slight groove, the upper one (and thus the upper limit of the corolla-filament-tube) lies at the level of the entrance to the faucal scales (Fig. 1). Distally the corolla tube and the short lobes follow. The entrance is c. 4–5 mm wide, the stigma lies ± at the level of the entrance.

The mature, intact anthers are c. 3.9–4.2 mm long (Fig. 5), open ones c. 2.9–3.2 mm (Fig. 7), they are not connected at their bases and bent toward the style forming a cone. The stiff, triangular, densely papillose faucal scales (c. 4.5–5 mm long) cover the anthers (view into corolla Fig. 2, side view Fig. 3). Thus the access to the interior is masked and only possible through the edges or the sides between two scales and further on between two neighbouring filaments. The short free parts of the filaments are c. 2.3–2.7 mm long and inserted c. 1.0–1.3 mm above the anther base.

Start of anthesis is clearly marked by the separation of the corolla lobes. Nectar secretion begins before flower opening. The nectar appears in the form of five or few drops on the ring of basal scales (hairy marginally) near the base of the corolla (Fig. 4). The origin of the nectar cannot be directly proven by the methods with a dissecting microscope but when shortly open corollas including the nectar are removed, a few minutes later drops can be observed on the whitish bulge at the base of the ovary.

Opening of the flowers ensues successively during the day, not synchronously. The opening of a single anther (from the base or from the tip) needs c. 1.5–4 hours (1.5–3, maximally 4 hours in the open, 2–4 hours under laboratory conditions). Anther opening starts on the first or second day of anthesis (not in the bud as Kirchner 1888: 556 and Knuth 1899: 106 wrongly write), occurs successively (Fig. 6) and usually all five anthers are open (Fig. 7) within two days (rarely one day).

The duration of anthesis apparently depends largely on weather conditions. The corolla wilts or drops off from day three to six after opening in unmanipulated flowers. In flowers which were manipulated to check anther dehiscence, the corolla dropped on day two on hot days, on day 5 under permanently cool weather and mostly on days three to four under intermediate conditions.

Thus anthesis of an individual flower lasts for c. (1?–)2–4(–5) days.

The flowering period of *S. officinale* in Graz lasts from end of April up to end of June or begin of July, in remontant (re-blooming) individuals up to August or September.

Furthermore, *S.* ×*uplandicum, S. asperum* and spontaneous backcrosses of *S.* ×*uplandicum* with *S. asperum* were grown. *S.* ×*uplandicum* was in all respects similar to *S. officinale* and Andrena symphyti was observed here too. *S. asperum* was never seen to be visited by A. symphyti.

Symphytum tuberosum is similar in floral ecological respects to *S. officinale*. The main differences are as follows. The sepals are 6.5–8.2 mm


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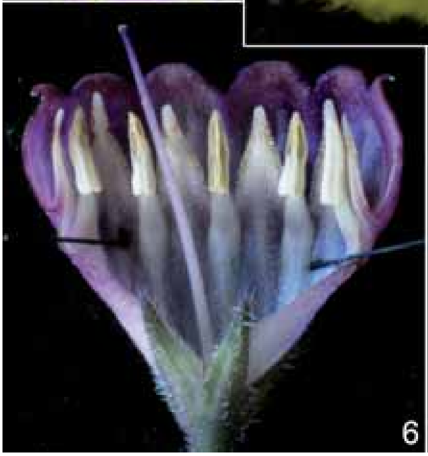
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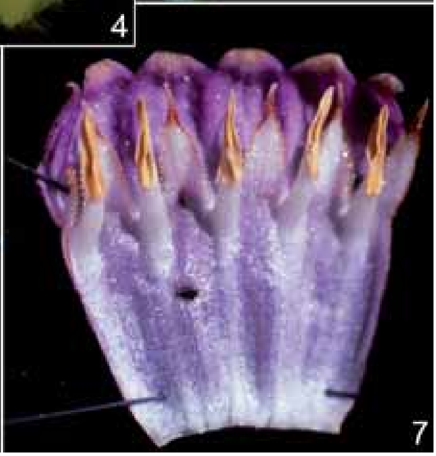
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Fig. 8–11. Andrena symphyti on *Symphytum officinale*. – Fig. 8. Pollen collection is interrupted by grooming pollen from the body and packing pollen into the transport structures. – Fig. 9–11. Concentrating nectar on the mouthparts. – Fig. 10–11. Packing pollen. – Fig. 10. The midleg transfers pollen to the hindleg. – Fig. 11. The hindlegs are rubbed against each other.

Fig. 1–7. *Symphytum officinale* (Fig. 4 excepted). – Fig. 1. Bud and flower. White arrow: entrance to a faucal scale, black arrow: upper limit of the corolla-filament-tube. – Fig. 2. View into the flower with the five converging faucal scales (note the space between the scales), style and stigma. – Fig. 3. Half of the corolla tube removed, converging faucal scales with bite marks of bumblebees in the distal part. – Fig. 4. *S.* × *uplandicum*, flower bud immediately before anthesis cut transversally near the base, nectar drops on the basal scales. – Fig. 5. Flower in early anthesis split longitudinally and opened, all anthers closed. – Fig. 6. Flower on the second day of anthesis, opened, one anther (left) at the begin of opening, two anthers open for $^{1}/_{2}$ it's length, one anther completely open, one anther (right) still closed. Bite marks on the faucal scales. – Fig. 7. Corolla on the third day of anthesis, all anthers open, the faucal scales with distinct bite marks of bumblebees.

Fig. 12–14. *Symphytum tuberosum*. – Fig. 12. View into flowers with the converging faucal scales (note the space between the scales). – Fig. 13. Flower in early anthesis, corolla split longitudinally and opened, all anthers closed. – Fig. 14. Ditto, later on the first day of anthesis, two anthers open, one half open, two anthers closed.

Fig. 15–18. Andrena symphyti on *Symphytum tuberosum*. – Fig. 15. Vibratory pollen collection. – Fig. 16. Nectar robbing. – Fig. 17. Two flowers with bite slits of Andrena near the corolla base and in the left one a bite hole of a bumblebee. – Fig. 18. Two bite slits of Andrena and one bite trace of a bumblebee. – In the flowers Fig. 17–18 one sepal each bent back manually.

long, connected basally for 0.5–1.0 mm (1.5–2 mm in fruit) bent outward or obliquely patent at anthesis (Fig. 12); during postanthesis the calyx is closed with sepals appressed together. The yellow corolla is c. 16.5–19 mm long, the entrance has c. 5–6.5 mm of diameter. The corolla-filament-tube measures c. 8.0–9.5 mm, i. e., c. one half of the tubular corolla.

The mature but closed anthers are c. 4–4.5 mm long (Fig. 13), the open ones c. 3–3.2 mm (Fig. 14) and the thick filaments measure c. 3–3.2 mm, the triangular faucal scales measure 6.0–7.5 mm (see Fig. 13, 14 and Troll 1928: 324–326) and allow an access between their distal halves (Fig. 12). Detachment of anthers from the filaments is much more difficult than in *S. officinale*. The style with the stigma is exserted.

Nectar secretion begins before corolla opening. The nectar appears as one or more drops above the basal scales (hairy marginally) of the corolla.

The opening of a single anther begins basally or apically (Fig. 14) and needs c. (1–)2–3(–4) hours. Opening of the five anthers of a flower begins at the first or second day of anthesis. The process of dehiscence of all five anthers of a flower may last one or two days. The anthesis of a flower lasts 3–4(–5) days.

The flowering period of *S. tuberosum* in the region of Graz lasts from mid of April to end of May or first days of June.

3.2. *Onosma* div. spec. (*Lithospermeae*)

The main characteristics of flowers with relevance to floral ecology are described in Teppner 1996, so that a relatively short statement may be sufficient here. A number of species were observed during the years, the most intensively studied ones are mentioned in chapter 2. Thus the characteristics are described in a more general manner, covering the species investigated.

Fig. 19–25. – Flowers of *Onosma* spec. div. – Fig. 19. *O. rigida*, two flowers of a cincinnus, entrance of the corolla, connivent anthers with connective tips and style. – Fig. 20. *O. paradoxa*, a flower on the first day of anthesis, corolla cut longitudinally and opened, anthers begin to open synchronously from the tips. Anthers connected side by side, one binding loosened manually. – Fig. 21. *O. isaurica*, corolla-filament-tube and corolla split longitudinally, anthers fully open and connected at their bases, style. – Fig. 22. *O. isaurica* view into the flower, “revolver” with five channels. In the centre the anther cone. – Fig. 23. *O. helvetica*, flower bud immediately before anthesis, cut transversally near the base, nectar drop on the basal scales and the corolla-filament-tube. – Fig. 24. *O. gehardica*, flower on the first day of anthesis (anthers $^2/_3{}^{rd}$ open), one nectar drop on basal scales and corolla-filament-tube, basal scales reaching the style. – Fig. 25. *O. erecta* subsp. *erecta*, calyx and corolla-filament-tube of a bud cut longitudinally, nectar drop on a narrow ring of basal scales and the corolla-filament-tube.

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Fig. 31. Bite slits of Andrena symphyti in the corolla-filament-tubes of *Onosma stojanoffii*. One sepal each bent back manually. – Fig. 32. Detail from Fig. 31. In the right flower three bites closely approximated.

Fig. 33. A worker bee of Bombus hortorum visits a flower of *Onosma gehardica*. The proboscis introduced in one channel of the flower shimmers through corolla and corolla-filament-tube (dark shade).

Fig. 26–30. – Andrena symphyti on flowers of *Onosma stojanoffii*. – Fig. 26. Vibatory pollen collection. – Fig. 27. Pollen grooming and packing. – Fig. 28. Nectar robbing. – Fig. 29–30. Nectar concentrating. – Fig. 29. Nectar regurgitated, drop on the galeae. – Fig. 30. Nectar drop swallowed.

The flowers are similar to *Symphytum* only superficially. There are many important differences. The free ± narrow triangular calyx lobes (connate in subg. *Aponosma* and other species not considered here) are stiff (Fig. 19, 33), often nearly cartilaginous basally, covered inside with long appressed hairs at least in the apical part and are appressed to the corolla (Fig. 25)! The pale to bright yellow corollas are usually 18–26 mm long and consist also of a corolla-filament-tube and an apical part of free corolla (Fig. 21). A ring of largely connected basal scales (glabrous, hairy in species not considered here), narrow or reaching the style, sits near the base of the corolla and covers the ovary (Fig. 23–25). The five anthers are connected at their base side by side (Fig. 20, 21) (connected along their whole length in species not considered here) and are bent towards the style (Fig. 19), forming a cone (movement of the style or of one anther leads to movements of the whole cone). The anthers are c. 6–10 mm long and end into a more or less long (0.5–2.0 mm), dry, membranous connective tip (Fig. 19–21). The style with the stigma is exserted.

Anthers, filaments and the inward protruding parts of the corolla-filament-tube form five separate entrances to the nectar, so the flowers have the characteristics of a revolver flower (Fig. 22). But the bees use only one entrance: either, they “know” that all entrances lead to the same nectar source or they learn so quickly that the other entrances of the same flower do not give additional nectar, that the observer has little chance to discern such a learning process.

The anthers of a flower develop synchronously and ripening and opening starts always from the tip (Fig. 20) and progresses successively to the base. The whole opening process of an anther needs two days, rarely one or three days (in evening-opening flowers) and the start depends on the beginning of the flower opening. Usually on the first day c. $^1/_2$ to $^1/_4$ of the anther length ripens and becomes open (Fig. 20 and Fig. 2 in TEPPNER 1996: 527), along the remaining basal part the process is continued on the next day.

Nectar secretion begins shortly before the opening of the corolla and the nectar appears usually as one drop on the basal scales (Fig. 23–25), it grows until it fills the whole flower base. Origin of the drops is also difficult to prove; after the removing of the corollas of shortly open flowers sometimes small droplets can be detected on the bulge at the base of the ovary.

Anthesis begins with the separation of the corolla tips. In some species (for e. g., *O. mattirolii*) the style-tip appears between the closed lobes shortly before opening. Anthesis lasts for c. 2–4(–5) days, then the corolla is seen wilting or dropping off.

Many *Onosma* species were grown during the past years, flowering time can be summarized as April to July, in remontant species (*O. echioides, O. rigida, O. heterophylla, O. frutescens* etc.) up to August or September.

3.3. *Cerinthe minor (Lithospermeae)*

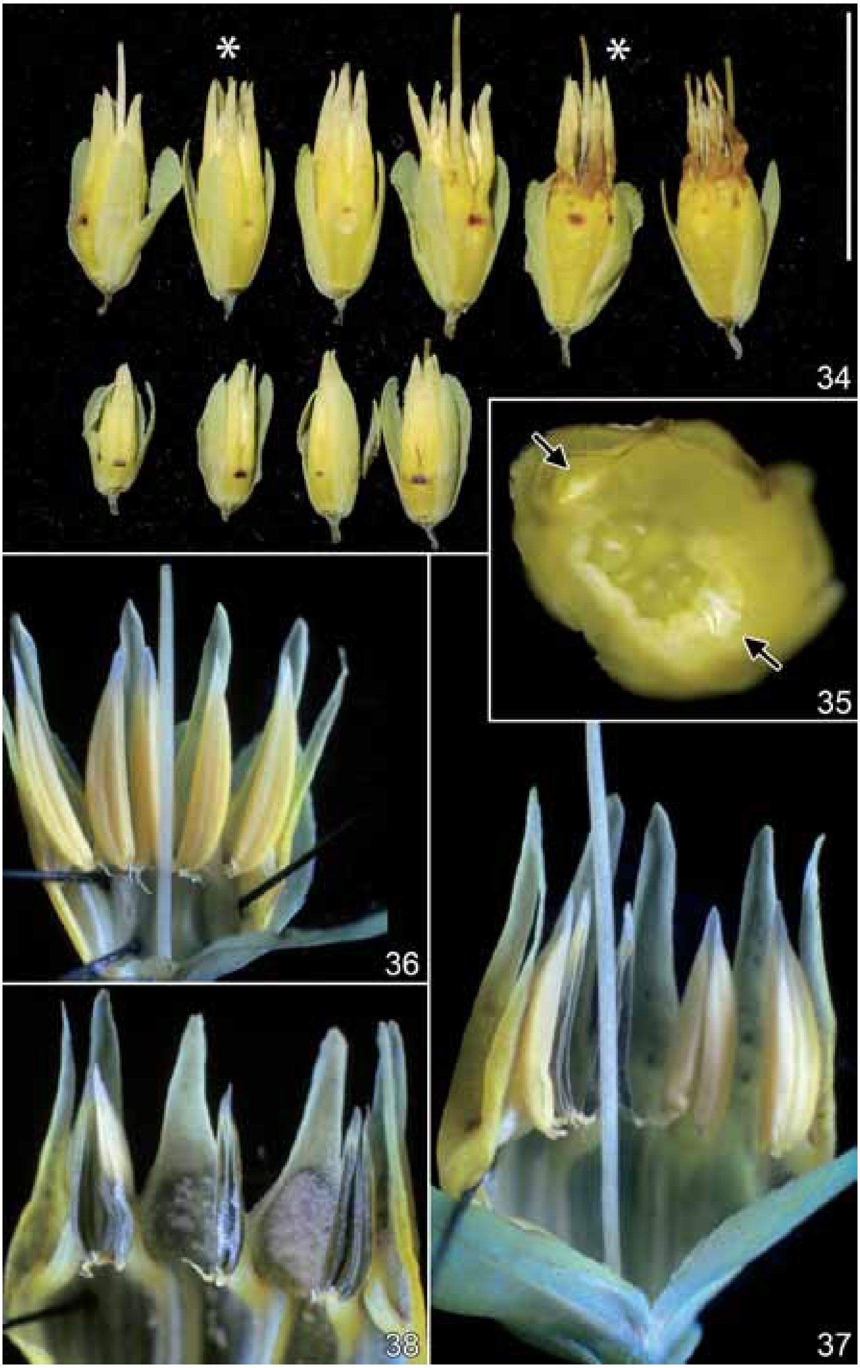
The broad, free sepals are delicate, glabrous on the faces (with minute hairs on the margin only) and up to c. 8–9 mm long (Fig. 34). The sympetal basal part of the corolla (approximately oviform) is formed mainly by the corolla-filament-tube; the depressions with the brown patches mark the insertion of the free parts of the filaments, thus also the upper end of the corolla-filament-tube. Distally a short corolla tube (c. 1.4 mm) and then the narrow triangular corolla lobes are developed (Fig. 34). The delicate lobes are bent inward marginally and thus canaliculate, overlap a little bit laterally and are bent to the centre like a cone, so that only a small opening remains [early in flower development, from c. (5–) 6 mm corolla length onwards, Fig. 34].

The full grown anthers are c. 5 mm (4.0–5.3) long (a sterile part of c. 0.7 mm and the connective tips of 0.2–0.3 mm included). The anthers are connected together basally by connective protrusions (basal tips of the thecae, the porting base of the fringes; not connected by the fringes itself) (Fig. 36, 37) and are also bent to the style forming a cone. The constriction of the corolla tube supports the anther cone. The filaments are short [(1–) 1.5–2.0 mm] and are inserted c. 1.0–1.5 mm above the anther base (Fig. 37, 38). The style with the stigma is exserted usually.

The nectar secretion in the flowers begins at a corolla length of c. 7 mm (fifth flower in Fig. 34). At this time the greenish lobes approximate to their final length, whereas the tube is short (c. 3.5 mm). Two nectar drops (Fig. 35) stand in the base of the flower on the ovary and the basal corolla scales or on the ovary only, usually above the furrow between the two mericarps grown together. Flowers at this stage are not visited by insects, thus the start of nectar secretion does not mark the start of anthesis. The following development is very gradual and is characterised mainly by a stretching of the corolla-filament-tube and a slow and indistinct change of the colour of the lobes from greenish to yellowish; the style stretches too so that the stigma lies at the height of the tips of the corolla lobes and later is exserted for up to 2.0 (–2.5) mm.

It seems that a corolla length of c. 9.0–9.5 mm (tube 4.8–5.0 mm, free lobes 4.5–4.7 mm), the turn of the colour of the lobes from greenish to yellowish and the appearance of the stigma between the tips of the corolla lobes, can be assumed as the begin of anthesis (sixth flower in Fig. 34). Soon stigmas can be exserted at this time. All anthers are closed (Fig. 36), thus the anthesis starts apparently with a female stage. The final length of the corolla is c. 11.5–12.0 mm (tube c. 7 mm, lobes 4.5–4.7 mm), or up to c. 8–10 mm in the last flowers at the ends of the cincinni.

The opening of the single anthers from the base to the top (Fig. 38; sometimes in the other direction too) lasts for 1–2 hours approximately. The five anthers open successively during 1–3 days. On the first day after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the supposed start of anthesis 0–4 (–5) anthers may open, mostly 1–3 (Fig. 37), the remaining anthers open on the second day (Fig. 38). Sometimes only the last anther opens during the third day (probably in the case of the start of anthesis late on the first day).

From the begin of the insect visitation the corolla lobes show an increasing number of brown marks, the larger ones (approximately 0.5–1 mm long and up to 0.8 mm wide) are bite marks (also on the anthers), whereas many small dots or small stripes come from the clasping of the bees with their claws (Fig. 34). Finally the bases of the corolla lobes are so chewed up, that the lobes often diverge. At this stage the flowers are no longer visited in spite of the remains of nectar at the flower base. Apparently the corolla persists during 1–3 days of postanthesis. Because of the indistinct and gradual transition between praeanthesis and anthesis as well as anthesis and postanthesis, the duration of anthesis of a single flower can only be estimated as three or eventually four days.

The plants in the Botanic Garden Graz grow within the natural area of *C. minor.* But actually only one small population is known within Graz. The flowering period lasts here from end of April to begin of July, in remontant individuals up to August.

4. Andrena symphyti
(A. subg. Euandrena, A. symphyti group)

4.1. Morphology, Activity Period and Activity Time

The body length of Andrena symphyti females measures c. 8.0–10.5 (–11.5) mm. It possesses a very short proboscis (Fig. 45) which measures c. 2 mm in length in extended condition (Fig. 30). The galeae (Fig. 46) are c. 0.9 mm long (without hairs), nearly glabrous on the upper side, have short, straight hairs on the outer margins; the long, slightly curved hairs on the tips are c. 200 μm long, this is approximately the width in the middle of a galea. Maxillary and labial palpi are much longer than the galeae (Fig. 45,

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Fig. 34–38. *Cerinthe minor.* – Fig. 34. Late developmental stages of flowers arranged according to age, the largest sepal removed. Flowers 1–4 (from below left) without nectar, 5–9 with nectar, 10 with remains of nectar only. From flower 6 on with marks of claws and/or biting marks. Flower 7: The first anther open for $^1/_4$. Thus flowers 1–5 are interpreted to be in preanthesis, 6–9 (asterisks) in anthesis and 10 in postanthesis. – The scale bar equals 1 cm. – Fig. 35. Flower on the first day of anthesis (one anther open), cut transversally near the base. Two nectar drops (arrows) on basal scales and ovary. – Fig. 36. Flower in early anthesis, split longitudinally and opened, all anthers closed. Three bindings at the anther's base loosened manually. – Fig. 37. Flower later on the first day of anthesis split longitudinally and opened, two anthers open, in the left anther opening starts at the base. – Fig. 38. Flower on the second day of anthesis, four anthers open, one opened in the lower half. During the preparation the large amount of powdery pollen has fallen into the grooves of the corolla.

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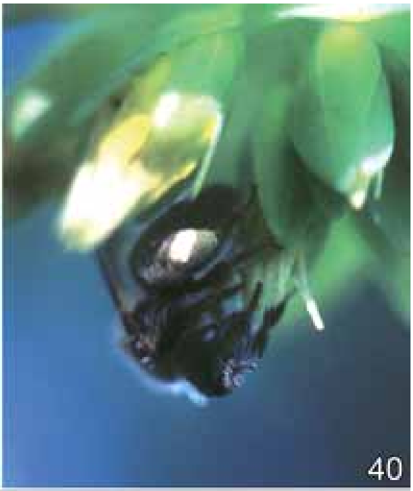

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46). If these characteristics are essential for the function of pollen collecting is not known. It could be that the glabrous upper side of the galeae and the nearly hairless palpi are important for the ability of nectar concentrating.

The basitarsus of the foreleg (Fig. 47–49) bears a brush of stout, straight, finely grooved, acute hairs as in other Andrena species too. There are no specialised hairs with curved or hooked tips, neither on the galeae and other parts of the proboscis (as in few other Andrena) nor on the palpi or on the forelegs (as in some other bees). Thus, in contrast to A. (Scoliandreana) osmioides COCKERELL 1916 (THORP 1979: 798) and A. (Didonia) nasuta GIRAUD 1863 (MÜLLER 1995), A. symphyti is not adapted to scrape pollen from anthers hidden in narrow corolla tubes.

Pollen is transported on the hindlegs only (Fig. 10, 16, 27, 28), in the corbicula on trochanter and femur (Fig. 50) and in the scopa on the tibia (Fig. 50, 51). The corbicula on the propodeum is covered with long, thin hairs on its surface [similar as in A. (Biareolina) haemorrhoa] and seems not to be used for the pollen transport in this species.

A. symphyti was seen in the Botanic Garden and in different parts of middle Styria between April 24 and June 8. Flower visitation was observed between 7:45 and 15:15 (CET, Central European normal time).

The main observations were made in the years 1996 and 2006. In 1994 and 1995 no A. symphyti was seen. 1997–2005 and 2007–2009 no observations were made too in spite of spot checks. In 2010 only two bite slits were observed on *Symphytum tuberosum* in the Botanic Garden, in spite of many controls on *Pulmonaria, Symphytum, Onosma* and *Cerinthe*. A key for an understanding of the strong fluctuations of the population size could be the fate of the nesting sites, but unfortunately not a single one has been discovered till now within the investigated area.

4.2. Pollen Collection

4.2.1. *Symphytum*

The females usually penetrate the flower of *S. officinale* and *S. tuberosum* with their head, the anterior part of the thorax and the forelegs (Fig. 15) and manipulate the faucal scales and the anthers by the man-

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Fig. 39–42. Andrena symphyti females and *Cerinthe minor*. – Fig. 39. Nectar robbing. – Fig. 40. Pollen collection. – Fig. 41. A single flower with a bite slit, one sepal bent back manually. – Fig. 42. A sample of corolla-filament-tubes and corolla with one to more bite slits.

Fig. 43. Anthophora plumipes female on *C. minor*, introducing the proboscis in the edge between two corolla lobes, during vibratory pollen collection. – Fig. 44. A worker bee of Bombus lapidarius, proboscis introduced under a corolla lobe, during vibratory pollen collection.

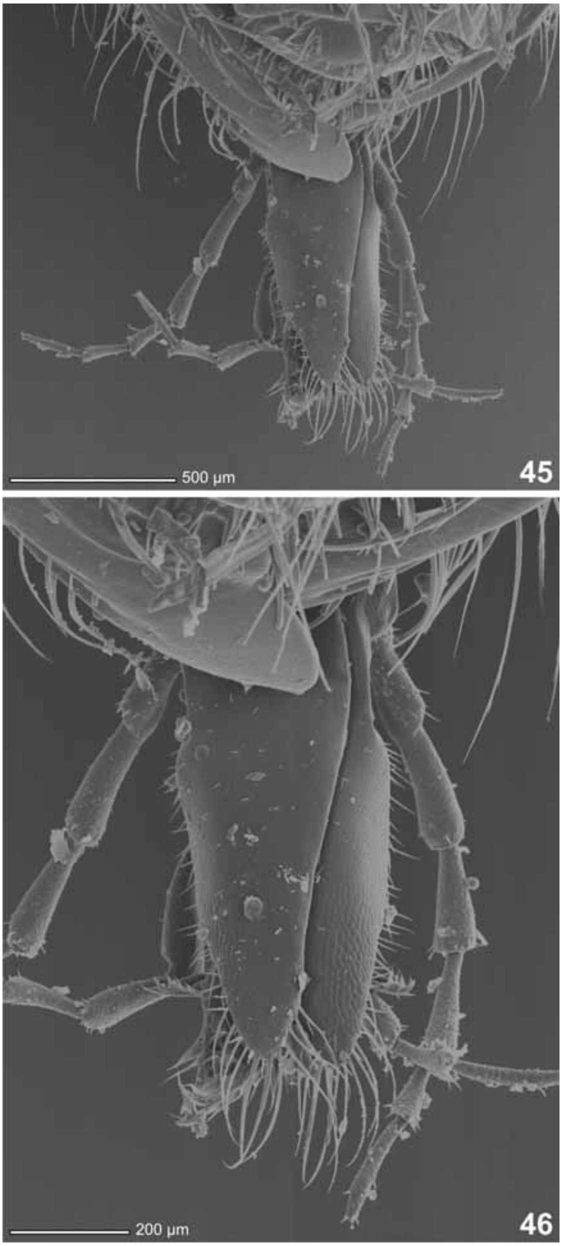


Fig. 45–46. Andrena symphyti female, mouthparts in front view, SEM images. – Fig. 45. Labrum, mandibles, galeae and palpi. – Fig. 46. Detail from Fig. 45: galeae and palpi. Tip of the glossa accidentally bent to the right side of the bee. – Phot. E. STABENTHEINER.

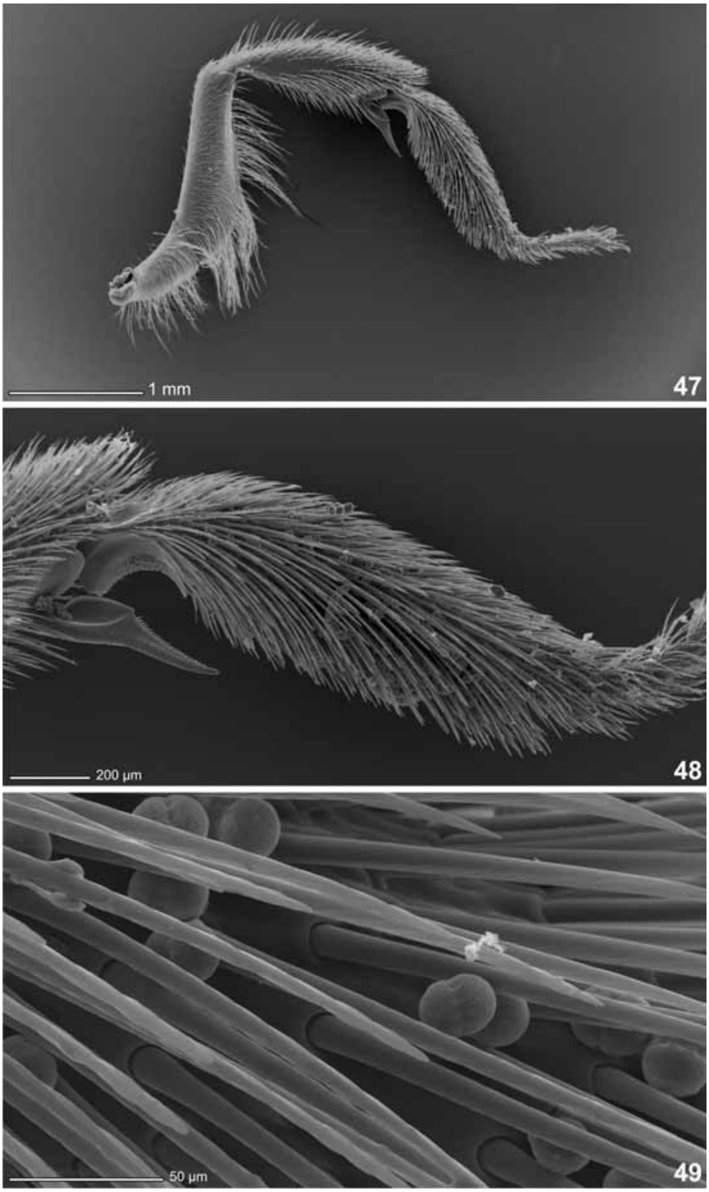


Fig. 47–49. Andrena symphyti female, SEM images of the left foreleg, anterior side. – Fig. 47. Overview. – Fig. 48. Basitarsus with a brush of stout, straight-tipped, simple hairs. Left the tibio-tarsal antenna cleaner (for the latter compare SCHÖNITZER & RENNER 1980: 122, 124 with A. ovatula as example). – Fig. 49. Detail of Fig. 48, simple hairs of the basitarsus and pollen grains of *Symphytum tuberosum*. – Phot. E. STABENTHEINER.

dibles (and the forelegs?). These activities in the interior of the flowers cannot be observed directly but can be concluded from the fact that sometimes in *S. officinale* anthers drop off during the manipulations of the bees (up to three anthers during one visit of one flower) and from the noises caused by the movements of the faucal scales. In *S. officinale* the anthers break off with relative ease from their filaments. Vibratory pollen collection is applied, often more than one sonication phase occurs during the visit of a flower altered with the mentioned manipulations. The scratching noises of the manipulations are often difficult to distinguish from the sonication. Pollen collection in a flower may be interrupted once or more than once by short backing off and grooming of pollen from the head and packing into the corbiculae on trochanter and femur as well as the scopa on the tibia in a curved (Fig. 8), rarely stretched position of the body. These manipulations must cause marks on faucal scales and anthers, but this is not to be discerned because of all possible marks are masked by the far overwhelming number of marks from the many visits of bumblebees and Anthophora plumipes.

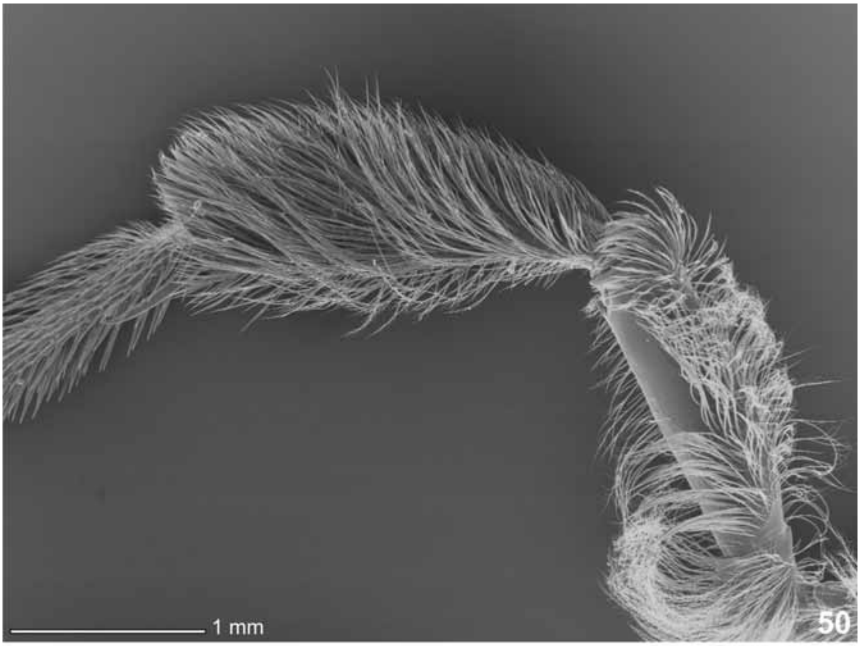
4.2.2. *Onosma*

For collecting pollen the bee penetrates the flower with head, anterior part of the thorax and forelegs (Fig. 26). The midlegs grasp within the corolla, on the reflexed bulge of the entrance or outside on the corolla. The head pushes against the style which leads to a movement of the anthers within the cone. The bee manipulates the anthers, whose dry, membraneous connective tips give a rustling noise. Buzzing (= sonication) is used in pollen collection. With some experience it is possible to distinguish between the rustling of the connective tips and the sonication. Pollen packing (Fig. 27) often interrupts the collecting.

Usually after pollen collection the bee turns for nectar robbing on the same flower but pollen cropping on more flowers (without nectar robbing in between) also occurs. The highest visitation rates were observed on *O. stojanoffii*, to a lesser extent on *O. kaheirei* and *O. mattirolii*.

4.2.3. *Cerinthe*

A. symphyti penetrates the flower between the delicate, narrow corolla lobes and manipulates the easily accessible anthers with the mandibles and the forelegs (Fig. 40). By the pressure of the head the style is often bent. Due to the more or less spread corolla lobes these manipulations can be seen directly. In *Cerinthe* pollen is effectively collected but an exact proof of vibration did not succeed because of the relatively small number of observations.



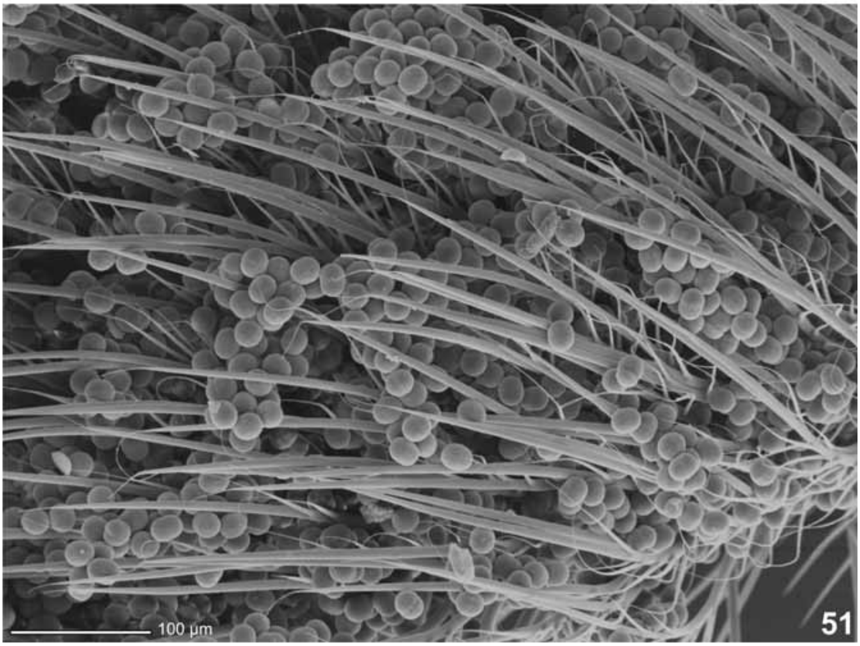


Fig. 50–51. Andrena symphyti female, SEM images of the right hindleg, anterior side. – Fig. 50. Trochanter and femur with corbicula, tibia with scopa and basitarsus. – Fig. 51. Detail of a tibial scopa with hairs branched near the base, filled with pollen of *Symphytum tuberosum*. – Phot. E. STABENTHEINER.

4.3. Nectar Robbing

Because of the short proboscis and the long corolla tubes of the pollen sources, the whole need of nectar for the short-tongued (Fig. 30, 45) A. symphyti must be covered by nectar robbing. The females put their body between calyx and corolla and bite a characteristic transversal slit near the base of the corolla-filament-tube. The males, patrolling between the potential plants, from time to time also suck nectar in the same manner as the females. Since the males appear prior to the females, they should be able to bite the slits themselves. In A. subg. Taeniandrena the biting of the males was observed directly (chapter 6.1.).

4.3.1. *Symphytum*

Usually after vibratory pollen collection from a flower, A. symphyti females turn to the base of the flower for nectar robbing. But also more than one flower can be visited for nectar, without pollen collecting in between. The bee pushes itself to the base of the flower which is not very difficult because of the ± diverging calyx lobes. Nevertheless some efforts are necessary: often vehement struggling of the hind and middle legs against the corolla to force the head under a sepal, can be seen. Reaching the correct position, the bee bites the characteristic transversal slits c. (1.6–)2.0–2.8 mm above the corolla base (Fig. 16).

The characteristic bite slits (Fig. 17, 18), distinctly different from the bite holes of bumblebees, usually permit to prove the presence of a bee before they can be seen. So the distribution of A. symphyti can be recorded at every daytime and also in short periods of bad weather conditions (for 1–2 days, not longer, then the method becomes imprecise, because of the dropping off of the corollas). The bite holes of bumblebees were not used by A. symphyti.

4.3.2. *Onosma*

After collecting pollen in a flower or independently from it, A. symphyti turns to the calyx and tries to penetrate between a sepal and the corolla. This seems to be troublesome for the bee, not only due to the stiff sepals but most probably also due to the long stiff hairs on the inner side of the sepal tips (oriented to the tip, i. e. against the bee). Often more than one attempt is necessary to put the head under a sepal. When successful, the bee pushes itself to near the base of the corolla-filament-tube (Fig. 28) and bites the characteristic transversal, c. 1 mm long slit c. 2.5–4.3(–6.1) mm above the base (Fig. 31, 32).

Biting holes of other insects were very rare in our cultivated plants and no perpetrator nor user was seen during the years.

4.3.3. *Cerinthe*

In *Cerinthe minor* A. symphyti clambers (often after pollen collecting) to the base of the flower and then forces itself between calyx and corolla so that one sepal is raised; because of the glabrous, delicate calyx this does not seem to be difficult. Then the bee bites the transversal slit c. 1–3 mm above the corolla base (Fig. 39, 41). The bees apparently do not use the slits of their predecessors, so not only one, but 2–3 or more biting slits in one corolla are possible (Fig. 42).

4.4. Nectar Concentrating

During the visitation of *Onosma* and *Symphytum* flowers, concentrating nectar by bees could be observed (Fig. 9–11, 29, 30). After visits on a number of flowers the bee chooses a sunny place on the plant or elsewhere within the area of the plants. The mouth parts are stretched, the nectar is regurgitated, pushed up to the galea tips (Fig. 9, 29), exposed to the sun, swallowed again (Fig. 30), regurgitated once more etc. The durations of these concentrating procedures, with rhythmic movements of the mouthparts, were observed for five to ten minutes, sometimes also longer. During this behaviour, grooming of pollen from the body and pollen packing into the corbiculae and scopae also occurs (Fig. 10, 11).

5. Other Visitors

In Central Europe the main pollinators of *Symphytum, Onosma,* and *Cerinthe* are the polylectic (generalists) Anthophora plumipes and some Bombus species. They collect nectar and pollen during the same visit, pollen usually by buzzing.

5.1. *Symphytum*

The main visitors, Anthophora plumipes females (to a lesser extent males) and queens and worker bees of Bombus terrestris s. l. (means B. terrestris s. str. and B. lucorum), B. pratorum, B. hypnorum, B. pascuorum and B. hortorum put – depending on the body size - head, thorax, and forelegs into the corolla. For vibratory pollen collection, additionally to the legs, they tightly hold onto the flower by biting the faucal scales and anthers (bite marks: Fig. 3, 6, 7). Besides this Bombus terrestris sometimes also uses a second method: the bees press the entrance of the corolla against the lower side of the body, bite on the outside of the corolla and then sonicate (e. g. King 1993: 44–45). B. hypnorum sometimes rotated on a flower using a number of buzzes. More or less high numbers of flowers can be visited for nectar only (empty of pollen already?); this is given at least in the case of diverging-wing habit (not closed over the back) during the visit.

The short-tongued B. terrestris and most probably B. pratorum (compare for e. g. MÜLLER 1873) are primary nectar robbers and bite holes in the corolla-filament-tube which are used by secondary robbers too (B. hypnorum, abundantly by Apis mellifera, rarely also by syrphid flies). Nectar robbing Bombus collect pollen too, thus are also pollinators. Very surprising is the note of GOULSON & al. 1998: 504, that bumblebees did not collect pollen at the time of their experiments. During the present studies the bumblebees collected pollen during the whole season (with little variance depending on daytime and weather). The availability of pollen per flower is usually not considered in floral ecological studies. The percentage of flower visitations with buzzing during the day (CORBET & al. 1988: 150–151) reflects the prevailing daytimes with anther opening.

The following bees were observed as more or less sporadic visitors: Bombus haematurus worker (*S. o.*, TEPPNER 2010), Eucera nigrescens male (*S. o.*), Megachile ericetorum male (*S. o.*), Megachile willughbiella female and male (*S. ×u.*, nectar robbing), Andrena nitida female (*S. t.*), Halictus spec. female (*S. o.*, vibratory pollen collection), Nomada flava female (*S. ×u.*)

5.2. *Onosma*

The flower visitors – very different in the cultivated plants in Central Europe and within the natural distribution area of *Onosma* (in Greece) – are treated in TEPPNER 1996. Visits of Eucera nigrescens males for nectar in the Botanic Garden can be added. The bees reach the nectar through one of the fife “channels” of the flower (Fig. 33).

The nectar robbers in *Symphytum* collect only pollen in *Onosma* and do not perforate the corolla-filament-tubes (TEPPNER 2005, BRIQUET 1896: 355). Only one author maintained, that B. terrestris should be a robber in natural stands of *O. helvetica* BOISS. near Bozen (SCHULZ as *O. “stellulata”*, cited after KNUTH 1899: 112).

5.3. *Cerinthe*

The main pollinators are Anthophora plumipes females (to a lesser extent males) and workers of Bombus pratorum and B. pascuorum (rarely also queens). The bees introduce the proboscis in the edge between the corolla lobes (Fig. 43) or under a lobe and then raise the lobe (Fig. 44). The bees bite the base of the corolla lobes or the freely accessible anthers and then vibrate the flowers for pollen. B. pratorum was observed sporadically to rotate partially or completely around the flowers. In visits without vibration only nectar is sucked. The visits occur so quickly, that for the details of the behaviour a special study would be necessary.

Sporadic visitors are Bombus hortorum, B. hypnorum and B. lapidarius workers, Osmia cornuta and O. bicornis (=rufa) females. Osmia cerinthidis (known to occur in Styria: SCHWARZ & al. 1996: 310), oligolectic on *Cerinthe*, was never seen, neither at the natural stand in Graz-Fölling nor in the Botanic Garden. Apis mellifera, mentioned by MÜLLER 1882: 9–14 and KRAUS 1996: 111, was never observed. This is especially curious, because *Cerinthe* pollen can reach high percentages in some Austrian honey types (FOSSEL & RUTTNER 1966). Does the high visitation rate of Anthophora and bumblebees make the flowers unattractive?

6. Nectar Robbing by Other Andrena Species

6.1. Andrena subg. Taeniandrena

Nectar robbing after longitudinal splitting of the calyx by the mandibles in some *Fabaceae* is well documented in the literature for A. lathyri ALFKEN 1899 (A. lathyri group; WESTRICH 1989: 271, 272). Own experience with this species in the Botanic Garden in Graz showed these activities of males and females in *Vicia sepium* and *V. sativa* flowers.

Fig. 52. Andrena ovatula female on a flower head of *Trifolium pratense*. The bee has split open the corolla tube on the left side of a flower nearly to the base and now sucks the nectar.

A. ovatula KIRBY 1802 and A. similis SMITH 1849, both from the A. ovatula group (s. str., SCHWARZ & al. 1996: 26–27), visit a number of *Fabaceae* genera. When seeking on *Trifolium pratense* (Red Clover) the bee is confronted by another problem: The calyx is relatively short, but in *Trifolium* the long corolla is united – in contrast to most other *Fabaceae*. So the bees (males and females) bite with the mandibles on one side of the flower in the edge between standard and wing petal (the same place on which the corolla would tear if one would pull apart the standard and the wing-keel-complex). With the mandibles the bee cuts the corolla tube and proceeds near the base of the corolla for sucking the nectar (Fig. 52). In a flower head visited by A. similis containing 78 flowers, 9 of them were split on the left side, 12 on the right and 2 on both sides. Another head with an actual visit of A. ovatula showed a similar situation.

The action of these bees is also a longitudinally splitting of narrow, tubular flower organs (calyx or corolla) for reaching nectar which, otherwise, would not be accessible for these short-tongued bees. Pollen collection (A. ovatula: Fig. 9 in TEPPNER 2003) occurs as to be expected without buzzing.

6.2.

For other Andrena groups I could not find any information about nectar robbing.

7. Discussion

7.1. Notes on Andrena symphyti

A. symphyti was known till now only from *Symphytum* with *S. tuberosum* as the main pollen and nectar source and *S. officinale* as an additional one (e. g., DUCKE 1900: 9 , SCHMIEDEKNECHT 1930: 918, WESTRICH 1989: 539). EBMER 2009: 61 indicates *S. bulbosum* SCHIMP. A. symphyti visits both, *S. tuberosum* and *S. officinale*, as well as *S.* × *uplandicum* in the same manner, depending on the availability of their flowers. The use of *Cerinthe minor* was recorded for the first time by KOCOUREK 1966:64 without any details. The visits on cultivated *Onosma* were mentioned for the first time in TEPPNER 2005: 230 and a photo was published in TEPPNER 1997: 21. It is worth mentioning that A. symphyti subsp. symphyti occurs also in Greece (rich in *Onosma* species, TEPPNER 1991) and the distribution area of subsp. furcata FRIESE 1921 covers the diversity centre of *Onosma* in Anatolia up to the Caspian Sea (map of A. symphyti: GUSENLEITNER & SCHWARZ 2002: 1186, maps of *Onosma*: MEUSEL & al. 1978: 361, 362). Thus observations from these parts of the natural area would be highly desirable. Oligoleges may have often access to only one of the possible pollen hosts and thus seem to be monolectic. “Where closely related pollen hosts bloom together, specialists typically use all of them.” (WCISLO & CANE 1996: 262).

For the visits on *Spiraea* and *Gentiana* flowers (KOCOUREK 1966:64) no details, e. g., if nectar or pollen was collected or the females have bathed in the sun only, are mentioned. Before *Symphytum* blooms, A. symphyti males visit flowers of *Ajuga reptans, Nonea pulla* or *Gentiana* (KOCOUREK 1966: 64).

My first observation of an A. symphyti was that of a nectar robbing female on *Pulmonaria officinalis* (*Boragineae*) in 1993; in spite of many controls of the flowers for the bee and for the bite slits at the original, natural stand and in the Botanic Garden I have not found any trace on *Pulmonaria* in all the years since then. May be that the secondary compounds are sufficient as attractants but that the inability of the bee to scrape pollen from the narrow tube, especially in pin-eyed flowers (cf. chapter 4.1.), leads to the abandonment of *Pulmonaria* flowers usually.

Finally, in this paragraph, a speculation should be permitted. The nectar robbing bumblebees of *Symphytum* do not learn or are not "willing" to perforate the corolla-filament-tubes of *Onosma*, protected by the stiff and setose sepals. Why does A. symphyti, also coming from *Symphytum* with flowers easier to handle, learn this? Isn't it more probable that A. symphyti brings along this ability due to its evolution in an *Onosma*-rich area?

7.2. Anthesis and Pollen Portioning

Variability in flower longevities is hardly considered in studies of floral ecology in spite of its consequences for pollination (PRIMACK 1985: 15, 35). The genera investigated here show a medium range of flower longevity (compared to table 1 in PRIMACK 1985:17).

In the last decennia much has been written about pollen portioning. So the impression could arise, that this must be an exceptional phenomenon. The contrary is true, I would estimate that pollen portioning in any form is the rule and the cases with simultaneously presentation of the whole pollen mass of a flower [as, for e. g. in *Hedera helix* (TEPPNER & al. 2009), *Mimosa pudica, Papaver, Campanula* and *Lilium* (the anthers of a *L. candidum* flower need in the morning c. $^1/_2$ hour for the simultaneously expanding of the theca valves of all six anthers, then the whole amount of pollen is presented)] are the minority. In all three genera, *Symphytum, Onosma* and *Cerinthe* pollen portioning is essentially pollen packaging in the sense of HARDER & THOMSON 1989. The three possess streukegel blossoms (= scatter-cone-blossoms) with nectar (*Borago* flower type: FAEGRI 1986). Most deviating from the other two is *Cerinthe* in having a short free corolla tube and long, narrow corolla lobes. In *Symphytum* the anther cone is more complex due to the support of faucal scales (see SCHAEFER 1942).

In all the three genera flower opening is scattered during the day. Thus a sort of portioning of the resources on the level of the flower is given.

Within a flower, each anther opens relatively quickly in *Symphytum* and *Cerinthe* (within 1–4 hours) and thus contribute little to pollen portioning; therefore if one opens the flowers accidentally, the probability to find incompletely open anthers is not high. The pollen portioning is given mainly by the successive opening of the five anthers of a flower within (1–) 2 (–3) days. Interesting is also the completely different way of pollen portioning in *Onosma* (*Onosma* and *Cerinthe* belong to the same tribe *Lithospermeae*), in which the anthers of a flower ripen and open completely synchronous and need for the complete opening approximately the same time span as *Cerinthe* (or *Symphytum*) for the successive opening. So at the end of the first day of anthesis often the part above the filament insertion only is open. The same effect is achieved with completely different methods in *Symphytum* and *Cerinthe* on the one side and *Onosma* on the other! In a figure of a *Lithospermum officinale* flower in SONNBERGER 2002:7 one anther is drawn open, the other four closed; this suggests successive opening, but the text reads as synchronous opening would occur.

7.3. Pollen Collection

A note on the terminology and a summary about the mechanism of vibratory pollen-collection (buzz-collection, sonication) is included in TEPPNER 2005: 219, 228-229. For the mechanics also the papers of KING & al. 1996, KING & BUCHMANN 1996 and 2003, not cited therein, are of great interest. The use of this technique by different bee groups is apparently very different.

In Andrenidae s. str. vibratory pollen collection is not often recorded. Within Andrena itself the North American A. (Melandrena) hilaris SMITH 1853 collecting pollen on *Vaccinium ashei* READE is probably the only proven record for vibratory pollen collection (NEFF & SIMPSON 1988: 242). CANE & al. 1985 were not able to decide if A. (Andrena) longifacies LA BERGE 1980 uses buzzing on *Vaccinium stamineum* L., in Tab. 2 (p. 137) they mention one record of buzzing for another Andrena species, but the species name seems not to be indicated.

A. symphyti manipulates the anthers with the mandibles (and forelegs ?) which is acoustically discernible by the noises from the movements of the faucal scales in *Symphytum* and the dry connective tips in *Onosma* as well as by the occasional dropping of of anthers in *S. officinale*. Besides this, vibratory pollen collection is used with one or more buzzes during one visit. Bending back of the body for grooming and packing of the pollen interrupts these actions. It is often difficult to distinguish between the noises from the manipulations and the sonication. With a little experience this is possible in the moments, when vibrations by bumblebees and contamination by noises in the surroundings are low.

Grooming of pollen from the body and packing of pollen into the corbiculae and scopae is also practised between flower visits and during nectar concentrating.

The question remains if A. symphyti is a good pollinator. Most likely this should be possible in *S. officinale*, which has relatively short styles and a stigma position more or less at the level of entrance into the corolla. In the other cases with longer styles there is a high probability that the stigma may miss the body of the bee; but pollen shaking out from the flower during manipulation and buzzing may reach the stigma and effect fertilization in the case of self-compatibility (at least in *Onosma*). If the stigma touches the head as in Fig. 27, pollination apparently occurs.

7.4. Nectary, Nectar, Nectar Robbing and Concentrating

In all three plant genera nectar secretion begins before anthesis and the drops appear on the basal scales. In *Symphytum* and *Onosma* the start of anthesis is clearly marked by the begin of the separation of the corolla lobes. Contrarily, in *Cerinthe* with its loose tapering and continuously developing corolla lobes the exact start of anthesis is masked by the early inset of nectar secretion. Since SPRENGEL 1793: 93, BEHRENS 1879: 245–246 and LOEW 1886: 173 (BONNIER 1879: 124–125 for other *Boraginaceae*) the generally accepted dogma is that nectar is produced by the bulge on the base of the ovary (nectary disc in HILGER 1985) but the exact place of origin is difficult to prove by the method of dissection under a dissection microscope. In *Symphytum* after removing the corolla, drops appear on the bulge, so it seems to be sure that this opinion is correct. In *Onosma* we have apparently the same situation but this is more difficult to prove because of lesser secretion after removing corollas; so secretion by the basal scales is also assumed in the literature (GÜRKE 1894: 124, 126, BRIQUET 1896: 356, RIEDL 1962: 54). FREI 1955: 93, TĂCINĂ 1973 and HILGER 1985: 343, 345 demonstrated the probability of nectar secretion of the nectary disc by anatomical methods, whereas SCHAEFER 1942: 319–320 ascertained the improbability of nectar secretion by the basal scales by anatomical methods too. The term annulus nectarifer / nectariferous ring for the basal scales (e. g. RIEDL 1962, 1967) is correct, if it is taken literally, not in the sense of nectar production. In *Cerinthe* the two nectar drops stand above the furrow between the two united mericarps, so that this (its outer side) should be the place of production. A reinvestigation of nectaries, their stomata and nectar secretion with modern methods (such as e. g. by WERYSZKO-CHMIELEWSKA 2003 for *Myosotis, Cynoglosseae* s.l. or GAFFAL & al. 1998 for *Digitalis, Antirrhinaceae*) would be not out of place.

Measurements of the fluctuations of the nectar volume between plants and between flowers of one plant (clearly present also in our material) as made by GILBERT & al. 1991 for *Cerinthe major* were out of the scope of our investigations. The discrimination of flowers on *C. major* by Anthophora plumipes is interpreted there as discrimination for nectar. I think, that the discrimination for pollen is more important and may be the reason that late anthesis flowers are not visited by Anthophora and bumblebees in spite of remains of nectar. BOËTIUS 1948: 292–294 has found a higher concentration of sugar in the nectar of *Symphytum officinale* during dry weather. According to the same author, nectar secretion in *S. asperum* decreases during anthesis (p. 262–264). Nectar amounts at one given time are indicated by GOULSON & al. 1998: 506 for *S. officinale* (0.26 µl in average). BRIQUET 1896: 356 indicated 2–3 mm^3 in *Onosma vaudense* GREMLI (= *O. arenaria* W. K. s. l.).

The movements of the mouthparts during nectar sucking are described by HARDER 1983 with the aid of Andrena (Melandrena) carlini COCKERELL 1901.

The nectar robbing by Andrena symphyti is proven here (as I know) for the first time. Probably the first hint is given by SCHREMMER 1955: 567-568, Fig. 12c; he depicted a bee on the way to the base of the corolla of *Symphytum officinale*, claiming to be a Halictus and erroneously indicating the use of bite holes of bumblebees by this bee. It is highly probable, that SCHREMMER described A. symphyti. Mag. F. GUSENLEITNER, as an Andrena specialist, has checked this figure and is also of the opinion (in litteris, 2010) that this never can be a Halictus; he suspects that the figure shows A. symphyti, but an exact determination of the species is not possible, because no morphological details are discernible.

Nectar robbing by Andrena as known till now is made by longitudinal splitting of tubular floral organs (see chapter 6.1.). Thus the biting of transversal slits near the corolla base by A. symphyti is a completely different method recorded here for the first time. The slits are also distinctly different from the often roundish bite holes of bumblebees and are in a different position, much nearer to the corolla base than the holes of bumblebees. All robbing Andrena species mentioned are primary nectar robbers (for the term see for e. g. GERNER 1972: 34, 36 or INOUYE 1980 and 1983: 153–155).

Concentrating nectar is widely distributed in bees. WESTRICH 1989: 273 mentions especially Hylaeus, Lasioglossum and Xylocopa and describes the process for the honey bee.

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