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Pollinators of Tomato, *Solanum lycopersicum* (*Solanaceae*), in Central Europe

By

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With 15 Figures

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Summary

TEPPNER H. 2005. Pollinators of tomato, *Solanum lycopersicum* (*Solanaceae*), in Central Europe. – *Phyton* (Horn, Austria) 45(2): 217 – 235, with 15 figures. – English with German summary.

The floral-ecology of *Solanum lycopersicum* L. (and *S. pimpinellifolium* JUSL.) was investigated on stands in two gardens in Graz (Styria, Austria, Central Europe). The anthesis of the individual flowers lasts two, partly up to three days, the anthers open from morning till afternoon of the first day. Typical buzz-collectors are the workers of four *Bombus*-species (main pollinators *B. pascuorum* and *B. terrestris*, third place *B. lapidarius*, rarely *B. sylvarum*) and *Megachile willughbiella*-females, the latter are also important tomato-pollinators. From the smaller bees the females of *Hylaeus gibbus* are good pollinators. In five *Lasioglossum* species buzzing is followed by the scraping-off the pollen adhering to the anther tube from their own vibration. The smallest bees which use buzzing are *Lasioglossum morio* and *L. politum* (body length c. 5–6 and 4–5 mm respectively), but because of the low sound it was not possible to observe the proportion of buzz-collection in relation to the scraping of pollen and gleaning. In the smallest species, *L. politum*, buzzing could be inferred only indirectly.

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Zusammenfassung

TEPPNER H. 2005. Bestäuber der Tomate, *Solanum lycopersicum* (Solanaceae), in Mitteleuropa. – *Phyton* (Horn, Austria) 45(2): 217 – 235, mit 15 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Blütenökologie von *Solanum lycopersicum* L. (und *S. pimpinellifolium* JUSL.) wurde in den Beständen in zwei Gärten in Graz (Steiermark, Österreich) untersucht. Die Anthese der einzelnen Blüten dauert zwei, zum Teil auch drei Tage, die Antheren öffnen sich vom Morgen bis zum Nachmittag des ersten Tages. Typische Vibrationssammler sind die Arbeiterinnen von vier *Bombus*-Arten (Hauptbestäuber *B. pascuorum* und *B. terrestris*, am dritten Platz *B. lapidarius*, sehr selten *B. sylvarum*) und die Weibchen von *Megachile willughbiella*, ebenfalls wichtige Bestäuber der Tomate. Unter den kleineren Bienen sind die Weibchen von *Hylaeus gibbus* gute Bestäuber. Bei fünf *Lasioglossum*-Arten folgt auf die Vibration das Absammeln des Pollens, der aufgrund der eigenen Vibration an oder in der Antherenröhre haften blieb. Die kleinsten Bienen, die Vibration einsetzen, sind die Weibchen von *Lasioglossum morio* und *L. politum* (Körperlänge ca. 5–6 bzw. 4–5 mm); leider war es wegen des sehr leisen Summtones nicht möglich, den genauen Anteil von Vibrationssammeln im Verhältnis zum Absammeln und Nachsammeln des Pollens zu ermitteln. Bei der kleinsten Art, *L. politum*, ist Vibration nur indirekt erschlossen worden.

1. Introduction

Lycopersicon MILLER as a separate genus is convenient for practical reasons. However, from the results of molecular analyses (e.g. SPOONER & al. 1993, OLMSTEAD & al. 1999, BOHS & OLMSTEAD 1999, CHILD & LESTER 2001) as well as anther morphology and anatomy (HARVEY 2004) natural relationships of tomatoes and related wild species clearly lie within *Solanum* L. subg. *Potatoe* (G. DON) D'ARCY sect. *Lycopersicum* (TOURN.) WETTST. and a separate genus can no longer be maintained.

The flowers of *Solanum* are nectarless pollen-only blossoms (*Solanum*-type of pollen-only blossoms after VOGEL 1978: 90). In *Solanum* sect. *Lycopersicum* the anthers are laterally bound together along the whole length to a tube by interlocking of the hairs in the dorso-lateral stripes of short hairs of adjoining anthers (sometimes also by ventro-lateral hairs) (e.g. BONNER & DICKINSON 1989, HARVEY 2004: 102–106, 126, SEM-images: ENDRESS 1994: 152). The thecae dehisce by longitudinal slits where the distal end dilates to form a pore-like opening (SEM-image: BONNER & DICKINSON 1989: 109); the pollen is released into the tube. Since the apical end of the anther is made up of a, more or less, long sterile part, usually the openings are not directly accessible for the pollinators.

The styles are exerted in self-sterile taxa and exerted or included in the anther tube in self-fertile ones. A summary of the importance of style length for pollination and fertilization type (self or cross) is included in TEPPNER 1993: 193–194, 205–206, see also RICK & DEMPSEY 1969.

The pollen retained in the anthers and the anther tube can be collected in a reasonable way only by bees with the ability of buzzing or buzz-collection. In the literature the term buzz pollination (BUCHMANN 1983; Vibrationsbestäubung WAGENITZ 2003: 346) is customary but it is not precise, because the buzzing is necessary only for the collection of pollen and not for the pollination. Thus, ROUBIK 1989: 48–49 uses buzz-collecting and buzz-collection and in TEPPNER 1993 the term “Vibrationsssammeln” was used. PROCTOR & al. 1996: e.g. 125, use vibratory pollen-collection and buzz-foraging along with buzz-pollination. Within the distribution area of the wild tomatoes in S. America, 17 species of bees out of 10 tribus are known as pollinators (RICK 1950, RICK & al. 1977, 1978; list in TEPPNER 1993: 207).

Because of the nearly world-wide distribution of *Solanum* species and other species which need buzz-collection (mainly streukegel-blossoms or flowers with poricidal anthers), tomatoes easily find facultative pollinators from the native bee faunas all over the world. Foremost all bumblebees are to be mentioned, of which commercially produced colonies of *Bombus terrestris* are used for pollination in industrial tomato-fruit production (e.g. DE RUIJTER 1997, VAN RAVESTEIJN & VAN DER SANDE 1991; short summary in MACFARLANE 1995: 33; *Bombus hypocrita* and *B. ignitus* in Japan: ASADA & ONO 1997, *B. impatiens* and *B. bimaculatus* in N. America: KEVAN & al. 1991; inhibition of queen hibernation: RÖSELER 1985).

In the years 1992–1997 special attention was given to the pollination of *Solanum lycopersicum* by wild bees in the Botanic Garden of the Institute of Botany and in a private garden in Graz (Styria, Austria) (for many days during the seasons; sporadic observations up to 2005). Surprisingly, in addition to the bumblebees, seven further species of bees were observed as more or less regular pollinators.

2. Material and Methods

The cultivated tomato species and cultivars were the same as listed in TEPPNER 1993: 192 plus some *S. lycopersicum* L. cultivars such as ‘Supersteak’, ‘Lukullus’, ‘Gardeners Delight’, ‘Blondköpfchen’ and others. *S. lycopersicum* ‘Mirabell’ is remarkable for its large numbers of flowers (up to more than 400 per axillary inflorescence). *S. pimpinellifolium* JUSL. refers to the Piura-Lambayeque-Type (large flowers, exerted styles). Indication of time is Central European normal time (CET). Vouchers of bees were determined by specialists (see acknowledgements) and are preserved in the collection of the author. Nomenclature of bee species follows SCHWARZ & al. 1996.

3. Anthesis

In our material on summer days (July, August) anthesis lasts usually two days, to a lesser extent three days. Splitting of the corolla often begins

on the evening before anthesis, in some cultivars ('Bonner Beste', 'Lukullus', San Marzano-Type) up to two days before anthesis. In the latter case it can be difficult to define the begin of anthesis; the day with wide-open corolla with reflexed lobes and with the turn of corolla colour from greenish to yellow was regarded as the first day of anthesis; in the stages before no insect visits were observed. Opening of the corolla takes place between 5:00 and 10:00 a.m., the daily closing of the corolla occurs between 14:00 and 19:00 p.m. Anthers open at the first day of anthesis between 6:30 a.m. and 16:00 p.m. Details in table 1. SMITH 1935: 6-7 reported an average of four days anthesis and anther opening beginning on the second day of anthesis (in some cases on the first day). This is in considerable contradiction to our results.

Table 1. Anthesis in *Solanum pimpinellifolium* and *S. lycopersicum* in the open during summer 1992

	Anthesis days	Corolla opening	Corolla closing	Anthers opening (first day)
<i>S. pimpinellifolium</i> Piura-Lambayeque-T.	2(-3 ¹)	5:00 – 8:00 (-9:00)	14:00 – 19:00	7:30 – 14:00
<i>S. lycopersicum cerasif.</i>	2	6:00 – 8:00	14:00 – 19:00	–
<i>S. lycopers.</i> 'Mirabell'	2	6:00 – 10:00 ³	14:00 – 17:00	6:30 – 14:00 ³
<i>S. l.</i> 'Gardeners Delight'	2(-3 ²)	6:00 – 9:00	16:00 – 19:00	– – 14:00
<i>S. lycopers.</i> 'Lukullus'	2 – 3	6:00 – 10:00	14:00 – 19:00	– – 14:00
<i>S. lycop.</i> 'Bonner Beste'	2	6:00 – 9:00	14:00 – 17:00	–
<i>S. l.</i> San Marzano-Type	2-3(-4 ?)	7:00 – 10:00	14:00 – 19:00	c. 13:00 – 16:00

¹ 20 %, mainly the first flowers of an inflorescence

² 10 %

³ Deviations see text

Since the corolla usually opens a little earlier than the anthers, the flower has a short female stage in the morning; in some cultivars the duration is longer. The complete opening of one anther needs some hours and the anthers do not open synchronously. Thus, a somewhat portioned pollen release occurs. But on the other hand, the available pollen is as it is not depleted completely through one collection-event, each flower can thus be visited several times by the same bee or bee species and/or different bee species. All anthers of a flower can be empty at the end of the first day or one or some anthers may still contain minute to large amounts of pollen on the second day of anthesis.

In cv. Mirabell with the many-flowered inflorescences a high variability in anthesis can be seen, which could not be observed in the usual,

few-flowered cultivars. This includes opening of a smaller number of flowers at midday and afternoon as well as flower buds in which, shortly before opening, 1–3 anthers are already open.

4. Bees

The following bees (and two hoverflies) were observed on *Solanum lycopersicum* and related species.

4.1. *Hylaeus gibbus* SAUNDERS (Colletidae-Hylaeinae)

Buzz-collection of pollen by females of *H. gibbus* (*Prosopis gibba*) (6.5–8 mm in length) is described in TEPPNER 1993: 207–208, Fig. 12, 13, 30–32. The bees were observed in July and August and in some years also at the begin of September; the females were active from c. 9:00 a.m. up to 17:00 p.m. CET and visited *S. pimpinellifolium* as well as different cultivars of *S. lycopersicum* with small and large flowers (Fig. 1 and 2). In June and July the males patrol around the plants.

During their visits the females adhere parallel to the anther tube, then, they put their head into the opening of the tube, or press the orifice against the lower side of their thorax and hold the tube with their mandibles (Fig. 1). In these two positions vibration occurs, which is to be clearly heard and seen (lens). After one buzz, the (in parts large amount of) pollen is groomed from head and thorax with the help of the forelegs and put to the mouth-parts (Fig. 2). Then the next buzz follows and so on. The duration of the single visits is very variable and lasts from seconds or parts of seconds (with 1–2 buzzes) to 2–3 minutes, sometimes even up to 6 minutes and more than 30 buzzes per flower visit. Buzzing is very effective; if the orifice of the tube is carelessly shielded, a copious jet of pollen grazes the body. Gleaning does not seem to occur. Before and/or during the pollen collecting the bees often turn to the base of the tube, move up and down or circumnavigate the anther tube once or repeatedly.

Hylaeus, most probably also *H. gibbus*, was also observed buzzing on *Solanum scabrum* flowers. Other polylectic *Hylaeus* species, abundant in the neighbourhood on *Allium porrum*, *A. tuberosum*, *Anemone japonica*, *Brassica rapa*, *Nepeta cataria*, *N. nepetella*, *Satureja montana*, *Tecoma radicans* and others (*H. brevicornis*, *H. communis*, *H. hyalinatus*, *H. leptocephalus*, *H. moricei*) were not observed on tomatoes, but sporadic visits can not be ruled out.

4.2. *Lasioglossum morio* (FABRICIUS) (Halictidae-Halictini)

The small species, *L. morio* and *L. politum* are difficult to be distinguished with the naked eye during their activities on the flowers. The a little larger body size (c. 1 mm) and a tinge of metallic shine of head and thorax (lens) of *L. morio* permit identification with some certainty. The

distinction between buzz-collection and gleaning is very difficult in these small species because the sound of vibration is very low and some noise always exists in the surroundings. To listen and hear this vibration, approximation of the ear at c. 5 cm near the flower would be necessary. The bees permit this rarely and so the exact acoustical proof of vibration was possible only once for *L. morio*. With the help of a lens, vibration can be seen to some extent.

L. morio (length of females c. 5.2–6.2 mm) is the second most-frequent species of *Lasioglossum* on *S. lycopersicum*. The bees manipulate the tip of the anther tube (sterile part) on the outer side as well as along the margin of the orifice with the mandibles and put the head and/or the forelegs into the tube (Fig. 3). The manipulations are violent, can take some time and seems to be interrupted by buzzes. Grooming of pollen from head and body takes place. Probably vibration is not sufficiently effective for ejaculation of a lot of pollen, which partly adheres in the orifice; therefore additional scraping is necessary. The growing of the pollen load in the scopae during the visit to a flower can be seen. Because of the difficulties and the uncertainties in the observation of buzzing, the importance of vibration and the relation of vibration to scraping pollen from the anthers after own vibrations and to gleaning remains unclear. *L. morio* was observed in July and August with an activity from 9:00 a.m. up to 17:00 p.m. CET; especially on cv. Mirabell it collected abundantly, but also on cultivars with large flowers and *S. pimpinellifolium*.

Otherwise, *L. morio* females were seen collecting pollen and pollinating *Lysimachia nummularia* and *L. punctata* and furthermore on flowers of *Bryonia alba*, *B. dioica* and *Digitalis laevigata*. Small *Lasioglossum*s (not captured, *L. morio* or *L. politum*) were abundant on flowers of *Allium porrum*, *Anemone japonica*, *Anethum graveolens*, *Brassica rapa*, *Verbascum densiflorum* and others.

4.3. *Lasioglossum politum* (SCHENCK) (Halictidae-Halictini)

See also the first and the last paragraph under *L. morio*. *L. politum* is the most abundant *Lasioglossum* species on tomato flowers. Females (length c. 4.2–5.3 mm) were observed in July and August and were seen on flowers from 8:00 a.m. to the afternoon. The females collect mainly on the small-flowered cv. Mirabell but also on all other cultivars, even with large flowers, and as well as on *S. pimpinellifolium*. In August even patrolling males were sometimes observed.

The behaviour on the flowers is very similar to that of *L. morio*. *L. politum* females land on the corolla or the anther tube, turn towards the tip, manipulate the outside with mandibles and legs, put the head and forelegs into the tube, hold the body in U-like form at the orifice of the tube and manipulate it with mandibles and legs (Fig. 4, 5; two positions

which make buzzing seem probable), insert and retract the forelegs in and out of the anther tube to collect pollen, bite the sterile tips with the mandibles and also between them, and bend apart the very tips of the tube, pass the pollen in the usual way from the head or from the orifice via forelegs and midlegs to the scopae. Although many efforts (also with the help of a lens) it was not possible to directly prove if buzzing occurs or not. However a whitish powder of pollen on the sternites of thorax, just like in *Hylaeus* after vibration (Fig. 2), appears to be present on the body opposite to the orifice of the anther tube in two slides of *L. politum* (Fig. 5). Thus I suppose that vibration occurs but statements on the importance of vibration and on the delimitation of buzz-collecting, scraping of pollen after own vibration and gleanings are not possible. In *S. pimpinellifolium* style and stigma were also cleaned with the mandibles; at least this latter behaviour seems to be a clear case of gleanings. All in all the bees receive large amounts of pollen which can be seen by the increase of the whitish pollen mass in the scopae.

Alongside of tomatoes *L. politum* females visited *Euphorbia lathyris* for pollen and nectar and males for nectar; furthermore females were observed on *Brassica juncea*, *Gypsophila paniculata*, *Hypericum perforatum* and *Salvia sclarea*.

4.4. *Lasioglossum zonulum* (SMITH) (Halictidae-Halictini)

This was the largest *Lasioglossum* species (females c. 8.5–10.3 mm) visiting *S. lycopersicum*. Sporadically observed in July between 10:00 a.m. and 15:00 p.m. CET on different *S. lycopersicum* cultivars with small and large flowers ('Mirabell', San Mazano-type, 'Supersteak'). Intensely collecting, clearly vibrating the flowers (Fig. 6; sound distinctly to be heard), several times during one visit, or head at the opening of the anther tube (Fig. 7) and apparently scraping pollen, accumulation of pollen in the scopae visible, and in between head also directed outside towards the base of the anther tube. Sometimes in *Cucurbita pepo* flowers. At the beginning of October also observed on a *Anthriscum majus* mutant with open flowers.

4.5. *Lasioglossum laticeps* (SCHENCK) (Halictidae-Halictini)

Observed only once in the Botanic Garden (1.8.1992), a female (length c. 6.3–7.4 mm) visiting consequently a number of flowers of *S. pimpinellifolium* (Fig. 8) and *S. lycopersicum* 'Mirabell'. Vibration not heard and no accumulation of pollen in the scopae observed (pollen foraged?). Females were also seen on *Brassica juncea* and *Scrophularia nodosa* and in off-flowering period of the tomatoes on *Actinidia deliciosa*, *Alyssum orientale*, *Osmaronia cerasiformis*, *Ribes fasciculatum*, *Taraxacum officinale* and *Veronica filiformis*.

4.6. *Lasioglossum nitidulum* (FABRICIUS) (Halictidae-Halictini)

Observed only once in the Botanic Garden (3.7.1993), a female (length c. 6.3–6.5 mm) visiting a number of flowers of *Solanum parviflorum* and apparently collecting pollen; vibration not heard. Females otherwise seen on *Lobelia erinus*, *Oenothera erythrosepala*, *Passiflora incarnata* and *Verbascum densiflorum*.

4.7. *Megachile willughbiella* (KIRBY) (Megachilidae-Megachilini)

The activity period of the relatively large bee (females c. 15–17 mm in length) lasts from beginning of June up to beginning of September; thus the whole flowering period of tomato is covered. The daily activity is from c. 8:00 a.m. up to 17:30 p.m. CET. The bee nests near the investigated tomato-stands in the soil between the stones in the rock garden, between the stone

Fig. 1–2. *Hylaeus gibbus* female on *Solanum lycopersicum* ‘Mirabell’. – Fig. 1. During vibration, thorax appressed to the orifice of the anther tube and mandibles biting it. – Fig. 2. Immediately after vibration, pollen eating, whitish tomato pollen on the lower side of the body.

Fig. 3. *Lasioglossum morio* female on cv. Mirabell immediately after vibration, manipulating the tip of the anther tube, mandibles and forelegs in the anther tube orifice. Scopae with whitish tomato pollen.

Fig. 4–5. *Lasioglossum politum* female on flowers of cv. Mirabell. – Fig. 4. In a position on the anther tube, which lets vibration seem possible. – Fig. 5. Similar position as in Fig. 4, but with a small space between body and anther tube as well with pollen which appears to be present opposite to the orifice. Scopae with tomato pollen.

Fig. 6–7. *Lasioglossum zonulum* female on a flower of cv. Mirabell. – Fig. 6. During buzzing, biting the anther tube with the mandibles. – Fig. 7. Shortly later on the same flower, with whitish tomato pollen on the lower side of the body and manipulating the orifice of the anther tube with the mandibles.

Fig. 8. *Lasioglossum laticeps* female on *Solanum pimpinellifolium*, cleaning the style. Brown bite marks of bumblebees on the anther tube.

Fig. 9–10. *Megachile willughbiella* female during vibration, with whitish tomato pollen on the lower side of the thorax. – Fig. 9. On *Solanum lycopersicum* ‘Supersteak’, in the distal third of the scopa whitish tomato pollen. – Fig. 10. On cv. Mirabell, the whole scopa full with tomato pollen.

Fig. 11. *Bombus terrestris* worker on cv. Mirabell vibrating the anther tube of a flower-bud successfully, with whitish tomato pollen on the lower side of thorax and abdomen as well as in the corbicula.

Fig. 12–13. *Bombus pascuorum* worker. – Fig. 12. During vibration on *Solanum parviflorum*. – Fig. 13. After vibration hanging on the flower and pollen packing on the hindlegs.

Fig. 14–15. *Bombus lapidarius* worker on cv. Mirabell. – Fig. 14. During vibration, mandibles biting the anther tube. – Fig. 15. Immediately after vibration, with the spot of whitish tomato pollen on the lower side of the abdomen.

The scale bars equal to 1 cm.

plates on paths, in the plant boxes on the balcony and even in the tubes prepared for the fruit tree pollinators *Osmia cornuta* and *O. rufa*. It is an impressive bee on tomato flowers. During vibration the bee holds on to the anther tube with the mandibles and the legs (Fig. 9–10), thus the pollen is ejected against the lower side of the thorax and the legs must bring the pollen in the scopa. This underlines the high flexibility of the bee in collecting pollen: in other cases the scopa is held directly against the pollen cloud and in non-buzzing flowers the scopa is brushed over the pollen presenting structures. All cultivars, regardless if small or large flowers, are visited, vibration is very well to hear, the sound is smoother and therefore easy to distinguish from bumblebees and is also louder than of the *B. pascuorum* and *B. lapidarius* workers. *M. willughbiella* is a very busy pollinator of tomatoes, they appear more times a day and pollinate all the suitable flowers in a stand. One female for c. 50 tomato plants would suffice easily for pollination of the open flowers repeatedly every day.

Nevertheless, the presence on tomato is sparse in relation to the abundance on *Lathyrus latifolius* and *L. sylvestris* in the neighbourhood, but this is explained by the continuous nectar production in *Lathyrus*. Furthermore the highly polylectic *M. willughbiella* (WESTRICH 1989: 204–205) is an important pollinator of many other plants like *Fabaceae*, *Campanulaceae*, *Lamiaceae*, *Boraginaceae* (*Borago*: TEPNER 1997a: 59), *Asteraceae*, *Asphodelaceae* (*Asphodeline lutea* and *A. liburnica*, pers. obs.) etc. Thus, one should be glad to have this nice bee in the garden and tolerate the fact that this bee cuts leaf sections from roses (and other plants, here *Cornus mas* and *Amphicarpaea bracteata*), which is needed for wall-paperying their cells (WESTRICH 1989: 204–205, O'TOOLE & RAW 1991: 77–81).

4.8. *Bombus terrestris* (LINNAEUS) (Apidae-Bombini)

B. terrestris workers are the classical pollinators of *S. lycopersicum* in Central Europe (e. g. RUTTER 1997) but are far from being evenly distributed and abundant over the years. In some years (e.g. 1997) *B. terrestris* is practically completely lacking on tomato flowers in our stands, probably caused by low density of colonies and therefore lower numbers of workers. In such years workers are present near the tomato stands and visit e.g. *Anemone japonica*, *Begonia semperflorens* and *Verbascum densiflorum* (all buzz-collections) and *Echinops*, but ignore tomato flowers. Rarely bumblebee visitation is so scarce, that tomato pollination is not assured by bumblebee species alone (1992). In other years *B. terrestris* can be the main pollinator. The workers visit tomato flowers, from the first ones in the second half of June until beginning of September, from c. 7:30 a.m. CET onwards during the whole day, on all species and cultivars. Not only open flowers are attractive; the bees often milk the tips of the buds (which are just about to open) especially in the morning till to the corolla

slits open, and then they squeeze themselves inside the bud and vibrate the anther tube (Fig. 11); thus they are the first visitors of the relevant flower and get a large amount of pollen.

4.9. *Bombus pascuorum* (SCOPOLI) (Apidae-Bombini)

B. pascuorum is an important, frequent pollinator of *S. lycopersicum* and is as busy as *B. terrestris*. It is often the second most-frequent visitor after *B. terrestris* and in the years of *B. terrestris* absence, *B. pascuorum* workers are the main pollinators which substitutes *B. terrestris* completely (e.g. 1997). They are also present on the flowers from the beginning of tomato anthesis up to mid of September and were seen on tomato from c. (6:00–) 8:00 a.m. CET during the whole day on all species and cultivars; sometimes I had the impression of a slight preference for cv. Mirabell and *S. pimpinellifolium*. The behaviour on the flowers is the same (Fig. 12, 13), this bee also clings with the mandibles onto the anther tube (giving brown bite marks), only the purposefully opening of buds was not observed. Sometimes the workers, during their flight on tomato, alternate with *Phaseolus coccineus* flowers (nectar present). For workers collecting on *Symphytum officinale* the wingbeat frequency and buzz frequency ranges of 165–207 Hz and 276–415 Hz, respectively, are indicated by CORBET & al. 1988: 151.

4.10. *Bombus lapidarius* (LINNAEUS) (Apidae-Bombini)

B. lapidarius is also a consistent visitor of tomato flowers of all species and cultivars. Over the season it is the third most-frequent *Bombus* species, but on particular days it may occur, that *B. lapidarius* workers are the most frequent ones. Activity period and behaviour on tomato-flowers (Fig. 13, 14) are the same as for *B. terrestris* and *B. pascuorum*; the opening of and squeeze themselves inside buds was observed only once. As in other *Bombus* species after vibration, pollen is groomed from the ventral side, transported to the hindlegs and packed in the corbiculae while hanging on the flower (Fig. 13, 15) or during flight, so that at the arrival on the next flower the ventral side seems to be clean.

4.11. *Bombus sylvarum* (LINNAEUS) (Apidae-Bombini)

B. sylvarum is not abundant in Graz. Only once a worker was observed on cv. Mirabell (23.7.1994). GLADIS & al. 1996:17 reported also one worker on *S. lycopersicum*.

4.12. Scarce Visits with no or Doubtful Effect

Halictus subauratus (ROSSI) (Halictidae-Halictini). Sporadically throughout the season, shortly searching on the anther tubes but apparently without receiving any pollen.

Lasioglossum calceatum (SCOPOLI) (Halictidae-Halictini) observed only once in the private garden on a flower of cv. Mirabell, mandibles in the orifice of the anther tube, no vibration heard (22.7.1993).

Anthidium septemspinosum (LEPELETIER) (Megachilidae-Anthidiini): a female was sitting shortly on the anther tube of four flowers, apparently nothing collected (23.7.1997).

Megachile rotundata (FABRICIUS) (Megachilidae-Megachilini): This species gathered on *Verbena officinalis* in the Botanic Garden and alternated with *Solanum chmielewskii* flowers. Some were visited holding the abdomen to the opening of the anther tube and the mandibles on its base. Not clear if pollen received, no vibration heard (2.7.1994).

Anthophora furcata (PANZER) (Apidae-Anthophorini): Observed only once in the Botanic Garden, a female hanging on a flower of *Solanum pimpinellifolium* and packing pollen with the hindlegs (30.7.1992). Curious, because this species is oligolectic on *Lamiaceae* according to WESTRICH 1989: 568. Also seen on *Gladiolus illyricus* for nectar exploitation in the Botanic Garden.

Apis mellifera LINNAEUS (Apidae-Apini): A number of flowers of *S. peruvianum* in the Bot. Garden searched and worked upon with the mandibles, at the inner and outer base (1.8.1994), a worker turns around the inner flower base of some *S. chmielewskii* flowers (21.8.1993). Another individual handles some flowers of *S. chilense* with the mandibles for a long time, splits the anther tube, seems to search for nectar and apparently collects pollen (accumulation of some whitish pollen in the corbicula) (22.7.1994); this latter behaviour seems to be similar to that described by CRIBB & al. 1993: 81–82 for honeybees on greenhouse tomatoes.

Syrpitta pipienes (LINNAEUS) (Diptera, Syrphidae): Observed once on cv. Mirabell in the private garden. This hoverfly first dabbed the outside of the anther tube with the proboscis and finally introduced the proboscis into the tube in a number of flowers (moving the proboscis back and forth; without vibration). Pollination may be possible in this way, but it is highly improbable, that any pollination, additionally to those of the bees, occurs. GLADIS & al. 1996: 17, 18 observed *Sphaerophoria scripta* “frequently feeding on tomato flowers”. BUCHMANN 1983: 98 describes buzzing of *Solanum douglasii* flowers by *Volucella mexicana* in S. California. NICKOL 1991: 208 observed vibration in one male of *Scaeva pyrastris* which was sitting on a window-sill, but not on flowers.

Heringia vitripennis MEIG., det. P. VOGTENHUBER, (Diptera, Syrphidae): A small, black hoverfly, sometimes on cv. Mirabell in the private garden. Behaviour the same as for *Syrpitta*.

5. Discussion

An important criterion for an extensive pollination of crop plants by wild bees is a rich differentiation of microhabitats for nesting sites of the different bee species (e.g. ROUBIK 1989: 185–192, WESTRICH 1989: 22–116) and a constantly rich flora over the seasons, which permits the development of sufficiently individual-rich populations of bees. In the parks and gardens of Graz (Austria, Europe) much more than hundred bee species are living (whole Austria 647 species, SCHWARZ & al. 1996:8).

Growing tomatoes in the open was never a severe problem in Central Europe in spite of the presence of *Phytophthora infestans* and relative high rainfall (Graz c. 865 mm/year, mainly in the vegetation period). For commercial purposes protected cultures (in greenhouses etc.) progressed very rapidly. Since c. 1998–2000 tomato growing in the open is nearly impossible in Styria without massive application of fungicides and therefore for commercial purposes is abandoned. The reason is probably the introduction of a second mating type of *Phytophthora infestans* into Europe and the appearance of more aggressive biotypes (ERWIN & RIBEIRO 1996, LEGARD & al. 1995). Nevertheless, plantations under roofs or in greenhouses with large openings are further accessible for wild bees in summer as well as in cultures in drier regions and therefore yet the relations between tomato flowers and wild bees will still remain of interest. The invasion of the noctuid *Helicoverpa armigera* (HÜBNER) (Noctuidae-Heliiothinae; det. H. HABELER) in 2003 in Styria, where the caterpillars gnawed away the tomato fruits in some places, was fortunately only of a passing nature, because it depends apparently on special weather conditions for the long distance dispersal from the South and the species seems not to be able to overwinter in our region.

For tomato seed production and for conservation of cultivars in the open, the activity of the wild bee fauna has to be taken in consideration because it contributes to cross-pollination which makes hybridisation possible. This is especially important in taxa with exerted styles or variable style length; in sorts with styles included in the anther tube, the “Königsblüten” possess also exerted styles usually. In a spot-check of 69 actual cultivars c. a third still had more or less exerted styles (TEPPNER 1994: 322).

From the anther tube of tomatoes a satisfying amount of pollen-harvest (from the point of view of the bee) is only to be achieved by vibration of the flower (buzz-collection). Much has been written on this subject (e.g., MICHENER 1962, BUCHMANN 1983, BUCHMANN & HURLEY 1978). The frequencies (fundamental frequency, Grundfrequenz) applied by bees for vibratory pollen-collection lie between 58–347 Hz (BUCHMANN & al. 1977). Measurements for *Bombus*, e.g.: *B. terrestris* workers 300–341 Hz, *B. pascuorum* up to 415 Hz: CORBET & al. 1988: 148,151; *B. terrestris* 260–

346 Hz, *B. hortorum* 323 Hz: KING 1993: 47. In the general indications for different bees of 50–2 000 Hz (BUCHMANN 1983: 75), 4–5 kHz (ROUBIK 1989: 48) and 4 500–6 000 Hz (KING 1993: 48) the harmonics (Harmonische, Obertöne; integer multiples of the fundamental frequency) are included, whereby the vibrations above 1 000 Hz have very small magnitudes (e.g. KING 1993: 46, 48). The fundamental frequencies of the buzz-sounds are higher than the wingbeat frequency of flight from flower to flower (e.g. *B. terrestris* workers 175–198 Hz, CORBET & al. 1988: 148). Very important is, that the indirect flight musculature vibrates at the natural frequency (Eigenfrequenz) of the sternites and tergites, so that resonance occurs, which generates a high magnitude (Amplitude) oscillation (KING 1993); it is transferred to the anthers by the contact of the head and/or the sternites with the anthers and is necessary to accelerate the anther (c. $140\text{--}300\text{ m s}^{-2}$, KING 1993: 47, KING & BUCHMANN 1996) and produce forces for sufficient acceleration of pollen grains within the anther for their release (ejection) (KING & BUCHMANN 1996). The buzz-frequencies lie lower or higher than the natural frequencies of flowers and anthers and are not adapted or adjusted to their natural frequencies. E.g., the natural frequency of the stamens on slender filaments in *Solanum laciniatum* is indicated as 124 Hz (KING & BUCHMANN 1996: 449) and as 4–20 kHz for the stiff anther tube in tomato flowers (DE TAR & al. 1968: 733). Tapetal fluid, drying up only successively in the anther, may be responsible for gradual pollen release over time according to KING & BUCHMANN 1996: 455. I have the impression, that the successive drying up of the anther wall also plays an important role as to the availability of pollen. KING 1993 has proven on *Actinidia deliciosa*, that bumblebees must not learn buzz-collection. The ability of bumblebees to recognize closed flower buds in which anthers are already open, and to avoid flowers with empty anthers, points towards some signals from the flower (comp. KNAPP 2002: 26–27). Pollen-collection from opening floral buds as a rule is described, e. g., for *Ptiloglossa arizonensis* females, who vibrate *Solanum elaeagnifolium* anthers at dawn in the deserts of Arizona (LINSLEY 1962).

It is easy to see, that bees react to the pollen mass in the anther tube and work longer and with more buzzes in fresh flowers (a detailed study on *Solanum elaeagnifolium*: BUCHMANN & CANE 1989). It is supposed, that there exists a limit in body length and weight for smaller bees to have the ability to vibrate. ROUBIK 1989: 49 mentions 7 mm and less than 30 mg for some Anthophorids, Halictidae and *Melipona*. This is also the dimension of *Hylaeus gibbus* (Colletidae); the sound of its vibration is heard clearly, though sometimes with some difficulty. The females of *Lasioglossum politum* and *L. morio* have a body length of c. 4–5 and c. 5–6 mm, respectively, and are most probably the smallest bees, in which buzz-collecting has been observed till now. The sound is very difficult to hear; a combination of buzz-collection and cleaning is apparent (as in

other Lasioglossums) but an exact investigation of the behaviour will only be possible with specialized technical equipment, because the necessary approximation of the ear to the flower is usually not tolerated by the small bees; and even if they would, the simultaneous visual observation would no longer be possible. The visual proof with the help of a lens is also difficult and often not unequivocal. In the smaller *L. politum* a clear decision for or against vibration was not possible – in spite of a bearing which lets buzzing seem to be possible. Thus the two species would be a convenient subject for a study concerning the existence of a limit in body length for the ability to buzz.

In larger bees (here *Bombus* and *Megachile*) vibration is loud and apparently very effective so that pollen is shoot against the ventral side of the body in sufficient quantities so that no further manipulation of the flower takes place. In smaller bees (here *Lasioglossum*) buzzing is combined in a characteristic manner with the scraping of the pollen, which remains adhered in and on the anther tube tip after the vibration, with the mandibles and the forelegs (somewhat similar in *Hibbertia*: BERNHARDT 1986: 236). Since there is a large amount of pollen in relation to the body size of the small bees, they are usually occupied for relatively long time with the handling of one single flower. [An analogous situation is described for Australian *Solanums*, where the vibrator bees stay for one to few seconds whereas the small (up to 5 mm) not vibrating *Trigona* spends up to one minute for one flower, ANDERSON & SYMON 1988: 845]. In the smallest *Lasioglossums*, because of the low vibration sound, it was not possible to distinguish this behaviour from true gleaning, which is the use of pollen remains from the visits of other bees (WILLE 1963: 207–208).

Colletidae are known for abundant use of vibration, e.g., *Ptiloglossa arizonensis* TIMBERLAKE on *Solanum elaeagnifolium* (LINSLEY 1962, BUCHMANN & CANE 1989). Two Colletids pollinate tomatoes in S. America. Thus the discovery of *Hylaeus gibbus* as pollinator of tomatoes (TEPPNER 1993: 207–208, Fig. 12, 13, 30–32; 4.1. in this paper) is consistent with the actual knowledge.

In Andrenidae buzz-collection is exceptional. It occurs in few species of *Protoandrena* (N. America) and *Parapsaenythia* (S. America) on *Solanum* (NEFF & SIMPSON 1988: 242). GLADIS & al. 1996: 17 observed one female of *Andrena bicolor* on tomato, unfortunately without any information on frequency of visits and behaviour on the flower. In spite of many *Andrena* species present around the tomato stands, I have never seen an *Andrena* on tomato. Principally, buzz-collection by *Andrena* is possible and has been proven (*A. hilaris* on *Vaccinium ashei*, NEFF & SIMPSON 1988: 242, *A. symphyti* on *Symphytum*, *Onosma* and seldom *Pulmonaria*: TEPPNER unpubl., photo in TEPPNER 1997b:21). In the small American subfamily *Oxaeinae* buzzing seems to be common (e.g. LINSLEY & CAZIER 1963, BUCHMANN 1983: 97, CAMARGO & al. 1984)

Many Halictidae are well-known for the use of vibratory pollen-collection in flowers with poricidal anthers, some also from tomatoes in America. Species of *Lasioglossum* itself are reported to vibrate flowers (BERNHARDT 1986, BUCHMANN 1983: 97) and also to visit *Solanum* flowers (MICHENER 1965). MICHENER 1962: 170 mentions a small *Lasioglossum* only scavenging anther tips of *Solanum wendlandii* from pollen. Observation of *Lasioglossum* species on tomatoes seems to be new. In the recorded *Lasioglossum* species buzzing is followed by collecting the remaining pollen adhering to the anther tube (see above). *L. morio* and *L. politum* are probably under the smallest bees which buzz flowers. BOHS 2000 reports only gleaning for four *Lasioglossum* species on *Witheringia* (*Solanaceae-Physaleae*).

On the one hand buzzing in Megachilidae seems to be very rare, but on the other hand, *Megachile willughbiella* is an early, well described example for buzz-collection of pollen. According to MEIDEL 1944: 9–10 *M. willughbiella* is an important visitor of *Melampyrum pratense*; in a position with the head downwards, the scopa nearly shuts the opening of the corolla and by two or three times of vibration the pollen is showered onto the scopa; then the bee turns to the upper side of the corolla tube, bites two slits and sucks the nectar. Our record seems to be the first one for this genus on tomato. For *Megachile mendica* on *Chamaecrista fasciculata* also buzz-collection is described (poricidal anthers, pollen-only blossom; NEFF & SIMPSON 1988). FELICOLI 1996 has written about the possibility to use *Osmia cornuta* for the pollination of greenhouse tomatoes, but the paper contains no information concerning the behaviour on tomato flowers, buzzing or the real success of pollination. In the open in Central Europe, at the end of May the activity period of the imagines of *O. cornuta* is over, so, there is no contact with tomato flowers at all. Since some other megachilids are reported to visit flowers with poricidal anthers, the number of buzz-collecting species may probably increase. In our tomato stands *M. willughbiella* was an effective and important pollinator, which, during fine weather conditions, is in no way inferior to the bumblebees.

From the former Anthophoridae, now usually included in Apidae, members of four tribus (Anthophorini, Centridini, Exomalopsini, Xylocopini) are often reported for vibration. *Anthophora* species are mentioned as regular pollinators and buzz-collectors on tomatoes and other *Solanums* in America. Therefore it was surprising not to have detected *Anthophoras* regularly on tomato flowers, especially because the polylectic *Anthophora quadrimaculata* (syn. *A. vulpina*), abundant around the tomato stands, is reported as a visitor of *Solanum nigrum* (WESTRICH 1989: 573). The single observation of *Anthophora furcata*, oligolectic on *Lamiaceae*, on a tomato flower was most probably accidental.

Apidae-Bombini. According to MACFARLANE 1995: 33 shorter- or medium-tongued bumblebees are better pollinators of *Solanum* species than longer-tongued ones. In accordance with this assumption *Bombus terrestris* and *B. lapidarius* are pollinators and *B. hortensis* and *B. argillaceus* are completely absent on tomato flowers in our stands. A remarkable exception is the long-tongued *B. pascuorum* which is an excellent pollinator of tomatoes, in the same manner as *B. terrestris*, and often substitutes it.

Apidae-Apini. In the open, *Apis mellifera* ignores the tomato flowers nearly completely; in the case of the rare visits it shows often curious behaviour. According e.g. MACFARLANE 1995: 33 and VAN RAVESTIJN & VAN DER SANDE 1991: 204, *A. mellifera* can only be used to some extent for greenhouse tomatoes in winter; as soon as other flowers appear, honeybees leave the tomatoes.

Bumblebees have the advantage to be active also during relatively bad weather conditions, whereas all other bees mentioned, also the excellent tomato pollinator *Megachile willughbiella*, are active only under fine weather. To check if pollination by bumblebees and *Megachile* is sufficient, the brown "bite marks" on the anther tube, where the bees hold it with the mandibles during buzzing, is a good proof. *Hylaeus gibbus* can be added to the group of "good" pollinators whereas the *Lasioglossum*'s vibration seems to be not so effective, in average the bees lasts longer on the flowers and in some species the visits are too rare.

Today there are many efforts for protection and promotion of wild bees. In this connection *S. lycopersicum* 'Mirabell' (Firma Julius Wagner, D-6900 Heidelberg) with its large, dichasial inflorescences with up to four-hundred flowers each, can be recommended as an excellent pollen source in summer for all bees, which can handle the flowers.

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