

The first records of vibratory pollen-collection by bees

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with 2 figures

Key words: *Apidae*, *Bombus*, *Megachile*, *Xylocopa*, bees, buzz collection, sonication, vibratory pollen-collection. – *Cassia* s.l., *Senna*, *Chamaecrista*, *Melampyrum*, *Physalis*, *Solanum*. – Floral ecology, history of botany.

Summary

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After a thorough analysis of the respective texts, the opinion that SPRENGEL 1793 or BURCK 1887 had discovered vibratory pollen-collection cannot be sustained. The first unambiguous descriptions of vibratory pollen-collection date back to LINDMAN 1902 for bumblebees (on *Senna alata*), to SCHROTTKY 1908 for *Oxaea*, *Augochlora*, *Xylocopa*, *Psaenythia*, *Ptiloglossa* and others (on *Senna occidentalis*, *Physalis viscosa* and *Solanum paniculatum*), and to MEIDELL 1944 for *Megachile willughbiella* and bumblebees (on *Melampyrum pratense*). Original texts and English translations are provided.

1. Introduction

The paper of BURCK 1887 is sometimes cited in connection with enantiostyly and the division of labor between the anthers within flowers of *Cassia* s.l. In NEFF & SIMPSON 1988, BURCK's paper is also regarded as the first record of vibratory pollen-collection (v. p.-c.), i.e. pollen-collection with the help of vibrations of the indirect flight musculature. This phenomenon is also known as buzz-collection, sonication, and often (erroneously) as 'buzz-pollination' (TEPPNER 2005: 219). For summaries see TEPPNER 2005: 228–232 and DE LUCA & VALLEJO-MARIN 2013, for the vibration frequencies see BURKART & al. 2011.

In spite of the results presented by ARCEO-GÓMEZ & al. 2011²⁾, we insist to prefer the term buzz-collection instead of buzz-pollination: From the perspective of the bee, only the collection is 'of interest', and – in the vast majority of cases – vibration is only necessary for collecting pollen, not for pollination. The problem may be more complicated only in the cases of internal stigmatic surfaces as in *Cassia* s.l. It is plausible that, in the experimental setup with the placement of cut anthers on the tip of the style, vibration is necessary to transfer pollen into the stigmatic cavity. But, in our understanding, this is not comparable with the natural process of

pollination where an insect's body loaded with pollen rubs against the tip of the style and where stigmatic hairs, secreted material and electrostatic forces also have to be considered; here, a contribution of vibration to the intrusion of pollen grains into the stigmatic cavities is under discussion (compare, e.g. DULBERGER & al. 1994, MARAZZI & al. 2007).

Everybody who looks at bees visiting flowers of *Solanum*, *Symphytum*, *Cassia*, *Chamaecrista*, *Senna*, etc., sees and hears vibratory pollen-collection. But the observation of the visits alone is no sign for the detection of v. p.-c. Records of v. p.-c. are only creditable if the description clearly separates v. p.-c. from the other behavior of the bees on the flowers, and if vibration is definitely interpreted in connection with pollen gathering.

The main purpose of the present paper is to draw attention to the earliest unequivocal records of vibratory pollen-collection found in the literature until now.

2. No details on the behavior of bees

SPRENGEL 1793: 93 describes abundant visits of bumblebees on the flowers of *Symphytum officinale*, but without any mention of sound or other conspicuous behavior. Concerning *Solanum nigrum*, he

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²⁾ ARCEO-GÓMEZ & al. 2011 apparently use the terms 'left-' and 'right-handed' style in the inverse sense, contrary to the definition in classical morphology (EICHLER 1875: 6) or, e.g., in JESSON & BARRETT 2002. Because of this ambiguity, the definition should be indicated in every case, e.g. by a figure.

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observed bees and bumblebees and writes (p. 129, translation): “But the bees [*Apis*!] seem to take only dust from the flowers. Those which I encountered on the blooms pushed with fierceness against the anthers that their dust should drop out”. Furthermore, for *Leucojum vernum* (p. 182) he mentions (translation): “The bees [again *Apis* is meant!] crawl entirely into the flower, stay for a long time in the bloom and cause a trembling movement, which is nice to see” [by movements of the legs of *Apis*, which never vibrates in flowers]. None of these three remarks by SPRENGEL suggests that he could have recognized vibratory pollen-collection. Thus we cannot follow ENDRESS 1992: 230 (*Leucojum*) and 1994: 151 (*Solanum*), who supposed this.

3. Misinterpretations

TODD 1882³, working with *Solanum rostratum* and *Chamaecrista fasciculata*, gives a short description of the behavior of a small bumblebee, who seizes the short anthers with the mandibles “and with a sort of milking motion crowds the pollen out of the terminal pores”. The long anther is bent back by the legs and when it rebounds into the original position, a cloud of pollen is discharged. Obviously, the firm adherence with the mandibles and legs to the flower to transmit the vibration has been misinterpreted as “milking” [squeezing-out of pollen]. This term often wanders through later published literature. It was negated and refuted by SCHROTTKY as early as 1908: 25 and recently by GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1988: 315.

The extensive paper of MÜLLER H. 1883 on the division of labor between the anthers of pollen-only flowers contains no details on the behavior of visitors relevant for v. p.-c. MÜLLER H. 1882: 22 noted that, in the case of strong agitation of the streukegel (scatter-cone) of *Solanum nigrum*, pollen falls out from the open ends of the anthers – without any mention of the nature of this agitation.

For *Heteranthera* (*Pontederiaceae*) and others (*Cassia* s.l. included), MÜLLER F. 1883 notes correctly that pollen of short stamens is gathered by bees, whilst pollen of long anthers is deposited on their backs – but without mentioning sounds.

The observations of MEEHAN 1886 for *Senna marilandica* seem not to be exact and do not mean any progress in relation to TODD 1882.

According to ROBERTSON 1890, the flowers of *Chamaecrista fasciculata* are exclusively exploited by bumblebees for pollen. Then he describes “a sort of milking motion” for obtaining pollen and mentions similar observations on *Senna marilandica*.

The essentials of the extensive writing on flower visits in HARRIS & KUCHS 1902: 24–30 can be summarized as follows: (i) many species of bumblebees are visitors of *Solanum rostratum* and *Chamaecrista fasciculata* and they squeeze out pollen from the short anthers by the mandibles; (ii) “A considerable quantity of pollen may be thrown from the terminal pores of the large stamen upon tapping it”. Also pollen-thieving by Halictids from the pores of the long anthers was recorded. There is not one word about sounds.

KNUTH in LOEW 1904: 361–380 describes the milking (“Ausmelken”) of feeding-anthers (“Beköstigungsantheren”) for a number of *Cassia* s.l. species.

Apparently, SHAW & al. 1939 and VAN DER PIJL 1939 (in Dutch language), who observed *Vaccinium* and *Melastomataceae*, respectively, did not perceive v. p.-c. either. In the case of *Osbeckia chinensis*, VAN DER PIJL stresses milking and bellows mechanism effected by the fore-legs(!), leading to a squirt-out of pollen. In *Melastoma malabathricum* the feeding-anthers should be pumped empty by quick pinching by mandibles and legs along the whole length of the anthers, whereas the pollination-anthers should set pollen free by springing back (catapult mechanism, slinger-anthers), when the bee flies away from the flower. Additionally, on p. 171 (bottom), there is a cryptic phrase (translated): ‘Probably the effect of the mechanism is important, when not a single deformation takes place, but a number of repetitive impulses lets vibrate [?? “snorren”] the spring [of the pollination-anthers]’. All this and also the back and forth motion of the body with strongly humming wings mentioned on p. 172 (top) seem to miss the point and do not speak in favor of the recognition of the essentials of v. p.-c.

As a curiosity HERBST 1918 should be mentioned. He interpreted the sounds of female bees on certain flowers as ejection of air, a sort of tracheal respiration, for cleaning the stigmata or tracheas from pollen and dust.

4. The paper of Burck 1887

BURCK objects decidedly to MÜLLER H. 1883 and believes that it is not debatable to regard every deviation from the normal type of a flower as a special adaption to body or life of an insect. With the example of *Cassia* s.l. (mainly *Senna*) species he claimed to demonstrate the trend of transformation of flowers towards self-pollination without mediation of insects.

For an analysis of BURCK 1887 in respect of the behavior of bees, the most relevant paragraphs con-

³) TODD 1882 and followers used the terms ‘left’ and ‘right’ in the inverse sense (compare the foot-note in the introduction).

cerning bees and flowers from p. 257–258 and 260 (*Cassia glauca* = *Senna sulfurea*) are worth to be reproduced here as original text followed by a translation:

(p. 257)

Les grandes abeilles, qui fréquentent les fleurs du *Cassia glauca*, s'approchent dans la direction de la flèche de la figure. Elles s'assoient au milieu de la fleur (vers x), courbent l'abdomen en bas et dévorent les grains de pollen des cinq courtes anthères, ou bien elles mangent en grande partie et quelquefois entièrement et les parois des sacs polliniques et le pollen. Seules les deux étamines allongées restent intactes. Elles ne sont pas mangées et leur pollen n'est pas dérobé.

De quelle manière les fleurs des *Cassia* sont-elles pollinisées?

Il n'est pas difficile de répondre à cette question. L'insecte, en se posant sur la fleur, change quelque peu la position normale des étamines. Lorsqu'il sort de la fleur ou bien lorsqu'il retire sa trompe de l'anthère, l'étamine rejaillit dans sa position primaire. Par ce brusque mouvement un petit nuage de pollen s'échappe de la fente du sac pollinique et quelques grains peuvent arriver sur le stigmate incliné.

En effet une telle disposition est fort incomplète et plus d'une fois il doit arriver que tout le pollen est dévoré sans qu'un seul grain se soit déposé sur le petit stigmate. L'allongement de deux des étamines doit être particulièrement favorable et à divers égards à une auto-pollinisation plus régulière. Le plus grand avantage résultant de cet allongement est que le pollen

(p. 258)

de ces deux anthères est mis hors de la portée des insectes; ceux-ci ne sont plus à même d'introduire leur trompe dans les fentes des sacs polliniques pour manger le contenu. En effet par cet allongement une division du travail entre les étamines est effectuée. Le pollen des grandes anthères ne sert qu'à la fécondation, tandis que celui des autres peut être mangé par les insectes visiteurs, qui à leur tour agitent les étamines pour faire échapper le pollen.

En second lieu les étamines allongées sont agitées plus énergiquement lors de la visite d'une abeille, qu'il ne pourrait être le cas sans l'allongement des filaments.

(p. 260)

Enfin j'ajouterai encore avoir vu les fleurs du *Cassia glauca* ainsi que celles des espèces suivantes, fréquentées par de grandes abeilles (*Xylocopa*, *Bombus*). Les abeilles se dirigent directement vers les petites étamines en n'effleurant que très rarement les grandes anthères. Dans les cas rares, où celles-ci sont touchées, le contact a lieu avec le côté ventral de l'insecte, à gauche ou à droite, et alors le pollen peut être déposé dans cet endroit. Pourtant je n'ai jamais vu le stigmate en contact avec le corps de l'insecte. On ne saurait nier que cela puisse arriver parfois, surtout au moment où l'insecte quitte la fleur; mais la chance que le dos de l'insecte touchera au stigmate est certainement beaucoup plus grande que celle d'un contact avec le ventre, auquel le pollen adhère.

(Plate XXXI Fig. 1)



Translation: (p. 257) The large bees, who visit the flowers of *Cassia glauca*, approach in the direction of the arrow in the figure [erroneously omitted in Fig. 1]. They rest in the center of the flower (toward x), bend the abdomen downward and devour the pollen grains of the five short anthers, or they eat a good portion or all of the walls of the pollen sacs as well as the pollen. Only the two elongated anthers remain intact. They are not eaten and their pollen is not thieved.

In which manner the flowers of *Cassia* are pollinated?

It is not difficult to answer this question. The insect, placed on the flower, changes slightly the normal position of the stamens. If it leaves the flower or if it retracts the proboscis from the anther, the stamen jumps back to its original position. Because of this abrupt movement, a small cloud of pollen escapes from the slit of the pollen sac and some grains can arrive on the inclined stigma.

In fact, such an arrangement is very imperfect and more than once it must occur that all pollen is devoured without a single grain being deposited on the small stigma. The elongation of two of the stamens must be especially favorable in consideration of a more regular self-pollination. The greatest advantage resulting from this elongation is that the pollen (p. 258) of these two anthers is out of the operating distance of the insects; they are no longer able to introduce their proboscis into the slits of pollen sacs to eat the content. Really, because of this elongation, a division of labor between the stamens is accomplished. The pollen of the large anthers serves only for the pollination, whereas the pollen of the others may be eaten by the visiting insects, which on their walk move the stamens to make the pollen escape.

Secondly, the elongated stamens are moved more vigorously by the visit of a bee, which could not be the case without the elongation of the filaments.

(p. 260) Finally, I would still like to add that I have seen flowers of *Cassia glauca*, as well as those of the following species, frequented by large bees (*Xylocopa*, *Bombus*). The bees approach directly the small stamens, and touch the long anthers very rarely. In the rare cases in which they are touched, the contact takes place with the ventral side of the insect, on the left or on the right, so the pollen can be deposited in this place. However, I have never seen the stigma in contact with the body of the insect. One cannot negate that this may occur sometimes, especially in the moment, when the insect leaves the flower; but the chance that the back of the insect will touch a stigma is certainly much more probable than the contact with the belly on which the pollen adheres.

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The treatment of eleven other *Cassia* s.l. species contains no additional facts important for our subject. The relevant points can be summarized as follows:

Firstly, BURCK has seen a cloud of pollen emerging from the long pollinating-anthers but he did not connect this with sonication, instead he presented another, to our current knowledge incorrect reason: the bees entering into the flower should distort the stamens and when the bee leaves the flower, the anthers should rebound into the original position what leads to a shake-out of pollen. Probably this opinion was influenced by TODD 1882. “Agiter les étamines” is clearly described as movements by crawling bees.

Secondly, it is described that the bees eat the short anthers with the feeding-pollen (Beköstigungspollen). In reality the bee holds on to the anthers (or staminodes) with the help of the mandibles for the transmission of the vibration to the flower and anthers, respectively. This leads to bite-marks on the anthers and, in the case of powerful bees, also to more severe damage of the anthers.

Thirdly, BURCK believes that the mentioned bees introduce their proboscis through the pores into the feeding-anthers for eating pollen. We believe that such a behavior is completely impossible.

Thus there is not any reason for the conclusion that BURCK should have recognized sonication as an element of the exploitation of *Cassia* s.l. flowers for pollen. The leitmotif throughout the paper is the attempt to prove self-pollination and the lack of any effects of the visitors on pollination.

5. Reports on vibratory pollen-collection

In the literature known to us, LINDMAN 1902: 21–24, who reports observations on *Senna* in South America (Brazil), is the first record (doubted by

LOEW 1904: 362). The most important lines for our subject are:

(p. 22)

Insektenbesuche habe ich hauptsächlich bei *Cassia alata* beobachtet, und zwar teils von grossen, teils von kleinen Hummeln und in grösster Menge. Trotzdem habe ich nicht ganz ins Reine bringen können, was die Insekten bei dem Besuche hier eigentlich vorhaben. Die Blüten dieser Art haben ziemlich nahe zusammenstehende Blumenblätter, so dass das Insekt während der Arbeit innerhalb der Blüte wie in

(p. 23)

einem kleinen Kämmerchen eingeschlossen sitzt. Man sieht indessen, dass der Besucher sich mit den Füßen an den vier kleineren centralen Staubgefässen festhält. Die eigentliche Arbeit besteht in einer gewaltsamen Vibration des Insektenkörpers und zugleich der ganzen Blüte; dies dauert in jeder Blüte mehrere Sekunden fort und macht sich durch ein prasselndes Geräusch kund, das man schon von weitem bemerkt und das den ganzen Tag über von allen Seiten in den heissen Campos cerrados ertönt. Es ist selbstverständlich, dass die Hummeln durch diese vibrirende Bewegung den Blütenstaub aus den Antheren herausschütteln

Translation: (p. 22) I observed visits of insects mainly on *Cassia alata*, namely partly of large, partly of small bumblebees and in greatest quantity. Anyway, I was not fully able to sort out what the insects actually intend during their visits. The flowers of this species possess petals that are quite close to each other so that the insect during his work within the flower sits enclosed like (p. 23) in a small cubbyhole. However, one can see that the visitor clings with the legs to the four smaller, central stamens. The proper work consists in a violent vibration of the insect-body and at the same time of the whole flower; this takes in every flower some seconds, and makes itself known by a crackling noise which one perceives already from far, and which resounds during the whole day from all directions in the hot Campos cerrados. It is self-evident that the bumblebees by this vibratory movement shake out the pollen from the anthers

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SCHROTTKY 1908 observed vibratory pollen-collection in *Senna*, *Physalis* and *Solanum* in Paraguay:

(p. 25)

Cassia occidentalis L. Genaue Beobachtungen, welche ich über die Art des Blütenbesuches lange Zeit hindurch anstellte, haben ergeben, dass von einem „Ausmelken der Antheren“ bei keiner der besuchenden Bienenarten die Rede sein kann. Freilich dauert der Besuch der einzelnen Blüten nur so geringe Zeit, dass es sehr schwer ist, alle damit zusammenhängenden Umstände zu bemerken; die Bienen, bis auf eine Ausnahme nur grosse und grösste Arten, versetzen die Blüte in starke Vibration, so dass der Pollen aus den Antheren herausschüttelt und von der gewöhnlich ungemein starken Behaarung der

Biene aufgefangen wird. Ueber die einzelnen Besucher folgendes: *Oxaea flavescens* Klug ♂ die am schwersten zu beobachtende Art; der Besuch jeder Blüte dauert selten länger als $\frac{1}{2}$ Sekunde; *Augochlora* (*Pseudaugochloropsis*) *nigromarginata* Spin. ♀, die kleinste der diese Pflanze besuchenden Arten; um die Blüte in Vibration zu versetzen muss diese Biene verhältnissmässig riesige Anstrengungen machen, und so dauert der Besuch jeder Blüte auch eine ganze Zeit. Gut beobachten lassen sich auch die *Xylocopa*-Arten *splendidula* Lep. und *augusti* Lep., deren Besuch jeder Blüte 1—1½ Sekunden dauert.

(p. 49)

Physalis viscosa L. Die hängenden Blüten werden vorwiegend von Bienen der Gattung *Psaenythia* Gerst. besucht und zwar in erster Linie von den ♂♂ der *P. picta* Gerst., die reichliche Mengen von Pollen entnehmen. Ob auch Honig genascht wird, konnte ich nicht feststellen, da die Bienen infolge des von oben nicht sichtbaren Blüteneinganges dem Auge des Beobachters verborgen bleiben; jedenfalls ist es anzunehmen, da auch die ♀♀ in die Blüten eindringen und diese es doch nur auf den Honig abgesehen haben. Die ♂♂ bringen bald nach dem Einfliegen einen eigentümlichen zirpenden Ton hervor unter gleichzeitigen vibrierenden Bewegungen, um den Pollen herauszuschütteln.

(p. 50)

Solanum paniculatum L. Am 11. April früh 6¼ Uhr bemerkte ich eine *Ptiloglossa matutina* Schr. ♂ an den Blüten dieser Art. Die Biene schüttelt unter vibrierender Bewegung den Pollen aus den Antheren, dabei ist der stark nach vorn gekrümmte Hinterleib fest angedrückt, mit den Mittel- und Hinterbeinen streicht sie den Pollen zurecht, die Hinterschenkel sind dick damit bepackt.

Translation: (p. 25) *Cassia occidentalis* L. Exact observations, which I have performed on the mode of flower visitation over long time, showed that a milking of anthers is by no means the case in any of the visiting bees. Of course, the visit of the single flowers lasts so short time that it is very difficult to perceive all related circumstances; the bees, all – except for one – large and largest species, put the flower in strong vibration so that the pollen is shaken out from the anthers and is caught in the usually extraordinarily strong hairiness of the bee. The following about the individual visitors: *Oxaea flavescens* KLUG ♀, the species most difficult to observe; the visit of each flower lasts rarely longer than $\frac{1}{2}$ second; *Augochlora* (*Pseudaugochloropsis*) *nigromarginata* SPIN. ♀, the smallest of the bees visiting this plant; for putting the flower in vibration, this bee must make relatively tremendous efforts, and so the visit of a flower needs a lot of time. Easy to observe are the *Xylocopa* species *splendidula* LEP. and *augusti* LEP., their visit of each flower lasts 1–1½ seconds.

(p. 49) *Physalis viscosa* L. The pendulous flowers were predominantly visited by bees of the genus *Psaenythia* GERST., in fact in first line by the ♀♀ of the *P. picta* GERST., which take away large amounts of pollen. Whether also honey is nibbled, I could not ascertain because bees remain hidden for the eye of the observer because of the entrance of the flower not visible from above; in any case this is to assume because also the ♂♂ enter the flowers and these look surely only for the honey. After entering, the ♀♀ generate a peculiar chirping sound under a simultaneous vibratory movement, for shaking out pollen.

(p. 50) *Solanum paniculatum* L. On 11 April early 6¼ o'clock I observed a *Ptiloglossa matutina* SCHR. ♀ on the flowers of this species. The bee shakes out pollen from the anthers under a vibratory movement, in doing so the strongly forward-bent abdomen is tightly appressed, with the middle and hind legs she spreads the pollen even, the hind femurs are thickly loaded with it.

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Observations of MEIDELL on the behavior of *Megachile willughbiella* and *Bombus* species exploiting flowers of *Melampyrum pratense* done in summer 1934 were published posthumously (MEIDELL 1944). Therein vibratory pollen-collection is clearly described, and it is the first report from Europe:

(p. 9)

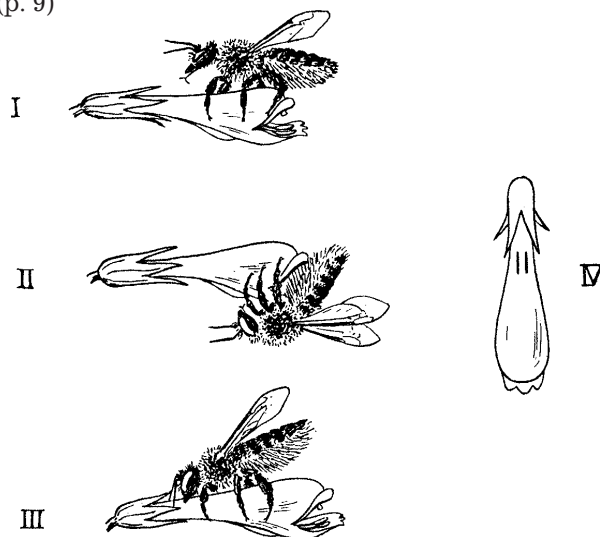


Fig. 1: *Megachile willughbiella* ♀. Collecting pollen (I and II) and nectar (III) on *Melampyrum pratense*.

All the four last-mentioned humble-bees are »active thieves« — they bite a hole in the corollar tube as soon as the flowers are big enough. In this field I gathered several samples of 50 plants each in full bloom, and it turned out that the corollae of more than 80 % were bitten open by humble-bees or by the bee *Megachile willughbiella*.

The latter also is an important visitor on *M. pratense*. Although its pro-

(p. 10)

boscis is sufficiently long to reach the nectary in the usual way, it appears, strangely enough, that on this plant it applies a special method of collecting nectar and pollen. (Fig. 1). The bee first places itself on the top of the flower (I), then turns swiftly round to the under side of the flower with the head downwards so that the scopa nearly shuts the opening of the flower. (II). In this position it whirs swiftly and vigorously two or three times, so that the flower is put into violent vibration: the pollen is showered out and is gathered in the scopa. Thereupon the bee turns round with lightning rapidity to the upper side of the flower (III), where it forces its head against the corollar tube, forcing the pointed mandibles through its wall. In this way two splits are made, (IV), through which the proboscis is put in. The whole process is carried out very quickly — all in all about 4 to 5 seconds.

Not so clear is MEIDELL's description for the bumblebees, whether the vibration is produced

with or without wing beat. But from own observations of bumblebee workers on *Melampyrum pratense* near Semriach (Styria, Austria), 21 Aug 1991, it can be confirmed that *Bombus lucorum* makes true v. p.-c. with the opening of the corolla pressed against the ventral side of the bee and with wings folded to the body. Bumblebees apparently show a comparable behavior on flowers of some *Pedicularis* species (MACIOR 1969, 1971; in the first paper the phrase “and wing motion ceased” together with the photos are clear indications for sonication).

The correctness of MEIDELL's observations was doubted by BUCHMANN 1985: 519 because they had not been confirmed by further studies until then. Besides, no sonication activity had been reported for *Megachilidae* up to that time. However, NEFF & SIMPSON 1988 who detected v. p.-c. in *Megachile mendica* on *Chamaecrista fasciculata* advocated MEIDELL. And since the proof of v. p.-c. by *Megachile willughbiella* itself on *Solanum lycopersicum* (TEPPNER 2005: 224–225, 231) any doubt on the findings of MEIDELL is no longer possible.

One author who must have been very familiar with v. p.-c. was OSORNO-MESA 1947 who has studied mainly *Bombus* on *Borago*, *Solanum*, *Monochaetum* and *Senna*. He published his short paper long before the new era of research in v. p.-c., which began in the early sixties, e.g., with MICHENER 1962.

In retrospect it is very surprising that authors who were somewhat ‘living’ with their bumblebees such as HOFFER (e.g. HOFFER 1885, on *Solanum dulcamara*, strong pressing of anthers by the mandibles), WAGNER 1907, and KUGLER (e.g. KUGLER 1938) did not discover or have not written about sonication (buzzing) as an essential element in flower visitation, different from the flight-sounds. At least we have not found any respective note in their comprehensive works till now.

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References

- ARCEO-GÓMEZ G., MARTÍNEZ M. L., PARRA-TABLA V. & GARCÍA-FRANCO J. G. 2011. Anther and stigma morphology in mirror-image flowers of *Chamaecrista chamaecristoides* (Fabaceae): implications for buzz pollination. – *Plant Biology* 13 (Suppl. 1): 19–24. – <<http://onlinelibrary.wiley.com/doi/10.1111/j.1438-8677.2010.00324.x/pdf>>.
- BUCHMANN S. L. 1985. Bees use vibration to aid pollen collection from non-porocidal flowers. – *Journal of the Kansas entomological Society* 58(3): 517–525. – <<https://www.jstor.org/stable/pdf/25084671.pdf>>.
- BURCK W. 1887. Notes biologiques. 2. Dispositions des organes dans les fleurs dans le but de favoriser l'auto-fécondation. – *Annales du Jardin botanique de Buitenzorg* 6: 254–265, 1 planche. – <<https://www.biodiversitylibrary.org/item/24940#page/266/mode/1up>>.
- BURKART A., LUNAU K. & SCHLINDWEIN C. 2011. Comparative bioacoustical studies on flight and buzzing of Neotropical bees. – *Journal of Pollination Ecology* 6(16): 118–124. – <<http://www.pollinationecology.org/index.php?journal=jpe&page=article&op=view&path%5B%5D=120>>.
- DE LUCA P. A. & VALLEJO-MARIN M. 2013. What's the ‘buzz’ about? The ecology and evolutionary significance of buzz-pollination. – *Current Opinion in Plant Biology* 16(4): 429–435. – <https://ac.els-cdn.com/S1369526613000630/1-s2.0-S1369526613000630-main.pdf?_tid=87974530-d764-11e7-beab-00000aab0f27&acdnat=1512221423_704a8eb85c79e727267c1c8e5a2bd9e6>.
- DULBERGER R., SMITH M. B. & BAWA K. S. 1994. The stigmatic orifice in *Cassia*, *Senna*, and *Chamaecrista* (Caesalpiniaceae): morphological variation, function during pollination, and possible adaptive significance. – *American Journal of Botany* 81(11): 1390–1396. – <<https://www.jstor.org/stable/pdf/2445310.pdf>>.
- ENDRESS P. K. 1992. Zu Christian Konrad SPRENGELS Werk nach zweihundert Jahren. – *Vierteljahrsschrift der naturforschenden Gesellschaft in Zürich* 137(4): 227–233. – <http://www.ngzh.ch/archiv/1992_137/137_4/137_26.pdf>.
- ENDRESS P. K. 1994 [first paperback edition (with corrections) 1996]. Diversity and evolutionary biology of tropical flowers. – Cambridge tropical Biology Series. – Cambridge University Press. – <https://books.google.at/books?id=8_DfMSS9r9cC&printsec=frontcover&hl=de&source=gb_s_ge_summary_r&cad=0#v=onepage&q&f=false>.
- EICHLER A. W. 1875. Blüthendiagramme, 1. – Engelmann, Leipzig. – Reprint Koeltz, Eppenhain, 1954. – <<https://www.biodiversitylibrary.org/item/45472#page/15/mode/1up>>.
- GOTTSBERGER G. & SILBERBAUER-GOTTSBERGER I. 1988. Evolution of flower structures and pollination in Neotropical *Cassiinae* (Caesalpiniaceae) species. – *Phyton* (Horn, Austria) 28(2):293–320. – <http://www.zobodat.at/pdf/PHY_28_2_0293-0320.pdf>.
- HARRIS J. A. & KUCHS O. M. 1902. Observations on the pollination of *Solanum rostratum* DUNAL and *Cassia chamaecrista* L. – *The University of Kansas Science Bulletin* 1(1): 15–43, 1 plate. – <<https://www.biodiversitylibrary.org/item/21218#page/25/mode/1up>>.
- HERBST P. 1918. Über Lautäusserungen einiger chilenischer Blumenwespen (*Apidae*). – *Deutsche entomologische Zeitschrift* 1918(1–2): 93–96. – <<https://www.biodiversitylibrary.org/item/103200#page/109/mode/1up>>.
- HOFFER E. 1885. Beobachtungen über blütenbesuchende Apiden. – *Kosmos* (Stuttgart) 17: 135–139. – <<https://www.biodiversitylibrary.org/item/88550#page/657/mode/1up>>.
- JESSON L. K. & BARRETT S. C. H. 2002. [Enantiostyly:] Solving the puzzle of mirror-image flowers. – *Nature* 417: 707. – <<http://www.nature.com/articles/417707a>>.
- KUGLER H. 1938. Blütenökologische Untersuchungen an Hummeln. IX. Die optische Nahwirkung von natürlich-

- chen Blüten und Blütenständen. – *Planta* (Berlin) 29(1): 47–66. – <https://link.springer.com/article/10.1007/BF01909090>.
- LINDMAN C. A. M. 1902. Die Blüteneinrichtungen einiger südamerikanischer Pflanzen. I. *Leguminosae*. – Bihang till kongl. svenska Vetenskaps-Akademiens Handlingar 27, Afdelingen III (14): 1–63. – <https://www.biodiversitylibrary.org/item/49807#page/739/mode/1up>.
- LOEW E. (ed.) 1904. KNUTH P., Handbuch der Blütenbiologie. III. Die bisher in aussereuropäischen Gebieten gemachten blütenbiologischen Beobachtungen, 1. – Leipzig. – <https://www.biodiversitylibrary.org/item/63950#page/7/mode/1up>.
- MACIOR L. W. 1969. Pollination adaption in *Pedicularis lanceolata*. – *American Journal of Botany* 56(8): 853–859. – <https://www.jstor.org/stable/pdf/2440626.pdf>.
- MACIOR L. W. 1971. Co-evolution of plants and animals – systematic insights from plant-insect interactions. – *Taxon* 20(1): 17–18. <https://www.jstor.org/stable/pdf/1218530.pdf>.
- MARAZZI B., CONTI E. & ENDRESS P. K. 2007. Diversity in anthers and stigmas in the buzz-pollinated genus *Senna* (*Leguminosae*, *Cassiinae*). – *International Journal of Plant Science* 168(4): 371–391. – <https://www.jstor.org/stable/pdf/10.1086/512105.pdf>.
- MEEHAN Th. 1886. On the fertilization of *Cassia marilandica*. – *Proceedings of the Academy of natural Sciences of Philadelphia* 38:314–318. – <https://www.jstor.org/stable/pdf/4061367.pdf>.
- MEIDELL O. 1944. Notes on the pollination of *Melampyrum pratense* and the “honeystealing” of humble-bees and bees. – *Bergens Museum Arbok Naturvitenskapelig Rekke* 11: 1–12.
- MICHENER Ch. D. 1962. An interesting method of pollen collecting by bees from flowers with tubular anthers. – *Revista de Biología tropical* 10(2):167–175. – <http://www.ots.ac.cr/rbt/attachments/volumes/vol10-2/06-Michener-Pollen.pdf>.
- MÜLLER F. 1883. Two kinds of stamens with different functions in the same flower. – *Nature* 27(694): 364–365. – <https://www.nature.com/articles/027364b0.pdf>.
- MÜLLER H. 1882. Weitere Beobachtungen über Befruchtung der Blumen durch Insekten. III. – *Verhandlungen des naturhistorischen Vereins der preussischen Rheinlande und Westfalens* 39. – Reprint with separate pagination, p. 1–104, 2 plates. https://archive.org/details/bub_gb_s5LAAAAYAAJ.
- MÜLLER H. 1883. Arbeitstheilung bei Staubgefäßen von Pollenblumen. – *Kosmos* (Stuttgart) 13: 241–259. – <https://www.biodiversitylibrary.org/item/88172#page/327/mode/1up>.
- NEFF J. L. & SIMPSON B. B. 1988. Vibratile pollen-harvesting by *Megachile mendica* CRESSON (*Hymenoptera*, *Megachilidae*). – *Journal of the Kansas entomological Society* 61(2): 242–244. – <https://www.jstor.org/stable/pdf/25084993.pdf>.
- OSORNO-MESA H. 1947. Observaciones antecológicas sobre recolección de polen por vibración. – *Caldasia* 4(20): 465–467. – <https://revistas.unal.edu.co/index.php/cal/article/view/32784/32779>.
- ROBERTSON Ch. 1890. Flowers and insects. V. – *Botanical Gazette* 15(8): 199–204. – <https://www.jstor.org/stable/pdf/2994757.pdf>.
- SCHROTTKY C. 1908. Blumen und Insekten in Paraguay. – *Zeitschrift für wissenschaftliche Insektenbiologie* 4 (1–2): 22–26, 47–52, (3): 73–78. – <https://www.biodiversitylibrary.org/item/43842#page/69/mode/1up>.
- SHAW F. R., BAILEY J. S. & BOURNE A. I. 1939. The comparative value of honeybees in the pollination of cultivated blueberries. – *Journal of economic Entomology* 32(6): 872–874. – <https://academic.oup.com/jee/article-abstract/32/6/872/2202171>.
- SPRENGEL Ch. K. 1793. Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. – Vieweg, Berlin. <https://www.biodiversitylibrary.org/item/105865#page/3/mode/1up>.
- TEPPNER H. 2005. Pollinators of tomato, *Solanum lycopersicum* (*Solanaceae*), in Central Europe. – *Phyton* (Horn, Austria) 45(2): 217–235. – https://static.uni-graz.at/fileadmin/_Persoenliche_Webseite/teppner_herwig/Phyton_45-2_217-235_Solanum_lyc.pdf.
- TODD, J. E. 1882. On the flowers of *Solanum rostratum* and *Cassia chamaecrista*. – *The American Naturalist* 16(4): 281–287. – <https://www.biodiversitylibrary.org/item/128882#page/293/mode/1up>.
- VAN DER PIJL L. 1939. Over de meeldraden van enkele *Melastomataceae*. – *De tropische Natuur* 28(10): 169–172. – <http://natuurtijdschriften.nl/download?type=document;docid=511512>.
- WAGNER W. 1907. Psycho-biologische Untersuchungen an Hummeln mit Bezugnahme auf die Frage der Geselligkeit im Tierreiche. – *Zoologica* (Stuttgart) 19(46), III + 239 p., 1 plate. – Schweizerbart, Stuttgart. <https://www.biodiversitylibrary.org/item/39519#page/75/mode/1up>.

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