Journal of Apicultural Research 32(3/4): 175-186 (1993)

The behaviour of honey bees (*Apis mellifera*) visiting avocado (Persea *americana*) flowers and their contribution to its pollination

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Keywords: honey bees, *Apis mellifera,* avocado, *Persea americana,* pollen, flowering, pollination, foraging, cross pollination, in-hive pollen transfer

SUMMARY

Observations of honey bee (*Apis mellifera*) foraging behaviour on five cultivars of avocado (*Persea americana*) were carried out in 1982-1984 and 1990-1992 in Galilee, Israel. Examination of the morphology of avocado flowers showed that the pistillate and staminate flower stages have similar structures. Bees collecting nectar, or nectar and pollen, visited both pistillate and staminate flowers, and due to the flower structure they were forced to touch both pistil and anthers. Only limited sites on a bee's body contacted the anthers, and these 'collection sites' also contacted the stigma, which occupied the same position as the anthers of the inner stamens. Most avocado pollen grains on bees visiting staminate flowers were clumped at the 'collection sites' and constituted the main pollen available for pollination. Some pollen grains randomly distributed over the entire bodies of bees visiting either pistillate or staminate flowers could have been acquired inside the hive, and did not play an important role in pollination. The observations suggest that pollination within a cultivar is accomplished during the overlapping phase of its pistillate and staminate flowering, during which bees collecting nectar and pollen move freely among neighbouring staminate and pistillate flowers. Pollination between cultivars of opposite flowering type is carried out by bees moving between them throughout the overlapping period of pistillate flowering of one cultivar and staminate flowering of the other. Bees which collect only pollen usually do not visit pistillate flowers and do not contribute to pollination.

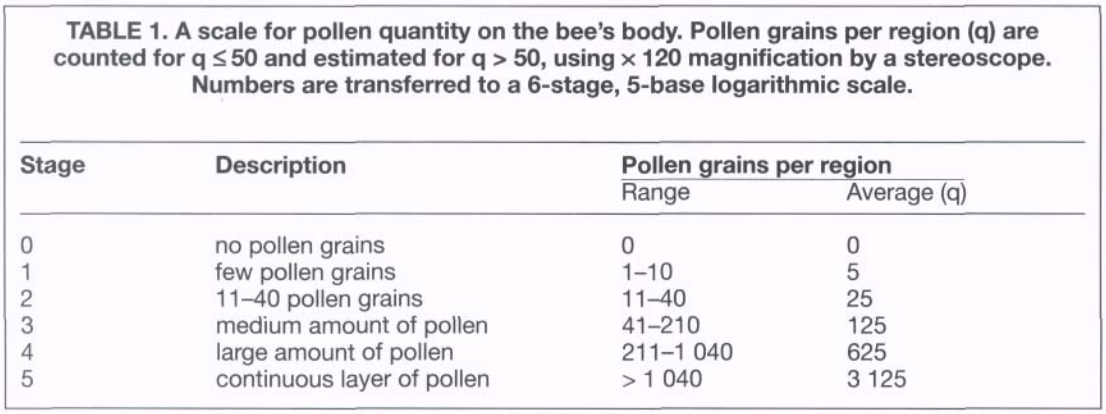

TABLE 1. A scale for pollen quantity on the bee's body. Pollen grains per region (q) are counted for q ≤ 50 and estimated for q > 50, using × 120 magnification by a stereoscope. Numbers are transferred to a 6-stage, 5-base logarithmic scale.

Stage	Description	Pollen grains per region	
		Range	Average (q)
0	no pollen grains	0	0
1	few pollen grains	1–10	5
2	11–40 pollen grains	11–40	25
3	medium amount of pollen	41–210	125
4	large amount of pollen	211–1 040	625
5	continuous layer of pollen	> 1 040	3 125

INTRODUCTION

Flower morphology

The avocado (*Persea americana*) has an androgynous, 1-cm diameter circular flower, which consists of six trimeric alternate whorls (two whorls of tepals, three of stamens and one of staminodes) and a pistil (fig. 1). Each stamen bears a terminal anther with four valves, that turn up while opening, drawing out the pollen grains with them. Each of the three inner filaments bears two nectaries, and the three staminodes function as nectaries by themselves.

The flowers are situated on terminal panicles, on which new flowers open daily during the flowering period. Each flower opens twice (dianthesis), usually on two successive days, in a protogynous rhythm. During the first (pistillate) opening the stigma is exposed and receptive. The closed valved stamens are attached to the tepals and the nectar is secreted by the three staminodes. Anther dehiscence follows the second (staminate) opening, while the stigma is covered by the three inner stamens and turns brown. The other six stamens bend to the pistil at about 45°, and nectar is secreted by the six nectaries (Stout, 1923,1933; Bergh, 1969; McGregor, 1976; Scholefield, 1982; Davenport, 1986,1991; Ish-Am & Eisikowitch, 1992a).

Flowering phenology

The flowering process is synchronous within a tree (and the cultivar). Two distinct flowering types have been described (Stout, 1923, 1933): 'A type' culti-vars open pistillate stage flowers in the morning and close at noon. These flowers reopen for the staminate stage on the next day at noon, and close on that same afternoon. 'B type' cultivars present an opposite flowering course: they open the pistillate stage flowers in the afternoon, close them at dusk, and reopen them for the staminate stage the next morning until noon (Bringhurst, 1951; Bergh, 1969; Papademetriou, 1976; Scholefield, 1982; Davenport, 1986, 1991).

Ish-Am and Eisikowitch (1992a) divided the daily flowering course of the tree into 15 phases, according to the flower stages it bears. They found that the commercial cultivars in Israel exhibit a daily bisexual phase, during which some of the morning flowers overlap with the afternoon ones (see also Stout, 1923, 1933; Bringhurst, 1951; Gustafson & Bergh, 1966; Papademetriou, 1976; Sedgley, 1985). The daily phase times are highly correlated with the daily average temperature (T_{avg}): a decrease of 1°C of T_{avg} delays flowering times by 30-60 min (Ish-Am & Eisikowitch, 1992a). Therefore, on cold days the morning phases are delayed until the afternoon, the afternoon phases appear during the next morning, and the whole course turns to 'an opposite flowering rhythm' (Stout, 1923,1933; Bringhurst, 1951; Lesley & Bringhurst, 1951; Bergh, 1969; Sedgley & Grant, 1983; Davenport, 1986).

Pollination

Due to its protogynous anthesis it is accepted that the avocado is unable to accomplish a fertile self-pollination within a single flower. On the other hand, according to its flowering rhythm and through a pollination agent, its flowers may be both cross-pollinated and close-pollinated (from flower to flower on the same tree, Stout (1933)), between cultivars and within the cultivar respectively (Stout, 1933; Lesley & Bringhurst, 1951; Gustafson & Bergh, 1966; Bergh, 1967; Davenport, 1986,1991; Ish-Am & Eisikowitch, 1991b). In Central America, where the avocado is native, it is pollinated by local social bees (Meliponinae) and wasps (Vespidae) (Free & Williams, 1976; Papademetriou, 1976; Davenport, 1986). However, away from this native region its main pollinator is the honey bee (*Apis mellifera*), and therefore colonies are regularly distributed within the orchards throughout the flowering period (Stout, 1923; Gustafson & Bergh, 1966; Bergh, 1967,1969,1977; Gazit, 1977; Davenport, 1986; Vithanage, 1990; Ish-Am & Eisikowitch, 1991b).

The efficacy of honey bees as avocado pollinators has been questioned however. Although beehives may be placed in an orchard, it is common to find the bees visiting competing flowers during a considerable part of the flowering season, leaving the avocado unvisited, unpollinated and with no fruitlets (Stout, 1923; Bergh, 1977; Gazit, 1977; Davenport, 1986; Vithanage, 1990; Ish-Am & Eisikowitch, 1992b).

The present study is aimed at investigating the behaviour of honey bees while visiting avocado flowers, and evaluating their suitability for and contribution to avocado pollination.

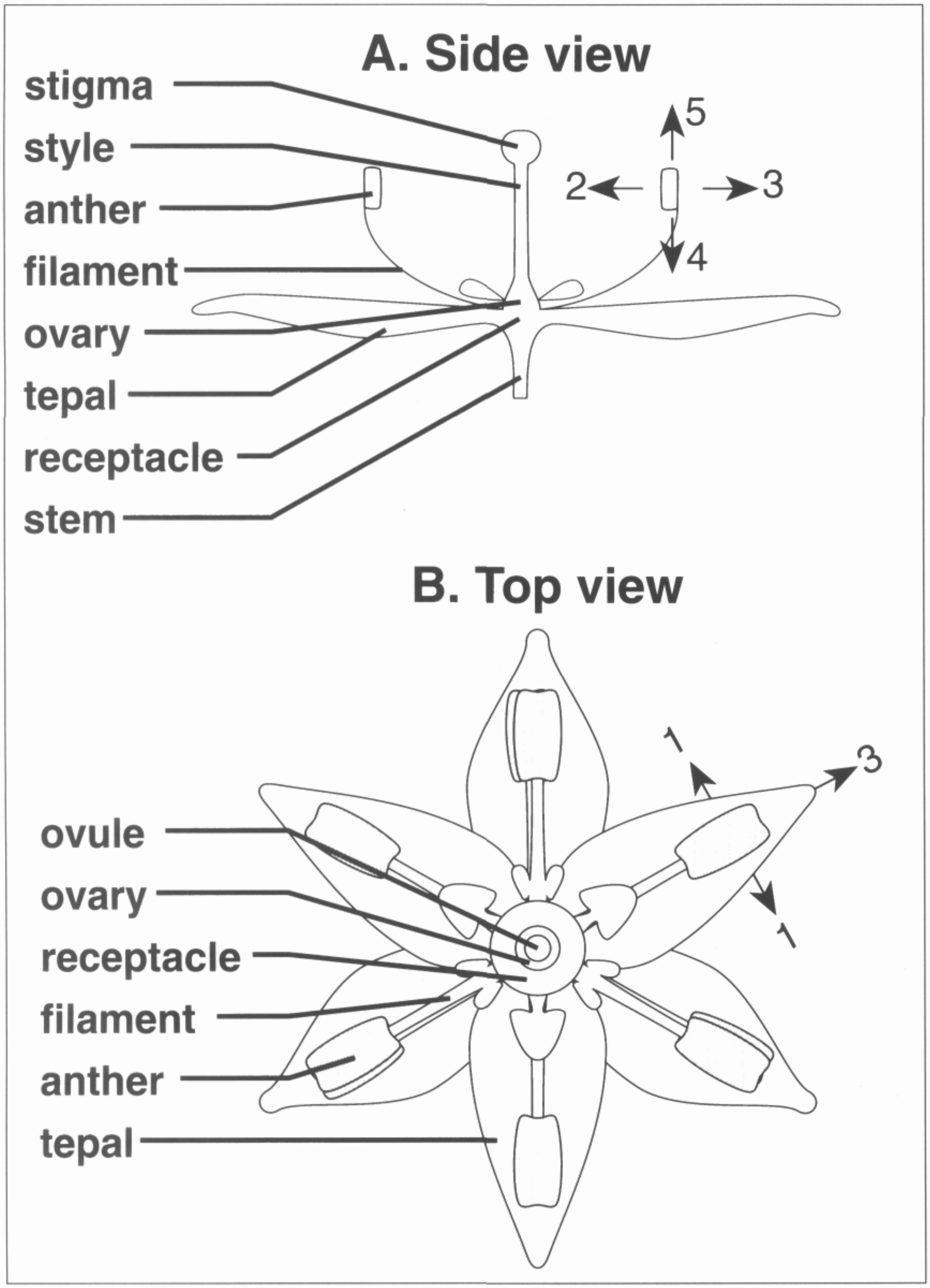

FIG. 1. Flower morphology and definition of directions of pollen exposure of a circular flower. 1: Tangential exposure. 2: Central exposure. 3: Peripheral exposure. 4: Basal exposure. 5: Distal exposure.

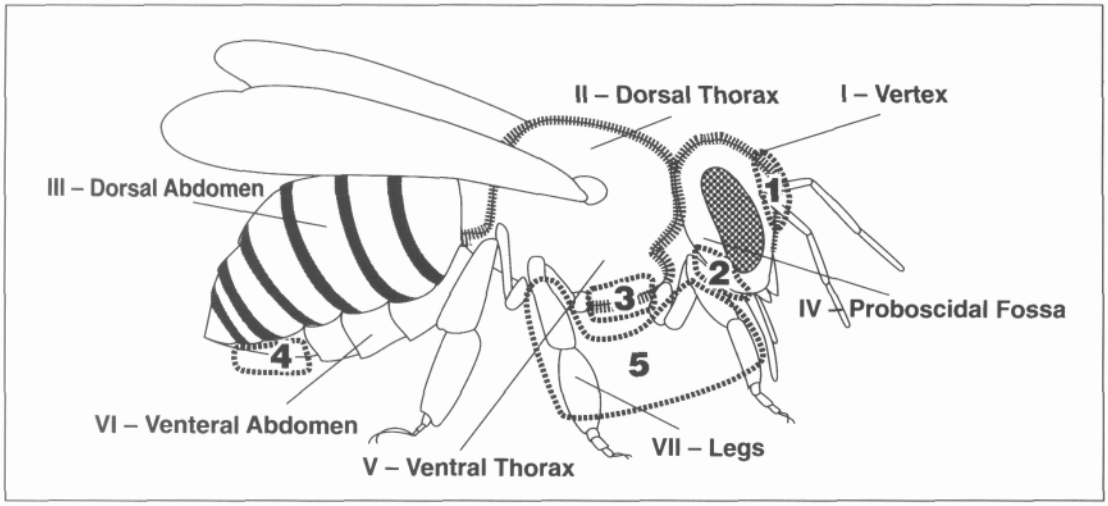

FIG. 2. Regions on the bee's body and the 'collection sites' of avocado pollen. Regions on the bee's body (dashed) are designated by Roman numerals I–VII. The leg region (VII) does not include the pollen-collecting apparatus. The avocado 'collection sites' (dotted, Arabic numerals) are: 1: Centre of vertex. 2: Proboscidal fossa. 3: Centre of ventral thorax. 4: Centre of VI and VII. 5: Inside surfaces of four forelegs.

MATERIALS AND METHODS

Observations were carried out during the flowering seasons of 1982-1984 and 1990-1992 in avocado orchards located in western Galilee, Israel, on the cultivars 'Fuerte', 'Hass', 'Ettinger', 'Nabal' and 'Reed'. Honey bee colonies were placed in the orchards during the flowering season.

Morphology of flowers is described according to field measurements (using a 0.5 mm scale and macro still photography) and laboratory measurements (stereoscope and SEM photography). Bees were tracked on the trees and their behaviour was recorded using audio tape, macro still photography and videotape.

Foraging bees were collected in a glass flask containing cotton wool with CCl_4 without direct touch. By means of this method bees were narcotized within 4 s, whilst grasping the cotton wool with their legs. After about 30 min bees were pinned laterally into an insect box, while their wings were held by forceps. Pollen grains were counted and mapped on the bee's body regions using x 120 magnification (fig. 2). The number of pollen grains per region may exceed 1 000, yet by this method one can safely count only 50-100 grains per region. Therefore, for more than 50 grains per region an estimation method was employed, and the figures were transformed to a 6-stage logarithmic scale, in which each stage is five times bigger than the previous one (table 1).

Temperature and humidity were recorded during field observations. Statistical calculations were implemented according to Sokal and Rohlf (1981).

RESULTS

Flower measurements

Measurements of pistillate and staminate flowers of the cultivars 'Fuerte', 'Ettinger' and 'Hass' are presented in table 2. A significant increase in flower size was measured during the two anthesis stages, and therefore only measurements of fully opened flowers were taken. On hot days (T_{max}> 32°C) and cold days (T_{max} < 18°C) some of the flowers were smaller and the variance was greater. Therefore, measurements were carried out on mild days (32°C > T_{max} > 18°C). 'Hass' had the biggest flower and 'Ettinger' had the smallest, while staminate flowers were significantly bigger than pistillate ones (by 10-17%) for all three cultivars. The 'Ettinger' pistil was the shortest, and had the widest stigma of the three cultivars (table 2).

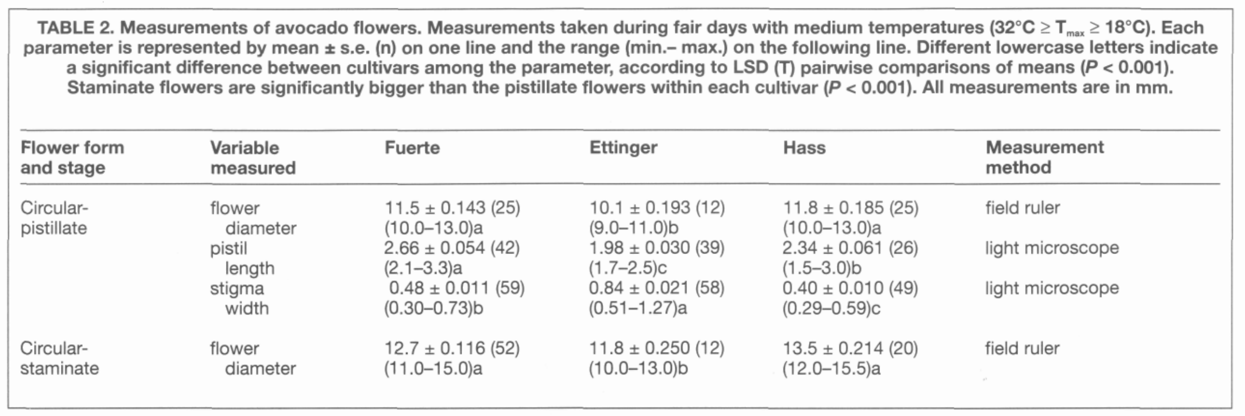

TABLE 2. Measurements of avocado flowers. Measurements taken during fair days with medium temperatures (32°C ≥ T_{max} ≥ 18°C). Each parameter is represented by mean ± s.e. (n) on one line and the range (min.– max.) on the following line. Different lowercase letters indicate a significant difference between cultivars among the parameter, according to LSD (T) pairwise comparisons of means ($P < 0.001$). Staminate flowers are significantly bigger than the pistillate flowers within each cultivar ($P < 0.001$). All measurements are in mm.

Flower form and stage	Variable measured	Fuerte	Ettinger	Hass	Measurement method
Circular-pistillate	flower diameter	11.5 ± 0.143 (25) (10.0–13.0)a	10.1 ± 0.193 (12) (9.0–11.0)b	11.8 ± 0.185 (25) (10.0–13.0)a	field ruler
	pistil length	2.66 ± 0.054 (42) (2.1–3.3)a	1.98 ± 0.030 (39) (1.7–2.5)c	2.34 ± 0.061 (26) (1.5–3.0)b	light microscope
	stigma width	0.48 ± 0.011 (59) (0.30–0.73)b	0.84 ± 0.021 (58) (0.51–1.27)a	0.40 ± 0.010 (49) (0.29–0.59)c	light microscope
Circular-staminate	flower diameter	12.7 ± 0.116 (52) (11.0–15.0)a	11.8 ± 0.250 (12) (10.0–13.0)b	13.5 ± 0.214 (20) (12.0–15.5)a	field ruler

Flower forms

We distinguished four main forms of the flower throughout its development (fig. 3).

1. **Circular form:** tepals spread at right angle to the pistil. This form appears in fully opened pistillate and staminate flowers. During hot and dry days the distal section of the tepals bends down towards the pedicel, and the flower turns to a narrow-circular form (fig. 4).
2. **Cup form:** tepals form a cup, in which the pistil occupies the centre. This form appears in opening and closing flowers, both pistillate and staminate.
3. **Oval form:** tepals almost closed, leaving an oval space around the pistil, stamens and nectaries. This form appears in both pistillate and staminate flowers.
4. **Closed form:** tepals completely closed. This form is characterized in flowers before the pistillate and after the staminate anthesis, as well as between the two anthesis stages.

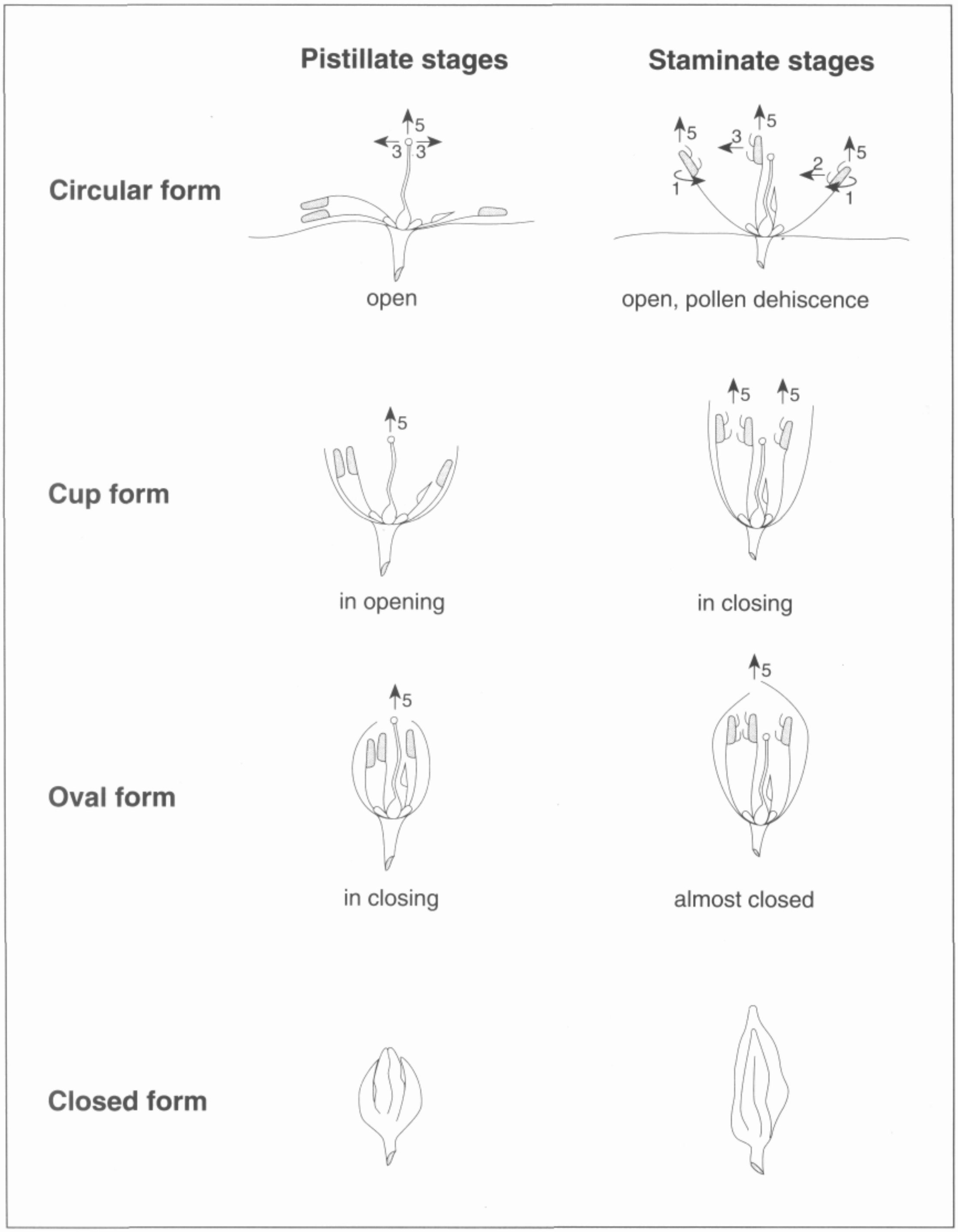

FIG. 3. Forms of the avocado flower. Arrows and figures indicate directions of pollen and stigma exposure (see also fig. 1). 1. Tangential exposure. 2: Central exposure. 3: Peripheral exposure. 4: Basal exposure. 5: Distal exposure.

Directions of stigma and pollen exposure

Five directions may be defined regarding a circular flower (figs 1 and 3):

1. **Tangential direction:** a course going tangentially to the flower circle.
2. **Central direction:** a radial course directed towards the pistil.
3. **Peripheral direction:** a radial course directed from the pistil towards the periphery.
4. **Basal direction:** a course directed perpendicularly from the distal part to the flower's receptacle.
5. **Distal direction:** a course directed from the receptacle towards the distal part of the flower.

The stigma is exposed distally throughout all the pistillate stages, and also peripherally during the circular opening (fig. 2). The pollen, being attached to the open valves, is exposed distally, peripherally, tangentially and centrally. Pollen is exposed peripherally, tangentially and distally by the inner stamens. The outer stamens expose the pollen centrally, tangentially and distally (fig. 5).

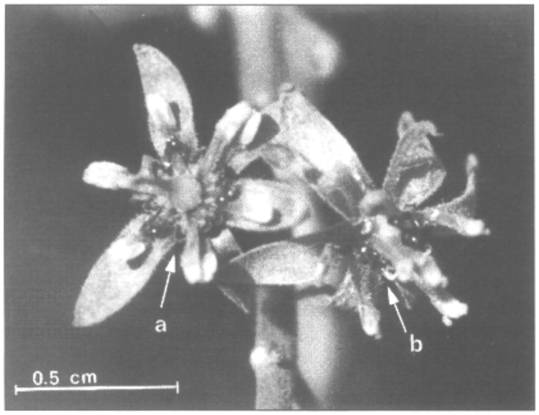

FIG. 4. Bisexual flowering of Hass. Field photography at noon (× 4). a: Circular pistillate flower from the morning, before closing. b: Narrow-circular staminate flower, lastly opened, releasing pollen.

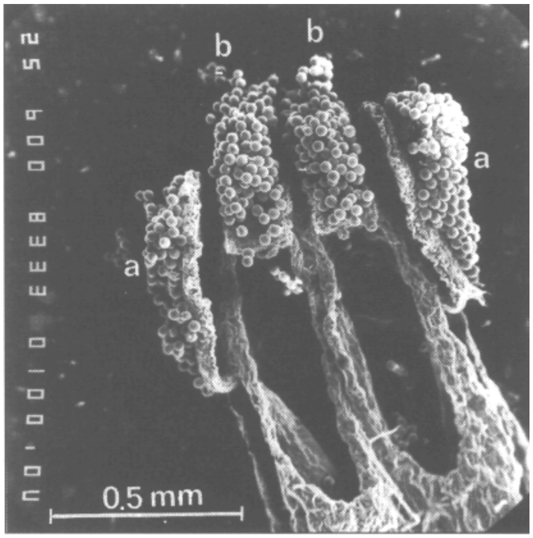

FIG. 5. Pollen exposure of Fuerte outer stamen. All 4 valves open (SEM × 47). a: Lower valve: tangential exposure. b: Upper valve: central and distal exposure.

Behaviour of honey bees

The bees walked among individual flowers of an inflorescence in full bloom, and flew between inflorescences. During the end of the flowering period only a few flowers were open in each inflorescence, and the bees flew among them as well. While visiting the relatively small flowers a bee often encountered some difficulties: sometimes it slipped while moving on the flower, and grasped other parts of the inflorescence with its hind-legs. This phenomenon was most pronounced on the relatively small flowers of 'Ettinger'. Otherwise, bee behaviour was similar on the cultivars observed.

Positions of bees collecting nectar, or nectar and pollen, were very similar while visiting pistillate and staminate flowers of equivalent form (fig. 6). On a circular flower a bee could occupy two positions, a side position and a top one, usually in that order. In the side position, the bee touched the near nectaries by turning its body left and right. Upon moving to the top position and collecting from the other nectaries, the bee turned around using the pistil as an axis (fig. 7). Sometimes a bee landed immediately in the top position, and then turned around, collecting from all the nectaries. Individual bees turned consistently to one direction, either clockwise or counter-clockwise.

While visiting a pistillate flower a bee was directed towards only three nectaries (the staminodes) and, therefore, its movements were faster and more precise than on a staminate flower presenting six nectaries. A bee visiting a cup-shaped, oval or closed flower reached the nectar by inserting its proboscis between neighbouring tepals, either through their distal tips (when occupying top or side position) or between their edges (while holding the basal position) (fig. 6).

Nectar-collecting bees visit both pistillate and staminate flowers for 2-10 s per visit (Ish-Am & Eisikowitch, unpublished data). While visiting a staminate flower a bee's body becomes dusted with pollen, which the bee cleans off after every 2-4 visits, whilst hovering or hanging on a leaf. Bees usually pack the pollen into their corbiculae, forming pellets, but some of them were seen 'deliberately' unloading the pollen, throwing it down while cleaning themselves, and collecting nectar only. Bees that collected only pollen also were observed; these bees visited almost exclusively circular staminate flowers. Their visits were very short, and in less than 1 s they touched the anthers while hovering, or whilst landing instantly in the top position. Their buzzes sounded lower than usual, and a small cloud of pollen could sometimes be seen around them during the visit. Sometimes pollen-collecting bees also collected some nectar. They performed 1-2 collections of nectar per 10 pollen collections, during which they sometimes visited pistillate flowers, if present in the vicinity.

Contact with pollen and stigmas Only limited and definite sites of a bee's body contacted the exposed pollen on the open valves ('collection sites' in fig. 2). A bee visiting a circular staminate flower made contact with the distally exposed pollen with its ventral regions, with the peripheral and central pollen with its vertex and proboscidal fossa and it approached the tangentially exposed pollen with its legs (figs 6 and 7). All these 'collection sites' also touched the stigma of the circular pistillate flower, due to the similarity of pistillate and staminate flowers and the identical location of the stigma and the anthers of the inner stamens (figs 3, 4 and 6). Additionally, when visiting a cup- or an oval-form flower, the bee's vertex and proboscidal fossa collected pollen and made contact with the stigmas.

Distribution of pollen on the bee's body Figure 8 presents the distribution of avocado pollen on a bee's body, according to flowering phase and cultivar. We found that most of the avocado pollen was located in the 'collection sites' in a clumped distribution (fig. 9) and only a few pollen grains were randomly distributed throughout all the body regions. The amounts of clumped pollen matched the flowering course of each cultivar: it was high on bees visiting staminate flowers, reached the maximum during pollen dehiscence, decreased after dehiscence and was not found during the pistillate flowering phase. The amount pf randomly distributed pollen, though much less than clumped pollen, matched the flowering course as well. Non-avocado pollen was observed on most bees, usually in random distribution, and only rarely were bees found carrying clumped non-avocado pollen (fig. 9).

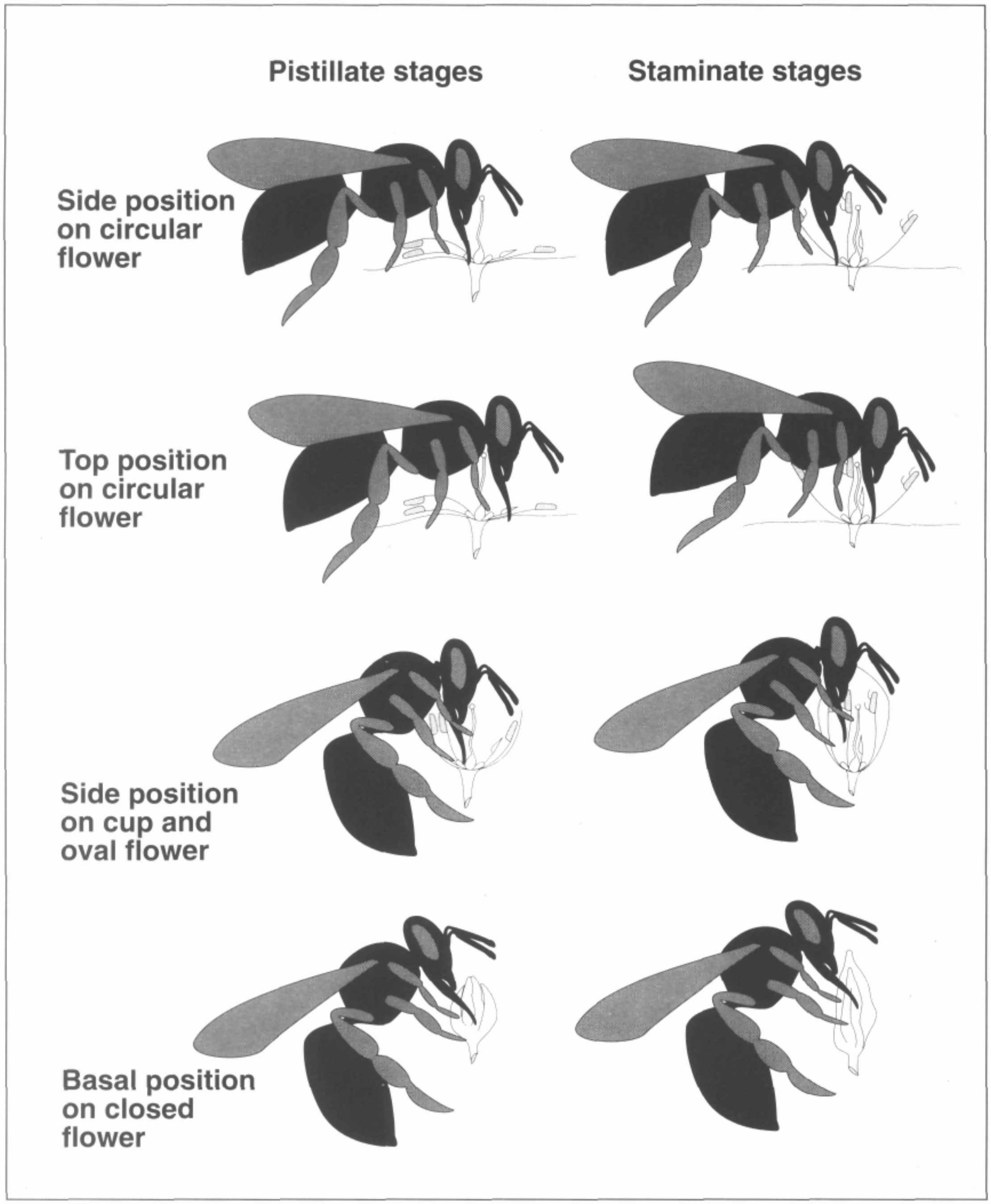

FIG. 6. The positions of bees on the flower forms.

FIG. 7. Top position of a bee on a circular staminate flower. Field photography of an Ettinger flower with all valves open (× 4.5). The bee collects nectar and pollen, and carries pellets.

DISCUSSION

The avocado flower seems not well suited for honey bee pollination (Vithanage, 1990) and seems to resemble a 'fly flower', rather than a typical 'honey bee flower' (Faegri & Pijl, 1979): the flower is shallow, greenish-yellow, has a light bitter smell and the nectar is fully exposed; the pollen and nectar, although easily collected, are not very attractive to bees; the flower has a radial symmetry, lacks a landing platform and is somewhat small for the bee; the inflorescence is too sparse to be visited as a unit, and bees seem to have difficulties holding tightly to the single flower (Davenport, 1986; Vithanage, 1990; Ish-Am & Eisikowitch, 1992b). This lack of suitability may explain the low level of attraction of avocado flowers for honey bees, which, in turn, has been identified as an important limiting factor of avocado fruitfulness outside its countries of origin (Vithanage, 1990; Ish-Am & Eisikowitch, 1992b).

However, when not competing with more attractive flowers of other species (usually during the second half of the flowering season), avocado flowers are well visited by honey bees (Ish-Am & Eisikowitch, 1992b), and nectar-collecting bees pollinate them efficiently, presumably because of the following factors:

1. The morphology of the open flower forms does not enable access by the bees without them touching the stigmas and anthers of both pistillate and staminate flowers

(fig.6).

2.Visiting bees touch both stigmas and anthers with the same 'collection sites', and therefore may transfer pollen effectively.

3.Nectar (or nectar and pollen) collectors move readily between staminate and pistillate flowers during foraging. Such movement is essential for avocado pollination, due to the absence of self fertilization within the flower.

4. Most importantly, the very high correlations between honey bee activity and both pollination and fruit set of avocado that have been found in Israel (Ish-Am & Eisikowitch, 1991 b, 1992b), indicate that honey bees are almost the sole pollinator there.

Although nectar-collecting bees show no constancy while visiting pistillate and staminate flowers, foragers can discriminate between flower types, since pollen-collecting bees prefer staminate over pistillate flowers. Both staminate and pistillate flowers contain a reward for visiting bees, and therefore their resemblance does not serve as a 'cheating' mechanism and a form of Mullerian mimicry (Baker, 1976; Vane-Wright, 1976). In fact, we suggest that this similarity serves to ease the transition between the different flower forms, as well as ensuring contact of both pollen and stigmas by the same 'collection sites'.

Bees which collect nectar or nectar and pollen play the major role in the pollination of avocado (Stout, 1933; Free, 1970; Davenport, 1986; Vithanage, 1990). They accomplish pollination within a cultivar (close-pollination) during its daily bisexual phase, moving freely among neighbouring pistillate and staminate flowers in an inflorescence (fig. 4) (Ish-Am & Eisikowitch, 1991 a, 1991b). The available pollen at that phase is carried mainly on the vertex and pro-boscidal fossa of bees since the pistillate flowers are mostly cup-formed, either closing or opening (A and B type cultivars, respectively) (figs 6 and 8).

Cross pollination, on the other hand, is performed by bees moving among trees of different cultivars, throughout the relatively long period of overlap of pistillate and staminate flowering (Stout, 1923,1933; Bergh, 1969, 1977; McGregor, 1976; Ish-Am & Eisikowitch, 1991 a, 1991b, 1992a). During these phases all 'collection sites' bear available pollen for pollination, since both pistillate and staminate flowers are in circular form (figs 6 and 8). Cross pollination is crucial for cultivars of partial self-incompatibility (Stout, 1923,1933; Gustafson & Bergh, 1966; Free, 1970; Bergh, 1977; Gazit, 1977; Degani *et al.*, 1989). Its efficacy depends mainly on both distance and bees' mobility between the cultivars (Ish-Am & Eisikowitch, 1991b).

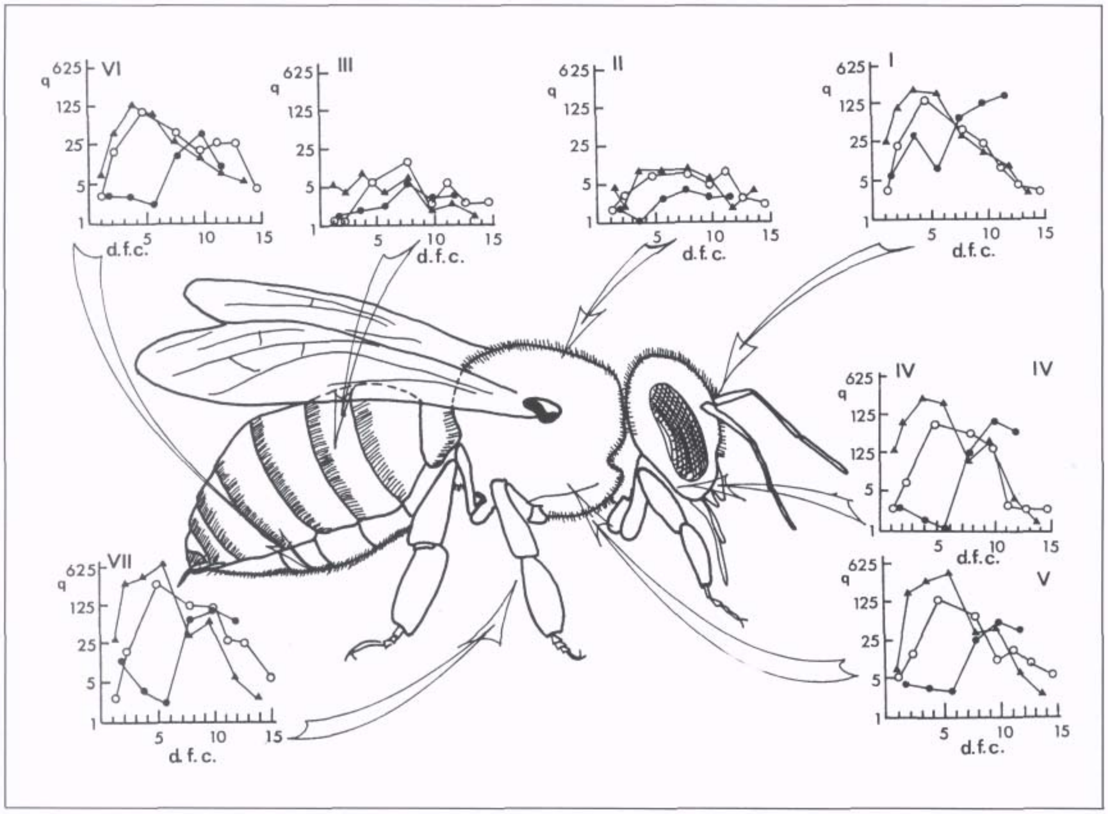

FIG. 8. Distribution of pollen grains on the bee's body during the daily flowering course. q: Number of pollen grains per region (logarithmic scale). Daily flowering course (d. f. c.) is divided into the following 15 phases:
Fuerte: 1–6 staminate, 7–10 bisexual, 11–15 pistillate (– ▲ –)
Ettinger: 1–6 staminate, 7–11 bisexual, 12–15 pistillate (– o –)
Hass: 1–6 pistillate, 7–8 bisexual, 9–15 staminate (– • –)
(After Ish-Am & Eisikowitch, 1992a). The regions of the bee's body are described in fig. 2.

Free and Williams (1972) showed that pollen transfer between flowers may be carried out not only directly, during the foraging flight, but also indirectly, through pollen exchange among bees within the hive. This idea gained more support from the works of DeGrandi-Hoffman *et al.* (1984a, 1984b, 1986), which show that most pollination of apples, and probably almonds, is a product of indirect pollen transfer in the hive. Some investigators have suggested this way of pollen transfer as an explanation for avocado pollination, both between cultivars (through pollen exchange among bees in the hive) and within the cultivar (by pollen grains retained on the body from the staminate to the pistillate flowering phase) (Free, 1970; Free & Williams, 1976; Bergh, 1977; Gazit, 1977; Davenport, 1986).

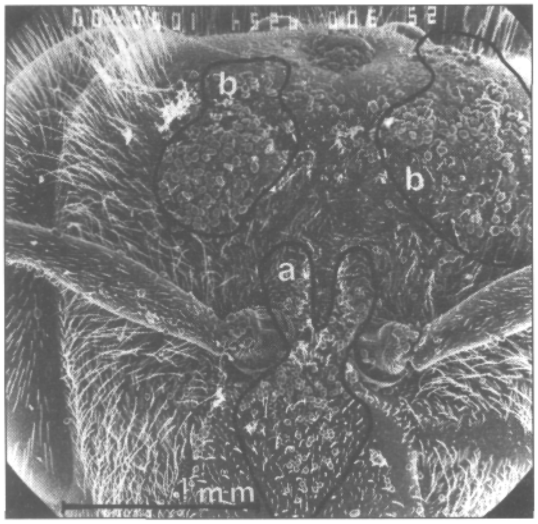

FIG. 9. Pollen on a bee's vertex (SEM × 34). The bee was active on staminate flowers of Fuerte during pollen dehiscence. a: Avocado pollen clamped between antennae. b: Clumped pollen of *Hirschfeldia incana* (Cruciferae), a spot above each antenna.

Nevertheless, our findings show that avocado pollination by honey bees is mainly a process of direct pollen transfer, and that indirect pollination plays a limited role, if any. Only avocado pollen that is carried on the 'collection sites' during visits to pistillate flowers is available for pollination (fig. 8). The clumped pollen may be accumulated only directly during foraging, while the randomly distributed pollen grains on the bodies of bees visiting pistillate flowers, consisting of only 0-5 grains per region (fig. 8), may explain only a small amount of pollination. Furthermore, checks of honey bees departing the hive showed that only a small portion of the randomly distributed avocado pollen (about 10%, Ish-Am & Eisikowitch, unpublished) is attained within the hive, and most of it is probably spread over the bee's body whilst it cleans itself in the field (Free & Williams, 1972; DeGrandi-Hoffman *et al.,* 1984b). It seems that, in contrast to the pollen of many Rosaceae, Brassicaceae and others, honey bees efficiently clean avocado pollen from their bodies. This may be another aspect of the low suitability of honey bees for avocado pollination.

ACKNOWLEDGEMENTS

We wish to thank M Darom and R Teicher for statistical assistance, A Shub for field photography, the late M Ish-Am for helping in observations and R Direktor for useful comments.

This study was funded in part by the Israeli Beekeepers Memorial Fund, by the Israeli Fruit Growers Organization, by the 'New Projects' Fund of the Israeli Agriculture Ministry and by the David Ben-Gurion Fund of the Israeli General Workers Organization.

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(Received 24 February 1993, accepted subject to revision 17 April 1993, accepted for publication 7 September 1993)