Hajime TANAKA*: **Relationship between ultraviolet and visual spectral guidemarks of 93 species of flowers and the pollinators**

田中 肇*: 紫外線および可視光線による花のガイドマークと送粉者との関係

Through behavioural tests and conditioning experiments, v. Frisch (1914) showed that workers of the honeybee, *Apis mellifera*, possess colour vision. In 1958, Daumer, one of v. Frisch's disciples, investigated upper and lower limits of the visual spectrum of the bee and established that these insects perceive ultraviolet rays (the 300–400 nm waveband) as a distinct colour. Detailed electro-physiological studies by Autrum and co-worker (Autrum & Burkhardt 1961, Autrum 1968) completely verified the earlier behavioural reports and showed that the visual cells in the eye of the bee had response peaks to light of 340, 436–460, and 530 nm wavelengths. As shown by numerous other studies recently reviewed by Menzel (1980), it is now obvious that the bee is not only insect that perceives colours. To be able to distinguish ultraviolet, blue and green colours, appears to be a property of most insect species irrespective of the fact that they visit flowers or not.

Many flowers possess patterns on their petals visible to the human eye. However, in addition to these ' nectar guide ' there are often paterns which the human eye cannot perceive, but which can be observed using ultraviolet photographs (Daumer 1966) or television cameras (Eisner et al. 1969). The ultraviolet patterns are believed to be caused chiefly flavonols (Thompson et al. 1972). A further flower/ultraviolet interaction has been reported by Thorp et al. (1976) and Nakanishi (1980): nectar and anthers of *Prunus mume*, respectively, fluoresce under illumination with ultraviolet light.

The question whether the ultraviolet pattern could be related to ecological flower type (Blütengestalt oder Blumentypen) was investigated by Kugler (1963), who made observations on 361 species of flowers using ultraviolet photographs and photographs based on human visual spectrum (HVS). According to Kevan (1972, 1978) the colours of flowers plotted in a colour-triangle

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based on HVS form distinct clusters. When plotted in a triangle based on insect's perceptibility (ultraviolet-blue-green) the flowers are more widely distributed in the triangle. In other words, separation is enhanced and insects perceive more kinds of differently coloured flowers than humans. Utech & Kawano (1975), in a comparative analysis (HVS versus ultraviolet photographs) of flowers of 54 species representing 22 families, found that flowers of plants growing in exposed places absorb ultraviolet radiation more strongly than plants growing in sheltered regions.

All previous studies (reviewed by Kevan 1972, Proctor & Yeo 1973) seem to agree that the ultraviolet patterns of flowers are somehow aimed at insect, but a close inquiry into the special relatioship between the taxon of pollinator and the type of guidemark of a flower has, so far, not been undertaken. With this aim in mind 93 species of wild flowers representing 33 families, were investigated through HVS and ultraviolet photography.

Material and methods The flowers of 93 species of native Angiosperms, representing 33 families, were surveyed from February 17th through to May 5th, 1980. Most flowers were photographed on the living plant; a few were photographed within several minutes after cutting. The observations were carried out in Hidaka-cho, Iruma-gun and Han-no city (Saitama prefecture) and Nerima-ku, Tokyo.

The ultraviolet photography was similar to that used by Tanaka (1980). An Asahi Pentax MX camera with 50 mm macro-lens in combination with extension tubes or bellows, depending on the size of flowers, was used. For the exclusive use of ultraviolet rays, a Kodak Wratten 18A filter was fixed on the lens. Kodak Tri-X Pan film was used throughout the study. Pictures were taken under natural light conditions with the diaphragm set at f=5.6, 8 or 11. Exposure time varied between 1/8—16 sec.

Information supplied by Kodak showed that the filter used trasmits more than 10% of near ultraviolet rays between 325 and 390 nm, and that peak transmission (80%) is to radiation of 360 nm wavelength. Tri-X Pan film is sensitive to radiation ranging from infrared to ultraviolet (approximately 300 nm). According to information obtained from Asahi Optical Company the spectral transmission of the macro-lenses used was 0% for radiation lower than 340 nm wavelength, 50% at 360 nm and 81% at 380 nm. We can, therefore, assume that the pictures used in this study were photographed primarily in

Tab. 1. List of species examined, UV reflection of flower organs and existence of guidemarks.

Species	Fig.	UV reflection			Guidemark		Pollination type
		Perianth	Stamen	Pistil	UV	HVS	
Compositae							
Youngia japonica	3	+−	−	±	+	±	
Sonchus oleraceus	2	+−	−	−	+	−	
Ixeris japonica		+−	−	−	+	±	HDL
Taraxacum officinale	1	+−	−	−	+	−	Apogamy
T. platycarpum		+−	−	−	+	−	HDL
Hieracium japonicum		+−	−	−	+	−	HD
Lapsana humilis		+−	−	±	+	−	
Senecio pierotii (ray) (disk)		+ −	−	−	+	−	HD
S. vulgaris	4	−	−	−	−	−	D
Petasites japonicus		−	−	−	−	−	
Erigeron philadelphicus (ray) (disk)	5	± −	−	−	−	+	HD
Gnaphalium affine		−	−	−	−	−	
Caprifoliaceae							
Viburum phlebotrichum		±	−	−	−	−	
Rubiaceae							
Galium spurium		±	±	±	−	−	S
Scrophulariaceae							
Veronica didyma		±−	−	−	+	+	S
V. persica		±−	−	−	+	+	HD
V. arvensis	6	+−	−	−	+	+	S
Mazus japonicus (lower lip)		−+		+	+	+	H
M. miquelii (lower lip)		−		+	−	+	H
Labiatae							
Lamium purpureum	7	−+	+	+	+	+	H
L. amplexicaule		−±	−		+	+	H
Glechoma hederacea (lower lip)		−			−	+	H
Ajuga decumbens (lower lip)	9	±+	±	±	+	+	

Boraginaceae							
Trigonotis peduncularis		−+			+	+	
Convolvulaceae							
Calystegia hederacea	10	±−	−	−	+	+	H L
Gentianaceae							
Gentiana zollingeri		±−±	−	−	+	+	H
Ericaceae							
Pieris japonica		±			±	−	
Rhododendron kaempferi	8	+−	±	−	+	+	H L
Cornaceae							
Aucuba japonica (male)		±	±		−	−	D
(female)		±		−	±	±	
Stachyuraceae							
Stachyurus praecox	11	−	−	−	−	±	
Violaceae							
Viola verecunda		−		+	−	+	H
V. gripoceras		±				+	H
V. yedoensis	13	±−			±	+	H
V. mandshurica		±−			±	+	H
V. keiskei		±−			±	+	H
V. dissecta var. *eizanensis*		±+			±	+	H
Theaceae							
Camellia japonica	14	+	−		+	+	B
Oxalidaceae							
Oxalis corniculata	20	+−	±	±	+	±	H D
forma *rubrifolia*		+−	±	−	+	+	H D
O. articulata		+−	−	±	+	+	
Rutaceae							
Orixa japonica (male)		±	±		+	−	
(female)		±		−	+	−	
Zanthoxylum piperitum		−	+		−	−	
Leguminosae							
Astragalus sinicus		−	+	+	−	+	H
Vicia hirsuta		−			−	−	
V. tetrasperma		±−			+	+	
V. angustifolia	15	±−±			+	+	H
Wisteria floribunda		±+			+	+	H

Rosaceae							
Chaenomeles japonica		±	±		−	±	H B?
Rubus hirsutus	19	−	+	+−	±	±	H D
R. palmatus var. *coptophillus*		−+	±	±	+	±	H
R. microphillus		±+	+−		+	±	
Potentilla freyniana	16	+−	−	−	+	±	
P. kleiniana		+−	−	−	+	±	D
Duchesnea chrysantha	17	+	−	−	+	±	H D
Kerria japonica	18	+	−	−	+	−	H D
Spiraea thunbergii		±	−	−	+	+	
Saxifragaceae							
Chrysosplenium macro-stemon var. *atrandum*		+	−+	−	−	−	
Cruciferae							
Capsella bursa-pastoris		−	−	−	−	±	D
Rorippa indica		+	−	−	+	±	
Wasabia japonica	22	−	−	−	−	−	D
Cardamine flexuosa		±	−	−	−	−	
Orychophragmus violaceus		±	−		−	+	H
Papaveraceae							
Corydalis pallida var. *tenuis*	12	+−			+	±	H
C. incisa		±			−	+	H
C. decumbens		±−			+	+	H
Chelidonium majus		+	−	−	+	−	D
Magnoliaceae							
Magnolia kobus		−	−	−	−	±	
Lardizabalaceae							
Akebia quinata (male)		±	+		+	+	
(female)		±	+	−+	+	+	
Ranunculaceae							
Adonis amurensis		+−	−	−	+	−	D
Ranunculus cantoniensis		+−	±	−	+	±	
R. japonicus		+−	−	−	+	±	
R. sceleratus	21	+−	−	−	+	+	
Anemone flaccida		−	±		−	−	D
A. nikoensis		−	−	−	−	−	D

A. raddeana	23	−+	±	−	+	±	D
A. hepatica forma *variegata*		±	−	−	+	+	
Caryophyllaceae							
Stellaria alsine		±	−	−	+	±	
S. neglecta		±	−	−	±	±	D
S. media		±	−	−	±	±	D
Cerastium holosteoides var. *hallaisanense*	24	±	−	−	±	±	
Arenaria serpyllifolia		±	−	−	+	±	
Sagina japonica		±	±	±+	±	+	Ant
Spergularia marina		±	±	−	+	+	
Polygonaceae							
Rumex acetosa (male)		±	±				W
(female)		±		±			
Urticaceae							
Nanocnide japonica (male)		+−	+				W
Moraceae							
Broussonetia papyrifera (male)		−	±				W
(female)				−			
Fagaceae							
Quercus acutissima (male)		±	±				W
Salicaceae							
Salix gracilistyla (male)	25	−	±−		+	+	D
Lilliaceae							
Disporum smilacinum	26	±−	−	+−	+	±	
Juncaceae							
Luzula capitata		+−	−	−	−	+	W
Cyperaceae							
Carex ohwii		+−	−				W
Gramineae							
Poa annua	27	−	±				W
Alopecrus aequalis		−	+				W
Arundinaria chino		+−	±				W

UV reflection: +, strong reflection; ±, medium reflection; −, strong absorption. Guide marks: +, dstinct; ±, indistinct; −, absent. Pollination type: B, bird pollination; D, fly Pollination; H, bee pollination; L, butterfly and moth pollination; W, anemophilous. Perianth including bract.

Tab. 2. Guidemarks of 44 species and 1 forma of entomorphilous flowers and relation to type of pollinator.

			UV guidemarks +	UV guidemarks ±−
HVS guidemarks	+	H	7	10
		D	1	
		HD(L)	2	1
	±−	H	2	2 (9.5%)
		D	4	8 (61.5%)
		HD(L)	7	1 (9.1%)

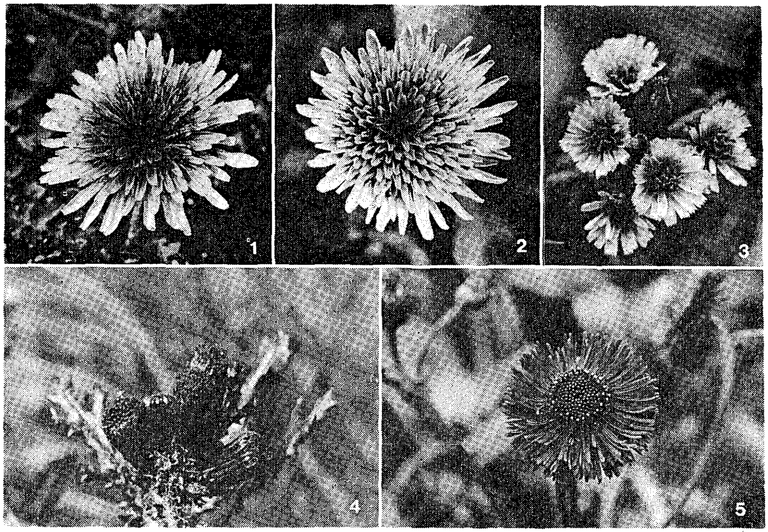
Symbols are explained in Tab. 1.

the 350-390 nm waveband (abbreviated as UV in this paper). The UV-photographs produced the complete range of tones from white and black. Based on the brightness of the pictures, I was able to classify them into the following three categories: strong reflection of UV, appearance white: +; medium reflection of UV, appearance grey: ±; strong absorption of UV, appearance black: −.

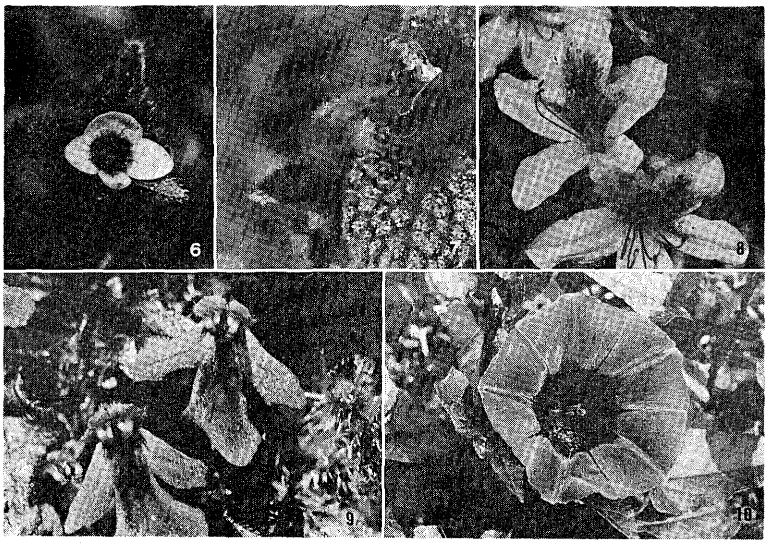
Observations Guidemarks (Holm 1979), here defined as a pattern different in colour and relative brightness, were found in a large number of flowers examined. In Table 1, which gives a summary of my observations, I have entered information on whether the plant species is autogamous or anemophilous, or whether pollination is achieved mainly by birds (B), flies (D), bees (H), or butterflies and moths (L).

UV-patterns of entomophilous flowers. Compositae: Ligulate florets of 7 species belonging to the Liguliflorae strongly absorbed UV at their bases, but the rest reflected UV. The heads (capitula) of the florets, therfore, combine to a pattern that resembles that of a series of concentric rings which were white at the periphery and black in the center. Flowers that appeared yellow to the human eye must have appeared to possess distinct guidemarks for flower-visiting insects (Figs. 1, 2, 3). Similar patterns were also found in the UV-absorbing tublar florets surrounded by UV-reflecting ligulate florets in the yellow heads of *Senecio pierotii*.

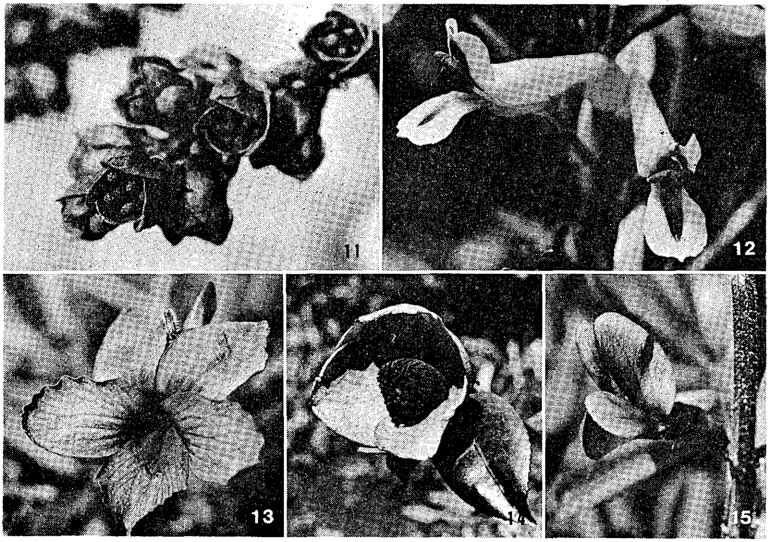
Scrophulariaceae: The entomophilous flowers of *Veronica persica* and the



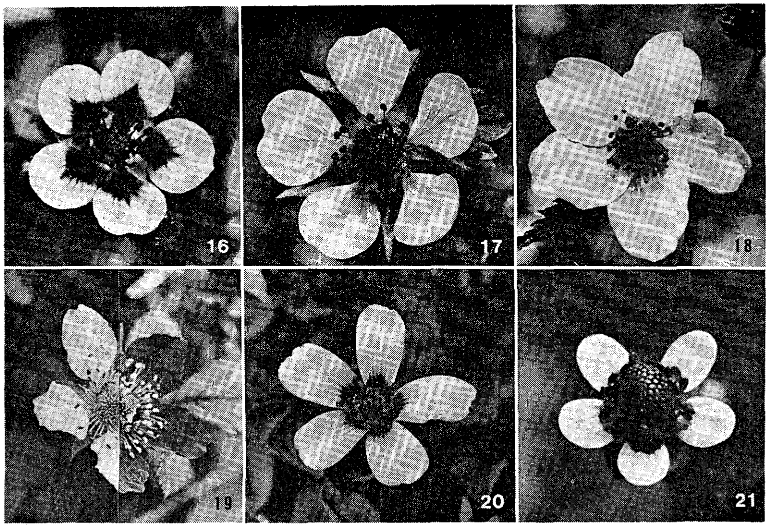
Figs. 1–5. UV photos of flowers. 1. *Taraxacum officinale*. 2. *Sonchus oleraceus*. 3. *Youngia japonica*. 4. *Senecio vulgaris*. 5. *Erigeron philadelphicus*.



Figs. 6–10. UV photos of flowers. 6. *Veronica arvensis*. 7. *Lamium purpureum*. 8. *Rhododendron kaempferi*. 9. *Ajuga decumbens*. 10. *Calystegia hederacea*.



Figs. 11–15. UV photos of flowers. 11. *Stachyurus praecox*. 12. *Corydalis pallida* var. *tenuis*. 13. *Viola yedoensis*. 14. *Camellia japonica*. 15. *Vicia angustifolia*.



Figs. 16–21. UV photos of flowers. 16. *Potentilla freyniana*. 17. *Duchesnea chrysantha*. 18. *Kerria japonica*. 19. *Rubus hirsutus* (the left half visible spectrum photo). 20. *Oxalis corniculata*. 21. *Ranunculus sceleratus*.

Figs. 22–27. UV photos of flowers. 22. *Wasabia japonica.* 23. *Anemone raddeana.* 24. *Cerastium holosteoides* var. *hallaisanense.* 25. Male inflorescens of *Salix gracilistyla.* 26. *Disporum smilacinum.* 27. Spiklets of *Poa annua.*

autogamous flowers of *V. didyma* and *V. arvensis* (Fig. 6) all showed the same patterns of high UV-absorption in the center.

Ericaceae: *Rhododendron kaempferi* (Fig. 8), a butterfly flower, has a very distinctive guidemarks. The corolla reflected UV, but in strong contrast to this, dark red spots inside it absorbed UV strongly.

Violaceae: In the case of each of the 6 species of *Viola,* the whole petals weakly reflected UV almost equally without regard to the colours of the flowers visible to human eye (Fig. 13).

Rosaceae: *Potentilla freyniana* (Fig. 16), *P. kleiniana* and *Duchesnea chrysantha* (Fig. 17) had yellow, five-petalous flowers which were very similar in shape. The flowers of the two species of *Potentilla* had UV guidemarks on their petals. *D. chrysantha* absorbed UV only with its stamens and pistils.

Cruciferae: Amongst 5 species studied UV guidemarks were not conspicuous, but at the base of the petals of the agricultural species *Brassica oleraceae* and *B. oleraceae* var. *capitata* UV guidemarks were found.

Papaveraceae: Strong UV absorption was observed at the front central part of the corolla of the yellow flower of *Corydalis pallida* var. *tenuis*

(Fig. 12).

Ranunculaceae: All the yellow flowers, such as those of *Adonis amurensis*, *Ranunculus cantoniensis*, *R. japonicus* and *R. sceleratus* (Fig. 22) absorbed UV at the bases of their petals, stamens and pistils. The white flowers of *Anemone nikoensis* and *A. flaccida* absorbed UV over almost the entire area.

UV-patterns of anemophilous flowers. The following 9 species of anemophilous flowers were surveyed: *Rumex acosta, Nanocnide japonica, Broussonetia papyrifera, Quercus acutissima, Luzula capitata, Carex ohwii, Poa annua* (Fig. 27), *Alopecrus aequalis* and *Arundinaria chino*. In *Luzula capitata*, which insects visited occasionally, guidemark patterns were visible in HVS examination. In the other species, however, there were no patterns recognizable either through HVS or UV photography that would show or direct toward the center of the flowers and advertise the inflorence to potential pollinators.

Discussion Flowers other than anemophilous ones that had distinct guidemarks, observable through HVS alone, belonged to 37 species (44.0% of examined species), but if we add those species that possessed guidemarks in the ultraviolet range the figure increases to 63 species (75.0% of examined species). The increase is considerably greater than what one would have expected: the HVS covers the wevelength band 400-700 nm, whereas the UV, made use of in this investigation (see Material and Methods), was mainly the 350-390 nm region. The result probably means that UV-reflection patterns are more powerful and efficient in attracting insect pollinators than patterns visible through HVS.

The major pollinators of the flowers studied in this investigation were bees, ants, flies, butterflies, birds or combinations of these. The three most important flower groups in relation to insect pollinators were 'bee-flowers', 'bee+fly-flowers' and 'fly-flowers'. If we correlate the HVS and UV guide marks with bee and fly pollinator, we find an interesting pattern (see Tab. 2). Only 2 species out of 21 bee- flowers (9.5%) and 1 species out of 11 bee+fly-flowers have guidemarks that are so insignificant that they cannot be recognized either through HVS or UV. On the other hand 8 species out of 13 fly-flowers (61.5%) have only weakly developed guidemarks or none at all.

It almost seems as if guidemarks are unnecessary if flies are the major pollinator. Yet, flies as well as dozens of other insect species tested behaviourally and electrophysiologically (Menzel 1980) see colours just as well as the bee or bumblebee (Meyer-Rochow 1981). In most insects colour vision, when developed, is tri- or tetra-chromatic and sensitivity peaks are usually present in the UV, blue and green parts of the spectrum. The difference in abundance of UV and HVS guidemarks between bee- and fly-flowers is, therefore, not likely to be a reflection of the fly's poorer colour discrimination, but appears to have other reasons.

Bees as well as bumblebees are social insects. They display a characteristic horming behaviour, return to a rich food source, and at least in the case of the honeybee recruit other worker bees. These Hymenopterans possess the ability to remember not only feeding sites, but also colours (Menzel 1968). I believe that plants employing specific guidemarks are interested in social Hymenopterans such as honeybees and bumblebees. These are not only very efficient pollinators, but also return to the plant bringing with them additional pollinators. One could almost say the plants with conspicuous guidemarks are taking advantage of the better brains and the higher social organization of bees.

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von Frish の学習法による研究でヨウシュミツバチではじめて昆虫の色の識別能力が証明された。その後の研究により，訪花昆虫を含む多数種の昆虫も，紫外線，青および緑色を区別できることが明らかにされてきた。また虫媒花を紫外線写真にし，肉眼では見ることのできないガイドマークの存在が知られるようになった。この紫外光のガイドマークの持つ意義については Daumer, Kugler, Kevan その他の研究者により各方面から論じられている。しかし，紫外線を含むガイドマークと送粉昆虫との関係は直接は論じられなかった。そこで私は，野生の被子植物 93 種の花を 350～390 nm の近紫外線 (UV) および可視光線 (HVS) で撮影し考察を試みた。撮影して得られた情報は Table 1 に示した。

風媒花以外の花で明瞭なガイドマークが認められた花はHVSのみでは37種(44.0%)であったが，これにUVによるデータを加えると63種(75.0%)となった。増加した26種は観察しうる波長が拡大した比から期待される種数の3.6倍にあたり，花がUVによるガイドマークにたよる比重が大きいことを示している。Table 2にはハナバチ媒花(H)，アブ・ハエ媒花(D)それにハナバチ・アブ・ハエ媒花(HD)とUVおよびHVSのガイドマークの明瞭度との関係を示した。この表から，ハナバチが受粉に関与する花ではUVでもHVSでもガイドマークが不明瞭(±)または認められない(−)花は9%台であるが，アブ・ハエ媒花では61.5%とその比が高いことが読みとれる。後者の花粉を媒花するハナアブやハエはハナバチを含む他の昆虫と同様に三または四元色の色覚を持つことが知られており，送粉者の違いによるガイドマークの存在比の相違を色覚に求めることはできない。それはさらに昆虫の脳内の別の情報処理能力に関連したものと考えられる。ハナバチはハナアブやハエより訪花・採餌能力が勝っており，ハナバチ媒花にガイドマークの出現率が高いのは，送粉者の視覚情報処理能力の高さを反映したものだと言える。

○*Ophiorrhiza staintonii* Hara について (D.B. デブ・D.C. モンダル)

D.B. Deb & D.C. Mondal: On the identity of *Ophiorrhiza staintonii* Hara (Rubiaceae)

Ophiorrhiza staintonii Hara in Jap. Journ. Bot. **52**(12): 358. 1977 was described on the basis of two gatherings—J. D. A. Stainton 6875 & 5380 from East Nepal and Sikkim respectively. In describing the species Hara (l. c.) observed that in general appearance it resembles some species of the genus *Mycetia* and that without fruiting material, the exact affinity of this plant is doubtful.

In connection with revision of Indian *Ophiorrhiza* L. the specimens received on loan from British Museum (Natural History), London, included the paratype Stainton 5380 of this species. It looks very different from all other specimens. A thorough examination of the specimen threw light on its proper identity, despite non availability of the fruit.

In the genus *Ophiorrhiza* the ovary is 2 locular with many ovules in axile placentation whereas in the plant concerned the ovary is 2 locular with one basal ovule in each locule. For this reason it cannot be treated under the genus *Ophiorrhiza*, nor can it represent the genus *Mycetia*.

On the other hand it is allied to *Psychotria* L. differing in comparatively longer flowers and corolla curved at the base in which respect the genus *Chassalia* differs from *Psychotria* L.