

Pollination of Four Sumatran *Impatiens* Species by Hawkmoths and Bees

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Abstract Flowering patterns and pollination syndromes were compared among four sympatric *Impatiens* species (Balsaminaceae) in tropical montane rain forests in Sumatra, Indonesia. Pink flowers with long filiform spurs of *I. platypetala* produced nectar of 26 % sugar both in the daytime and at night and were pollinated by crepuscular hawkmoths, *Macroglossum corythus*. Yellow flowers with gradually tapering spurs of *I. korthalsii*, *I. talangensis* and *I. eubotrya* produced nectar of 34-39 % sugar, mainly in the daytime, and were pollinated by two specialized long-tongued anthophorid bees and an unusually long-tongued halictid bee. Spur morphology essentially determined nectar accessibility. Although the three *Impatiens* species partially shared the three bee species, they partitioned their pollinators by differing in sites of pollen deposition on the bee's bodies. The low pollinator visitation rates per day were compensated by the extended flowering period of the four species. Nectar robbing by two anthophorid bee species was observed, for the first time in Southeast Asia.

Key Words: *Impatiens* / Sumatra / pollination / Halictidae / Anthophoridae

Deep flowers are thought to have coevolved with long-tongued, nectar-feeding organisms in various ecosystems in the world (Darwin, 1862). Many flowers having long-tubed or -spurred corollas are visited almost by long-tongued bumblebees and hawkmoths in the temperate zone (Heinrich, 1979), and by euglossine bees, hummingbirds and hawkmoths in the neotropics (Janzen, 1971; Dressler, 1982; Ackerman *et al.*, 1985; Roubik 1989). In the palaeotropics, there are many deep flowers especially on the forest floor, whereas detailed analyses on the pollination syndrome have not yet been done.

In general, *Impatiens* flowers (Balsaminaceae) have long-spurred sepals which secrete nectar. The spur structure of *Impatiens* is excessively prone to vary (Hooker, 1874). In the palaeotropics, there are more *Impatiens* species than in the temperate zone, where most *Impatiens* species are mainly pollinated by bumblebees (Heinrich, 1979; Rust, 1979; Kato, 1989). In Africa, there are 109 morphologically diverse *Impatiens* species, and out of these, 58 species were pollinated by butterflies, three by moths, 27 by birds and 21 by bees (Grey-Wilson, 1980).

Mountain area of Southeast Asia is also a center of diversification of *Impatiens* (Miquel, 1862; Ridley, 1922; Van Steenis, 1972). In Sumatra, Indonesia, 29 species are reported by Grey-Wilson (1989), and even in the province of Sumatera Barat 16 are found by Hotta (1989). This remarkable diversification is thought to be due to isolation by drier regimes (Grey-Wilson, 1989) or to sympatric speciation caused by polyploidy in chromosome number (Okada, 1989). In order to understand the diversification process, we need more information

on pollination and reproduction ecology of these tropical *Impatiens*.

In this paper, We report flowering patterns and pollination syndromes of four *Impatiens* species in the tropical montane forests in Sumatra. First, we compare nectar secretion patterns of the four species. Secondly, we describe four effective pollinators by comparing morphological characters of flowers and flower visitors. Furthermore, the pattern of pollinator visits to flowers and the effect of their behavior on seed set are analyzed. Pollination syndromes of deep flowers and long-tongued bees are also discussed among the three tropical regions.

MATERIALS AND METHODS

In and beside primary forests of Mt. Gadut and Mt. Talang areas in the province of Sumatera Barat, Sumatra, Indonesia, we found seven *Impatiens* species at elevations between 400 and 1800 m (Hotta, 1989). *Impatiens platypetala* has pink (rarely white) flowers, and the others have yellow flowers. Intensive field observations were carried out at Airsirah and Alahanpanjang (Fig. 1). There, four species, *I. platypetala* Lindley, *I. korthalsii* Miquel, *I. talangensis* Hotta, nom. nud. and *I. eubotrya* Miquel were relatively abundant. Airsirah was covered with a montane primary forest at an elevation of 950 m. The mountain slopes near small streams were covered with the vegetation of *Saurauja* spp. (Actinidiaceae), *Villebrunea rubescens* (Urticaceae) and others. *Impatiens korthalsii* were scattered in the forest understory near streams and *I. platypetala* grows in clumps in light gaps along the streams and/or road side open places. Alahanpanjang is located along a stream on the west slope of an active volcano, Mt. Talang, at an elevation of 1300 m. The study site is covered with primary and secondary mountain forests, the vegetation of which was largely the same with that of Airsirah. Along streams, three *Impatiens* species were abundant and partly grew together: *I. korthalsii* and *I. talangensis* were sparse, but *I. eubotrya* occurred in clumps.

To investigate the temporal patterns of flowering and the nectar production of *Impatiens*, at least five inflorescences were bagged with nylon nets to exclude visitors on January 11, 1988 at Airsirah, and on January 14, 1988 at Alahanpanjang. We estimated the nectar volume in each flower as a function of the depth of nectar in a spur. During the observations the depth of nectar of bagged flower was measured by backlighting. Simultaneously, unbagged flowers

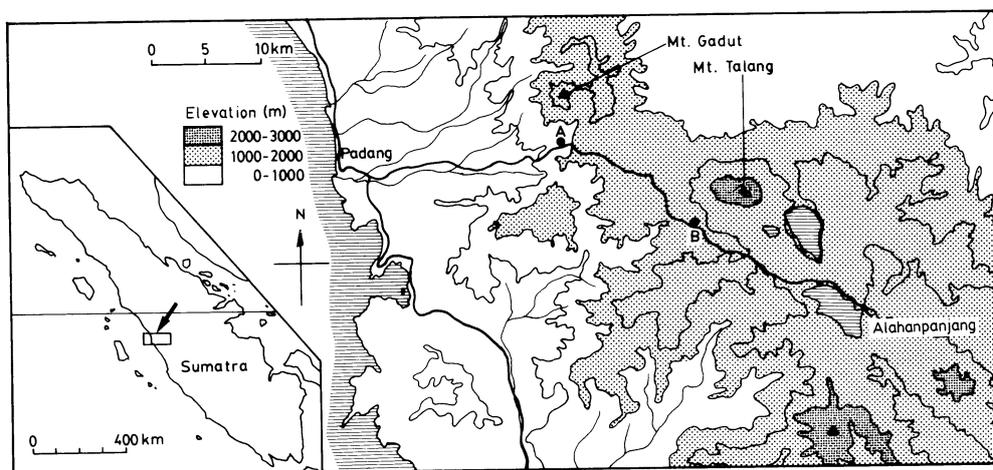


Fig. 1. The study sites (A, Airsirah; B, Alahanpanjang) in the province of Sumatera Barat and its location in Sumatra (inset).

were randomly sampled and the depth and volume of nectar were measured. At the end of observations, flowers were dissected to determine the relationship of the two variables. Measurements were made at about 5-hour intervals for >22 hours after flower opening. The nectar sugar concentration (weight/weight) was measured with a refractometer (Bellingham Stanley Ltd.). Bagged and unbagged inflorescences were sampled on 30 January 1988 to record fruit- and seed-set.

After preliminary observations and a haphazard collection of visitors to *Impatiens* during 21 - 31 December 1987, continuous periods of observation of insect visitors at *Impatiens* flowers were carried out from 6 to 30 January 1988. For each *Impatiens*, we selected a patch of flowering plants. We sat beside the patch for >8 hours to record the timing of visits, the flight paths of visitors between the flowers, and the time spent on each flower. Air temperature, relative humidity and light intensity were measured simultaneously. The temporal pattern of pollinator visits to flowers of *I. platypetala*, *I. korthalsii* and *I. eubotrya* were observed on 7-8, 12 and 15 January 1988, respectively. For *I. talangensis*, we only observed and collected pollinators for about 4 hours on 15 January 1988. All captured insects were examined for pollen with a microscope.

RESULTS

Floral morphology and flowering

The four *Impatiens* were distinct in their arrangement of petals and sepals, disposition of the peduncle and structure and curvature of the spur (Fig. 2). *I. platypetala* had a flattened flower with an erect dorsal petal and a shallow lower sepal, abruptly constricted into a long filiform spur. The others were slender funnel-type flowers with a hooded dorsal petal. The lower sepal of *I. korthalsii* and *I. talangensis* was shallowly boat-shaped, gradually tapering into a slightly curved spur, but that of *I. eubotrya* was narrowly sac-shaped and abruptly constricted into an incurved spur. The lower petals of *I. korthalsii* and *I. talangensis* were extended well beyond the tip of the lower sepals, thus forming prominent lips, but those of *I. eubotrya* were not so extended. The peduncle of *I. eubotrya* was distorted to leftside and the spur projected. Flower color was pink in *I. platypetala* and yellow in the other three species (Table 1). The

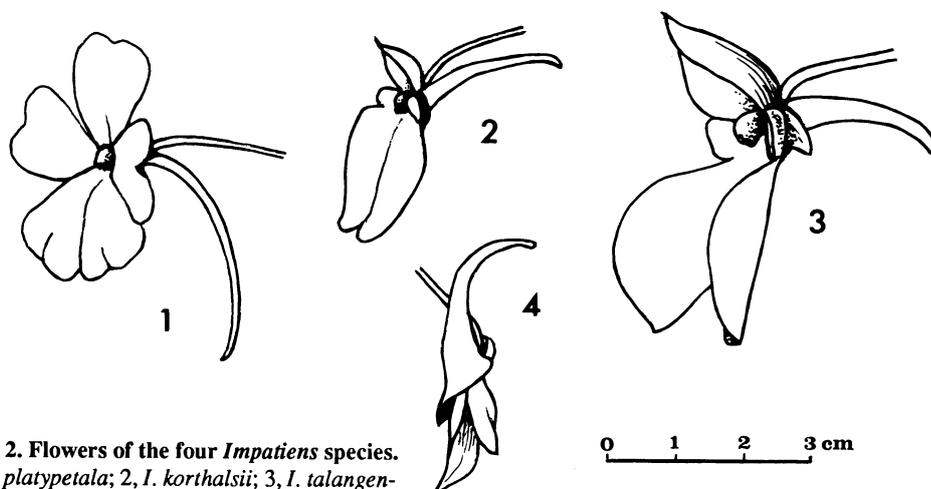


Fig. 2. Flowers of the four *Impatiens* species. 1, *I. platypetala*; 2, *I. korthalsii*; 3, *I. talangensis*; 4, *I. eubotrya*.

Table 1. Flower characters and nectar production patterns of the four *Impatiens* species. The mean is followed by the number of samples and the standard deviation (n, s.d.).

Characters	<i>Impatiens</i> species			
	<i>platypetala</i>	<i>korthalsii</i>	<i>talangensis</i>	<i>eubotrya</i>
Flower color	pink or white	yellow	yellow	yellow
Length of spur (mm)	31.5 (18, 2.0)	21.7 (14, 2.0)	22.9 (7, 1.0)	24.0 (9, 2.7)
Flowering duration (days)	3.8 (12, 0.6)	2.7 (9, 0.4)	4.1 (2, 0.5)	1.8 (58, 0.6)
Sugar concentration (%)	26.1 (21, 7.1)	37.9 (30, 6.3)	33.8 (2, 8.8)	39.4 (58, 3.2)
Nectar production rate (µl/h)				
Daytime (06:00-18:00 h)	0.047 (14, 0.025)	0.085 (11, 0.061)	0.176 (10, 0.061)	0.181 (25, 0.086)
Night (18:00-06:00 h)	0.039 (11, 0.015)	0.024 (9, 0.027)	0.093 (7, 0.054)	0.049 (14, 0.039)

spur length (we call the lower sepal the spur hereafter) was longest in *I. platypetala* followed by *I. eubotrya*, *I. talangensis* and *I. korthalsii* (Table 1). The spurs of the four *Impatiens* species were different not only in length but also in shape. Relationships between the depth (x mm) and the volume (y µl) of nectar stored in spurs of the four *Impatiens* species were well expressed by power functions: $y = 0.0121x^{1.73}$ ($r=0.92$) for *I. platypetala*; $y=0.00893x^{2.09}$ ($r=0.90$) for *I. korthalsii*; $y = 0.00472x^{2.46}$ ($r=0.98$) for *I. talangensis*; $y=0.0408x^{1.87}$ ($r=0.96$) for *I. eubotrya*.

These *Impatiens* species were perennials which bloomed all the year round. Anthesis of *I. platypetala* usually occurred at night whereas the others opened in daytime. Flowers of all four species were protandrous and the male phase (stigma embedded under androecium) lasted longer than the female phase (stigma protruding from androecium or androecium fallen); the functional sex ratio was biased to males (0.6-0.8). The mean life of a flower of *I. platypetala* was four days whereas those of the other species were two to three days (Table 1).

Nectar production

Each flower produced nectar steadily through its life. The sugar concentration of *I. platypetala* was significantly lower ($p<0.001$) than those of the others (Table 1).

The nectar production rate in daytime was highest (ca. 0.2 µl/h) in *I. eubotrya* and was followed by *I. talangensis*, *I. korthalsii* and *I. platypetala* (Fig. 3). In *I. platypetala*, nectar production rate was not significantly different between daytime (06:00 - 18:00 h) and night (18:00 - 06:00 h) ($df=23$, $t=1.25$, $p>0.1$). On the other hand, in *I. korthalsii*, *I. talangensis* and *I. eubotrya*, nectar production was higher in daytime than at night (*I. korthalsii* at Airsirah, $df=18$, $t=1.94$, $p<0.1$; *I. korthalsii* at Alahanpanjang, $df=17$, $t=1.89$, $P<0.1$; *I. talangensis*, $df=15$, $t=1.86$, $p<0.1$; *I. eubotrya*, $df=37$, $t=6.822$, $p<0.001$).

In *I. platypetala* the mean nectar volume of unbagged flowers (NU) was not significantly different from that of the bagged flowers (NB) both in the morning and evening (Table 2). In contrast, in *I. korthalsii*, NU was significantly less than NB in the morning and evening, and NU in the evening was significantly less than NU in the morning ($df=18$, $t=2.43$, $p<0.05$). In *I. talangensis*, NU was significantly less than NB in the evening (Table 2). In *I. eubotrya*, NU was significantly less than NB in the afternoon (13:00 h; $df=20$, $t=13.87$, $p<0.001$) and evening but not in the morning (Table 2), and NU in the afternoon was significantly less than NU in the morning ($df=22$, $t=7.69$, $p<0.001$). These data suggest that the nectar of the last three species was consumed by diurnal visitors.

Table 2. Comparison of the mean (n, s.d.) nectar volume (ml) between bagged and unbagged flowers of the four *Impatiens* species, by t-test.

<i>Impatiens</i> species	Morning (08:00 h)			Evening (16:00 h)		
	Bagged	Unbagged	t	Bagged	Unbagged	t
<i>platypetala</i>	1.95 (11, 0.61)	1.61 (9, 1.78)	0.38	1.82 (11, 0.56)	1.63 (7, 1.63)	1.09
<i>korthalsii</i>	1.98 (10, 0.92)	1.46 (9, 1.78)	3.24*	1.72 (9, 0.69)	0.99 (10, 0.79)	5.49**
<i>talangensis</i>	-	-	-	5.51 (3, 0.73)	1.20 (13, 1.21)	18.09***
<i>eubotrya</i>	1.98 (10, 1.26)	1.68 (12, 1.47)	1.87	2.22 (8, 1.67)	1.54 (11, 1.22)	3.52*

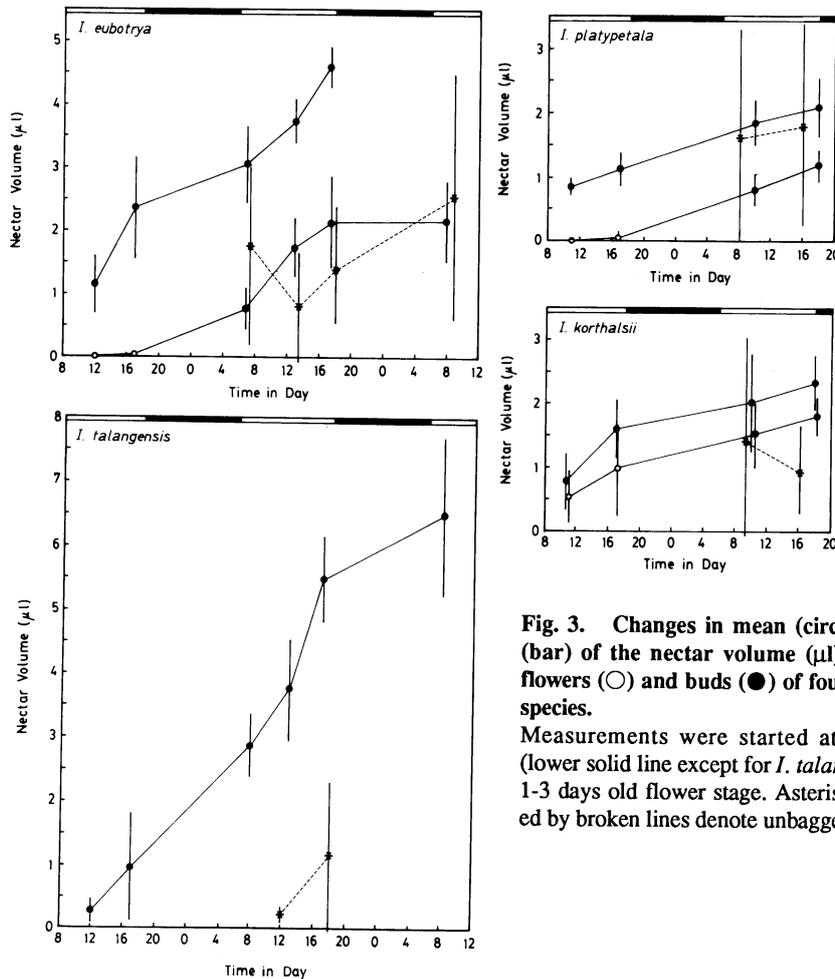


Fig. 3. Changes in mean (circle) and s.d. (bar) of the nectar volume (μ l) in bagged flowers (\circ) and buds (\bullet) of four *Impatiens* species. Measurements were started at bud stage (lower solid line except for *I. talangensis*) and 1-3 days old flower stage. Asterisks connected by broken lines denote unbagged flowers.

Insect visitors

Twenty-one insect species were collected on flowers of the four *Impatiens* species (Table 3). Each *Impatiens* species had pollinators that could legitimately extract nectar left in the long spur. Excluding *I. platypetala*, which was pollinated by the hawkmoth, *Macroglossum corythus*, the other three species were pollinated by solitary bees of Halictidae and Anthophoridae. Although *Thrinchostoma asianum* belongs to Halictidae, considered to be a

family of short-tongued bees, it had a long tongue (15 mm), and could extract nectar in the deep spur of *I. korthalsii*. Hairs on its thorax touched the androecium of *I. korthalsii* flowers during floral visits. *Amegilla sumatrana*, a medium-sized anthophorid bee with a long tongue, visited *I. korthalsii* and *I. eubotrya*. *Amegilla sumatrana* is placed in a subgenus *Glossamegilla*, which is characterized by brown pubescence and a long tongue (Brooks, 1988). *Elaphropoda impatiens* is also a medium-sized long-tongued anthophorid and is endemic to Sumatra (Lieftinck, 1944). This visited flowers of *I. korthalsii*, *I. talangensis* and *I. eubotrya*. *Amegilla sumatrana* also visited *Cyrtandra* sp. (Gesneriaceae) and *E. impatiens* visited *Globba variabilis* (Zingiberaceae) (Kato *et al.*, 1989). All three bee species inhabited the understory of the rain forest and never visited flowers in the open habitats which were studied by Inoue *et al.* (1990).

Amegilla andrewsi (bearing shining blue bands on abdomen) sometimes landed on spurs of *Impatiens* flowers to rob nectar by perforating the tip of the spur with the mandibles. *Protomelissa vulpecula*, putatively a cleptoparasite of *E. impatiens* (Lieftinck, 1944), robbed nectar of *I. korthalsii* and *I. eubotrya* in a similar manner as *A. andrewsi*. Interestingly, *P. vulpecula* is a parasite of both the host bee *E. impatiens* and its main food source. Other small bees, such as *Lasioglossum* spp. and *Ceratina* sp. 1 were pollen thieves and secondary nectar

Table 3. Insect visitors, their lengths of forewings and proboscises, the mean numbers of visits per hour per flower patch of the four *Impatiens* species. Anthecological status follows Inouye (1980).

ORDER	Family	Species	Length of		Mean number of visits per hour				Anthecological status*
			Fore-wing	Proboscis	<i>Impatiens</i> species				
					<i>platy-petala</i>	<i>korth-alsii</i>	<i>talang-ensis</i>	<i>eubo-trya</i>	
LEPIDOPTERA									
	Sphingidae	<i>Macroglossum corythus</i>	34.3	44.0	0.08	-	-	-	Pn
	Satyridae	<i>Mycalasis marginata</i>	24.1	5.7	-	0.66	-	-	Tn
DIPTERA									
	Syrphidae	<i>Episyrphus</i> sp.	7.9	1.1	1.43	0.43	-	0.09	Tn
		<i>Baccha</i> sp.	8.0	1.0	0.14	0.33	-	-	Tp
COLEOPTERA									
	Mordellidae	<i>Glipa</i> sp.	7.9	-	-	-	-	0.09	Tp
HYMENOPTERA									
	Formicidae	<i>Creumatogaster</i> sp. 1	-	-	-	0.33	-	-	Tn
		<i>Creumatogaster</i> sp. 2	-	-	0.14	-	-	-	Tn
		<i>Pratrechina</i> sp.	-	-	-	-	0.33	0.45	Tn
		<i>Monomorium pharaonis</i>	-	-	-	-	0.33	-	Tn
		<i>Pheidole</i> sp.	-	-	-	-	0.33	-	Tn
	Vespidae	<i>Polybioides raphigastra</i>	-	-	0.33	-	-	-	Tn
	Halictidae	<i>Thrinchostoma asianum</i>	11.5	14.9	-	3.85	-	-	Pn, Pp
		<i>Lasioglossum vulcanicum</i>	6.6	2.6	-	1.54	0.66	-	Tp
		<i>Lasioglossum</i> sp. 1	6.2	2.5	-	0.99	-	0.99	Tp
		<i>Lasioglossum</i> sp. 2	5.6	2.5	0.14	-	-	-	Tp
		Anthophoridae	<i>Amegilla sumatrana</i>	11.0	16.4	-	0.57	-	0.91
		<i>A. andrewsi</i>	9.5	13.2	0.33	0.33	-	0.09	Rpn, Pn
		<i>Elaphropoda impatiens</i>	10.2	16.5	-	3.08	1.33	3.91	Pn, Pp
		<i>Protomelissa vulpecula</i>	9.4	2.7	-	0.56	-	0.09	Rpn
		<i>Ceratina</i> sp.	5.5	2.0	0.14	-	-	-	Tp, Rsn
		<i>Braunsapis</i> sp.	6.0	2.3	-	-	-	0.09	Tp

* Pn, pollinator searching for nectar; Pp, pollinator searching for pollen; Rpn, primary nectar robber; Rsn, secondary nectar robber; Tn, nectar thief; Tp, pollen thief.

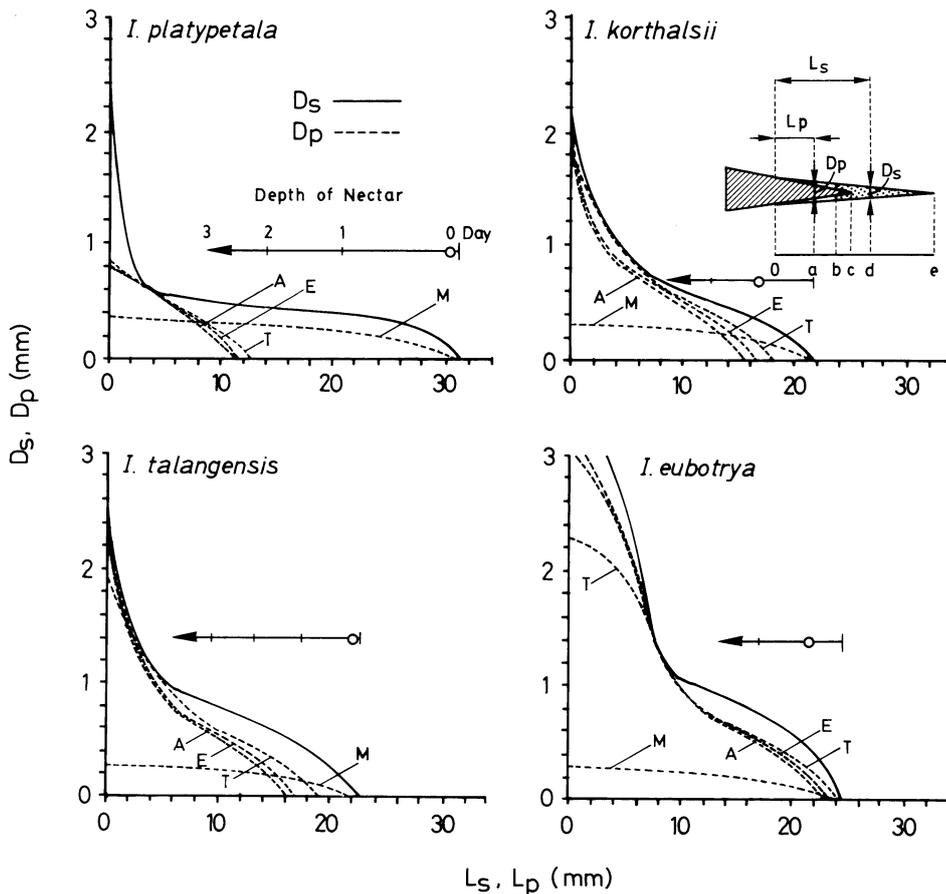


Fig. 4. The accessibility of spurs of the four *Impatiens* species by the four pollinator species. A, *Amegilla sumatrana*; E, *Elaphropoda impatiens*; T, *Thrincostruma asianum*; M, *Macroglossum corythus*. Ordinate denotes diameters of spur inner cavity (D_s) and pollinators' mouthparts (D_p) and abscissa denotes lengths of spur (L_s) and pollinator's mouthparts from entrance (L_p). Spurs and pollinators' mouthparts are shown by solid and broken lines, respectively. The upper right schema shows a vertical section of nectar (dotted area) in a spur and pollinator's mouthparts (shaded area). See text for details.

robbers. The percentage of perforated flowers was 8.3 % ($n=24$) on *I. platypetala*, 22.2 % ($n=36$) on *I. korthalsii* at Airsirah; 20.8 % ($n=24$) on *I. korthalsii*, 20.0 % ($n=15$) for *I. talangensis* and 20.5 % ($n=88$) for *I. eubotrya* at Alahanpanjang. A pollinator tried to insert its mouthparts, and sometimes even the head into a spur as deep as possible. The accessibility of nectar to the three bee species was examined as follows (Fig. 4): Let us call L_s length of the spur from the spur mouth to point d, D_s the inner diameter of the spur at d and e the length of the spur. The relationship between D_s and L_s of each *Impatiens* species shows that the spur cavity is not a simple cylinder but a swollen cone. When the pollinator inserted its mouthparts, it may not have access to all of the floral nectar. Calling L_p length of pollinator's mouthparts and D_p diameter of pollinator's mouthparts, D_p - L_p curve represents the mouthpart morphology. At the point that the D_p - L_p curve adjoins the D_s - L_s curve, the pollinator's insertion is thought to be blocked by the narrowness of the spur cavity. If the nectar is stored between e and b in a spur, the pollinator can extract nectar only between c and b.

The three bee species, *T. asianum*, *A. sumatrana* and *E. impatiens*, could exploit little nectar left in the slender spur of *I. platypetala* because their mouthparts were thicker than the spur diameter. The nectar of *I. platypetala* could be completely extracted only by *M. corythus*. Some portion of nectar of the three yellow *Impatiens* species could be extracted by the three bees, but their mouthparts did not reach the spur tip. *Thrincostruma asianum*, with a shorter proboscis than the other two anthophorids, could insert it deepest into spur because its mouthparts and head were more slender than the other two.

The posture of bees during nectar extraction determined the position of pollen attachment on a bee's body (Fig. 5). Pollen grains of *I. korthalsii* were attached to the dorsal part of thorax of *T. asianum* and to the clypeus, malar space, and rarely the dorsal thorax of *A. sumatrana* and *E. impatiens*. Pollen grains of *I. talangensis* were attached to the dorsal part of thorax of *E. impatiens*. On the other hand, pollen grains of *I. eubotrya* were attached to the ventral or lateral part of thorax of *A. sumatrana* and *E. impatiens*. The distortion of the peduncle and the particular curvature of the spur of *I. eubotrya* function to change the position of pollen attachment from that of the other *Impatiens* species.

Temporal patterns of visits

Only the hawkmoth, *Macroglossum corythus*, visited *I. platypetala* once at dawn (Fig. 6). We could not find any other insects visiting the flower legitimately in a total of 27 hours of observation. *Impatiens platypetala*, at the spur mouth, produced a thin liquid that was not nectar (volume = 3.17+1.60 ml and sugar concentration = 2.20 + 2.71 %, mean + s.d.; n=8). This liquid was found even during the bud stage. Pollen grains were often floating on this liquid. Thus, this liquid might help pollen grains adhere to the hawkmoth proboscis.

A flower patch of *I. korthalsii* was visited by both *A. sumatrana* and *T. asianum* several times per day (09:00-18:40 h, Fig. 7). Fast-flying males of *E. impatiens* visited 19 times per day but scarcely landed on the flowers (Fig. 7). These males are thought to come to the flowers for mating rather than solely to feed. The mean number of flowers visited by an *A. suma-*

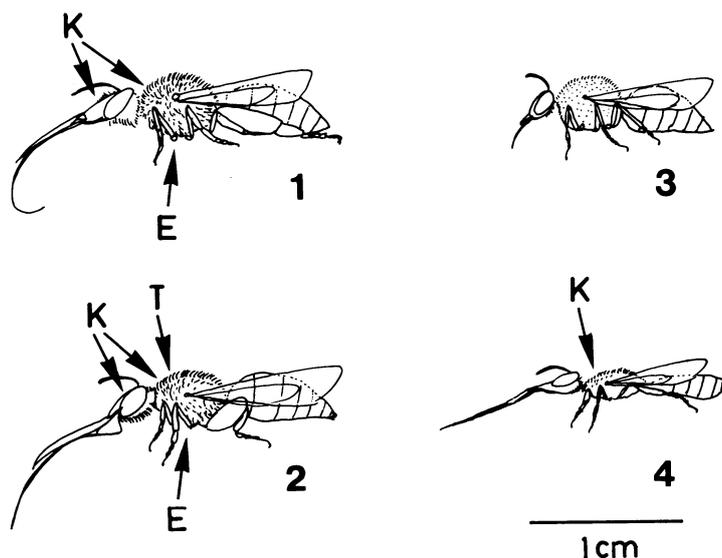


Fig. 5. Lateral view of the four bee species. 1, *Amegilla sumatrana*; 2, *Elaphropoda impatiens*; 3, *Protomelissa vulpecula*; 4, *Thrincostruma asianum*. Arrows show the positions of pollen grains attached to bees' bodies: E, *I. eubotrya*; K, *I. korthalsii*; T, *I. talangensis*.

trana female per visit to a patch was about 19 (about two thirds of flowers in the patch), and the mean time spent on a flower was about 1 second (Table 4). *Amegilla sumatrana* males were rare during our observation periods.

A flower patch of *I. eubotrya* was visited by females of both *A. sumatrana* and *E. impatiens* several times per day (07:00-18:30 h, Fig. 8). *Elaphropoda impatiens* females foraged more flowers per visit in a patch and stayed on a flower longer than *E. impatiens* males (Table 4). *E. impatiens* males flew swiftly and visited the patch frequently but they rarely landed on the flowers. The number of flowers visited by them per visit in a patch was usually one. Their activity increased at air temperature of >20°C.

As a result of bees' foraging, only a small part of flowers in a patch was visited by legitimate pollinators each day (Table 5). The frequency of pollinator visits to flowers of *I. eubotrya* may be underestimated because some effective visits by fast-flying males of *E.*

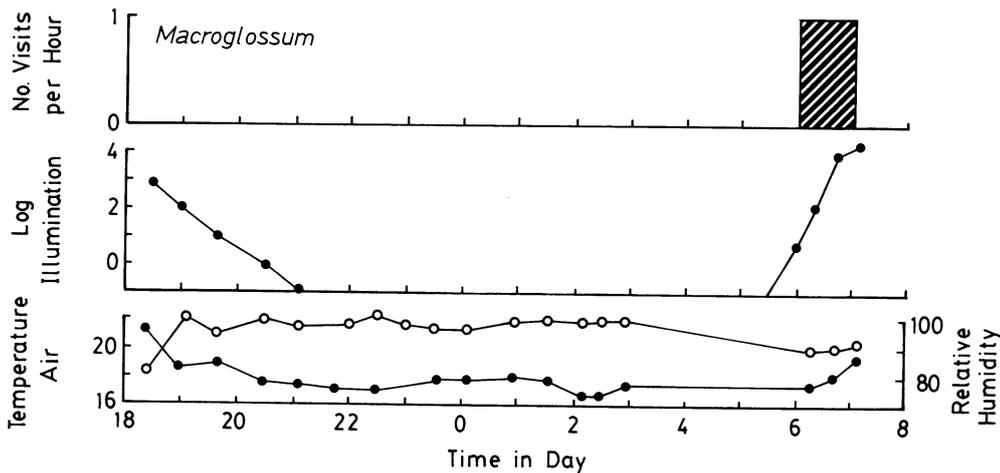


Fig. 6. Insect visits to an *Impatiens platypetala* flower patch and changes in light intensity (lx, logarithmic scale), air temperature (°C; solid circle) and relative humidity (%; open circle) at Airsirah on January 7-8, 1988.

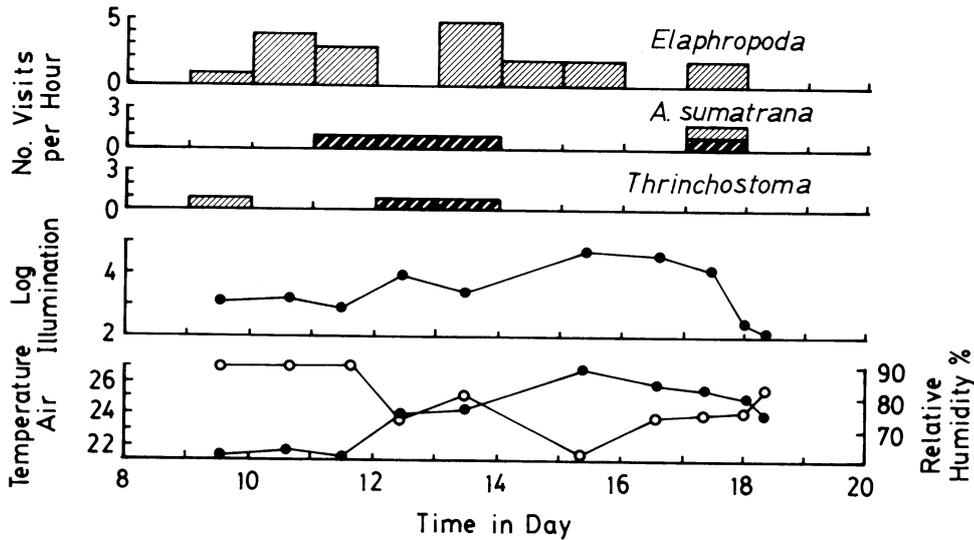


Fig. 7. Insect visits to an *Impatiens korthalsii* flower patch. Airsirah on January 12, 1988. Thick striped and shaded columns denote probing-visits and approach-visits, respectively.

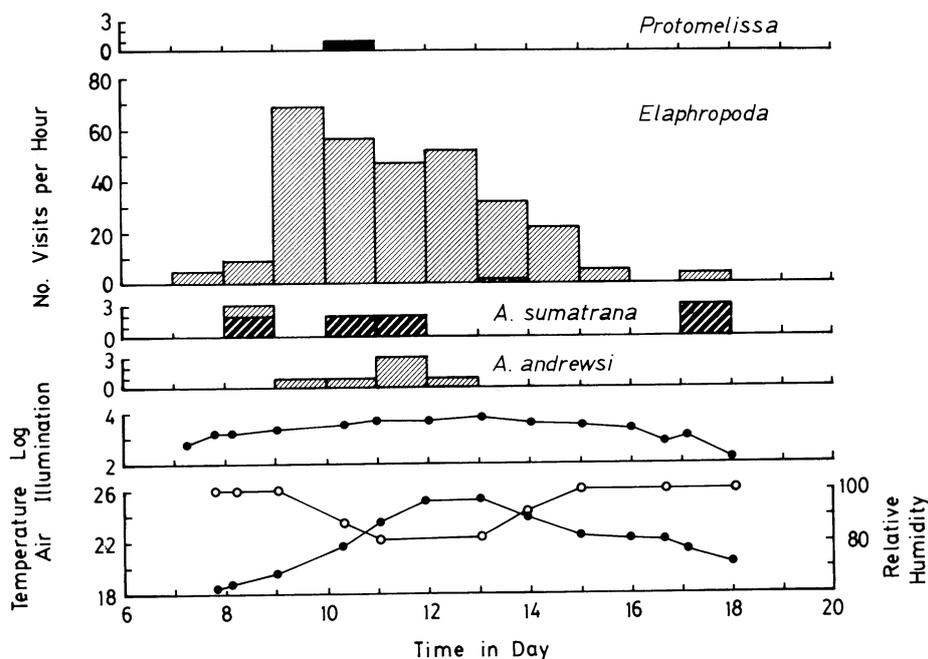


Fig. 8. Insect visits to an *Impatiens eubotrya* flower patch. Alahanpanjang on January 15, 1988. Thick striped, shaded and solid columns denote probing-visits, approach-visits and robbing-visits.

Table 4. Mean number of flowers visited per bout in a patch and the mean time spent on a flower by the four bee species.

Pollinators	Sexes	<i>Impatiens</i> Species	Number of flowers per patch	Number of flowers visited per bout in a patch			Time spent on a flower (sec.)		
				n	Mean	s.d.	n	Mean	s.d.
<i>Macrogrossum corythus</i>	F.	<i>platypetala</i>	20	1	15.0	-	15	2.0	0.0
<i>Thrincostruma asianum</i>	F.	<i>korthalsii</i>	28	1	1.0	-	1	21.0	-
	M.	<i>korthalsii</i>	28	10	1.1	0.3	12	3.3	3.9
<i>Amegilla sumatrana</i>	F.	<i>korthalsii</i>	28	9	19.4	11.9	99	1.1	1.0
<i>Elaphropoda impatiens</i>	F.	<i>eubotrya</i>	41	9	2.7	2.2	24	2.7	2.3
	M.	<i>eubotrya</i>	41	8	1.3	0.5	10	0.9	0.6

Table 5. Frequency distribution of the number of visits that one flower receives per day and the probability that the flower is visited by pollinators once or more per day.

<i>Impatiens</i> Species	Number of visits							n	No. of Visits		Probability of receiving ≥ 1 visit
	0	1	2	3	4	5	6		Mean	s.d.	
<i>platypetala</i>	80	15	0	0	0	0	0	95	0.16	0.37	0.16
<i>korthalsii</i>	4	10	12	8	1	5	0	40	2.18	1.45	0.90
<i>talangensis</i> *	2	2	1	0	0	0	0	5	0.80	0.84	0.60
<i>eubotrya</i>	22	14	3	1	0	0	0	40	0.58	0.75	0.45

* From a 4 hour observation and others from 12 hour observation.

impatiens might have been overlooked. The very low frequency of pollinator visitation at *I. platypetala* might be compensated by flower longevity (3.8 days, Table 1) or by self-pollination (autogamy, Table 6).

Table 6. Comparison of fruit-set between bagged and unbagged flowers, by Fisher's exact probability test.

<i>Impatiens</i> species	Fruit set (%)		Pro- bability	Number of seeds per fruit of unbagged flower (n, s.d.)
	unbagged (n)	bagged (n)		
<i>platyptala</i>	8.0 (25)	9.1 (55)	0.620	14.8 (12, 5.0)
<i>korthalsii</i>	36.4 (11)	0.0 (9)	0.068	18.0 (11, 8.7)
<i>talangensis</i>	20.0 (5)	0.0 (8)	0.385	13.3 (4, 3.87)
<i>eubotrya</i>	42.2 (19)	4.5 (22)	0.005	4.7 (3, 0.58)

Impatiens korthalsii and *I. talangensis* were self-incompatible (Table 6). While fruit sets of *I. eubotrya* and *I. platyptala* were not zero, seed sets of them were zero. All the species cultivated in Japan were self-incompatible. Fruit set in the field was positively correlated with the probability that a flower was visited by a pollinator at least once ($r=0.4$, $p>0.05$).

DISCUSSION

The four *Impatiens* showed two contrasting pollination syndromes: sphingophily and melitophily. *Impatiens platyptala* was visited by crepuscular hawkmoths and had pink flowers with long filiform spurs that produced dilute nectar (26 % sugar concentration). *Impatiens korthalsii*, *I. talangensis* and *I. eubotrya* had yellow flowers with long gradually tapering spurs that produced nectar of medium sugar concentration (38 %) mainly in daytime and were visited by long-tongued bees (*T. asianum*, *A. sumatrana* and *E. impatiens*) (Fig. 9). The higher nectar production rates by *I. talangensis* and *I. eubotrya* than *I. korthalsii* may be related to the larger sizes of the presumed pollinators (Anthophoridae vs. Halictidae). The higher rates of nectar robbing by *Amegilla andrewsi* and *Protomelissa vulpecula* may be another factor to increase their nectar production. But essentially the spur morphology and its matching to proboscis may ultimately determine which types of flowers are visited by bees (Roubik *et al.*, 1985).

The yellow species, *I. korthalsii*, *I. talangensis* and *I. eubotrya* are endemic to Sumatra, whereas *I. platyptala* is widely distributed from Malay to the Lesser Sunda Archipelago (Grey-Wilson, 1989; Hotta, 1989). Flowers of the two yellow species, *I. korthalsii* and *I. talangensis*, are symmetric, but those of *I. eubotrya* are twisted and asymmetric. These flower morphologies regulated the position on pollinators' bodies to which pollen grains attach. Thus, they could use the same bee species as pollen carriers as discussed below.

The three long-tongued bee species pollinated the three yellow flower species. *Thrinchostoma asianum* visited only *I. korthalsii*, *Amegilla sumatrana* visited *I. korthalsii* and *I. eubotrya*, and *Elaphropoda impatiens* visited all three plants. Although the three sympatric yellow *Impatiens* species shared pollinators, the morphology of flowers separated the position of pollen attachment on pollinators. Both symmetric flowers (*I. korthalsii* and *I. talangensis*) shared a common pollinator, *E. impatiens*, whereas *I. korthalsii* seemed to have more restricted relations with *T. asianum*, and was seldom visited by *A. sumatrana*. The reproductive isolation of these three *Impatiens* species due to pollination process might be incomplete.

Okada (1989) reported that these three *Impatiens* species had different chromosome numbers: *I. korthalsii* $2n=14$ (2x); *I. eubotrya*, $2n=28$ (4x); *I. talangensis*, $2n=ca. 60$ (8x?). The

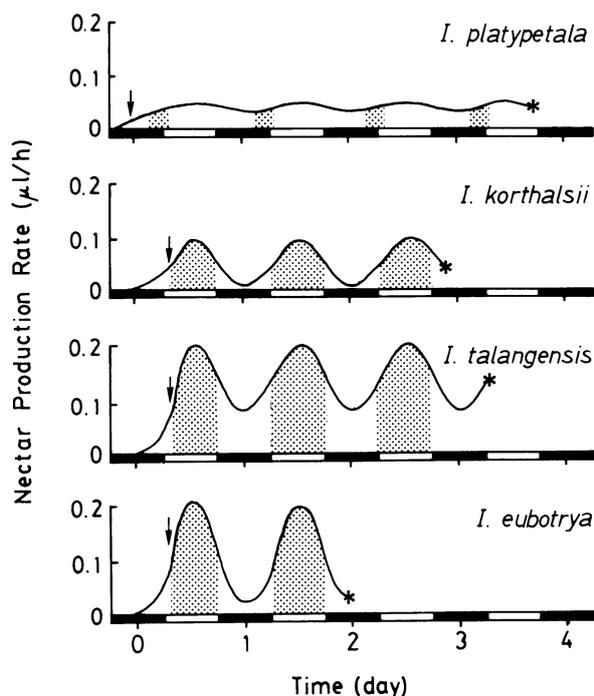


Fig. 9. Temporal patterns of flowering, nectar production of the four *Impatiens* species and insect visits (shaded areas) to them. Solid and open scales denote night and daytime, respectively. Opening and dropping of flowers are shown by arrows and asterisks, respectively.

polyploidy is the main cause of the reproductive isolation. At the study site in Alahanpanjang, there were other *Impatiens* species which were thought to be very close to *I. korthalsii* and *I. talangensis* but had different chromosome numbers (rheophilous *I. diepenhorstii* and ridge growing *I. beccarii*; both $2n=28$). The high diversity of *Impatiens* species in Sumatra (Grey-Wilson, 1980) should be studied from the standpoints of habitat segregation, polyploidy and pollination syndrome on regional and local scales.

The frequency of pollinator visits per day was much less in the Sumatran species than the Japanese species *I. textori* which is pollinated by bumblebees (Kato, 1988). The flowering span of the former (1.8-4.1 days) is equal or longer than the Japanese species (1.8 days, Kato, 1988). In spite of the low frequency of pollinator visitation, the outbreeding ratio of the Sumatran *Impatiens* species seemed to be high due to the extended flowering time.

Neotropical long-tubed flowers of Apocynaceae, Bignoniaceae, Convolvulaceae, Gesneriaceae, Leguminosae, Marantaceae, Polygalaceae, Rubiaceae, Verbenaceae and Zingiberaceae are pollinated by long-tongued euglossine bees (Janzen, 1971; Dressler, 1982; Roubik, 1989). In the palaeotropics, long-spurred or long-tubed flowers of Balsaminaceae, Gesneriaceae and Zingiberaceae are pollinated by long-tongued anthophorids, especially *Amegilla* (Kato *et al.*, 1989). Although detailed information on their behavior is lacking, some females and males of *Amegilla* seem to trapline as do euglossine bees. Some neotropical understory herbs of *Costus* spp. (Zingiberaceae) share common pollinators due to floral convergence or conservatism to compensate for low frequency of euglossine bee visitation (Schemske, 1981). Sumatran *Impatiens* spp. might have unusually long flower life and similarity in floral morphology to other species due to such limitations in pollinator availability. Patterns of nectar production (peak in daytime) and nectar sugar concentration (33-37 %) of *Costus* spp. (Schemske, 1981) are also similar to those of Sumatran *Impatiens*. In spite of differences between the continents and their pollinators (Euglossini, Apidae vs. Anthophorini, Anthophoridae), the pollination ecology of long-spurred and long-tubed flowers can be similar between the neotropics

and palaeotropics.

In 'short-tongued' bees the enormously elongated mouthparts have been known in Colletidae and Andrenidae from Australia and New Guinea (Houston, 1983) and temperate America (LaBerge, 1978; Laroca & Almeida, 1985). The long proboscis of the newly discovered *T. asianum* is the first example of such mouthparts in Halictidae in Southeast Asia (Sakagami *et al.*, 1991). Elongation of the proboscis of this halictid may be a secondary adaptation to long-spurred or long-tubed flowers that had coevolved with other partners, e.g., long-billed nectarinid birds in Australia and the long-tongued anthophorid bees in Sumatra.

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REFERENCES

- Ackerman, J. D. 1985. Euglossine bees and their nectar hosts. *In* W. G. D'Arcy & M. D. Correa A. (eds), *The Botany and Natural History of Panamá*, 225-233. Missouri Botanical Garden, St. Louis.
- Brooks, R. W. 1988. Systematics and phylogeny of the anthophorine bees (Hymenoptera; Anthophoridae; Anthophorini). *University of Kansas Science Bulletin* 53: 436-575.
- Darwin, C. 1862. *The Various Contrivances by which Orchids are Fertilised*. Murray, London.
- Dressler, R. D. 1982. Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics* 13: 373-394.
- Grey-Wilson, C. 1980. *Impatiens of Africa*. A. A. Balkema, Rotterdam.
- . 1989. A revision of Sumatran *Impatiens*. Studies in Balsaminaceae VII. *Kew Bulletin* 44: 67-106.
- Hooker, J. D. 1875. *Flora of British India* 1: 440-483. L. Reeve, Kent, England.
- Hotta, M. 1989. Identification list of *Impatiens* (Balsaminaceae) in West Sumatra and G. Kerinci area. *Occasional Papers of the Kagoshima University Reserch Center for the South Pacific* no. 16: 59-66.
- Houston, T. F. 1983. An extraordinary new bee and adaptation of palpi for nectar-feeding in some Australian Colletidae and Pergidae (Hymenoptera). *Journal of Australian Entmological Society* 22: 263-270.
- Inoue, T., Salmah, S., Sakagami, S. F., Yamane, Sk. & Kato, M. 1990. An analysis of anthophilous insects in central Sumatra. *In* Sakagami, S. F., Ohgushi, R. & Roubik, D. W.

- (eds), *Natural History of Social Wasps and Bees in Equatorial Sumatra*, 175-200. Hokkaido University Press, Sapporo.
- Inouye, D. W. 1980. The terminology of floral larceny. *Ecology* **61**: 1251-1253.
- Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* **171**: 203-205.
- Kato, M. 1988. Bumblebee visits to *Impatiens* spp.: pattern and efficiency. *Oecologia* **76**: 364-370.
- , Itino, I., Hotta, M., Abbas, I. & Okada, H. 1989. Flower visitors of 32 plant species in West Sumatra. *Occasional Papers of the Kagoshima University Research Center for the South Pacific* no. 16: 15-31.
- LaBerge, W. E. 1978. *Andrena* (*Callandrena*) *micheneriana*, a remarkable new bee from Arizona and Mexico (Apoidea: Andrenidae). *Journal of Kansas Entomological Society* **51**: 592-596.
- Laroca, S. & Almeida, M. C. 1985. Adaptação dos palpos labiais de *Niltonia virgillii* (Hymenoptera, Apoidea, Colletidae) para coleta de néctar em *Jacaranda puberula* (Bignoniaceae), com descrição do macho. *Revista Brasileira de Entomologia* **29**: 289-297.
- Lieftinck, M. A. 1944. Some Malaysian bees of the family Anthophoridae. *Treubia hors série*: 57-139.
- Miquel, F. A. W. 1862. *Sumatra, Zijne Plantenwereld*, 395-398. C. G. van der Post, Amsterdam.
- Okada, H. 1989. Chromosome counts of some plants collected from West Sumatra. *Occasional Papers of the Kagoshima University Research Center for the South Pacific* no. 16: 11-14.
- Ridley, H. N. 1922. *The Flora of the Malay Peninsula* **1**: 335-339 (Balsaminaceae). A. Asher & Co., Amsterdam.
- Roubik, D. W. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge.
- Rust, R. W. 1979. Pollination of *Impatiens capensis*: pollinators and nectar robbers. *Journal of Kansas Entomology Society* **52**: 297-308.
- Sakagami, S. F., Kato, M. & Itino T. 1991. *Thrinchostoma* (*Diagonozus*) *asianum* sp. nov.: Discovery of an african subgenus of long-malared halictine bees from Sumatra, with some observations on the oligotrophy to *Impatiens*. *Tropics* **1**: 47-56.
- Salmah, S., Inoue, T. & Sakagami, S. F. 1990. An analysis of apid bee richness (Apidae) in central Sumatra. In Sakagami, S. F., Ohgushi, R. & Roubik, D. W. (eds), *Natural History of Social Wasps and Bees in Equatorial Sumatra*, 139-174. Hokkaido University Press, Sapporo.
- Schemske, D. W. 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. *Ecology* **62**: 946-954.
- Van Steenis, C. G. G. J. 1972. *The Mountain Flora of Java*. E. J. Brill, Leiden. 222 pp.

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加藤真, 市野隆雄, 堀田満, 井上民二 スマトラ産ツリフネソウ属 (*Impatiens*) 4種のスズメガとハナバチによる送粉

インドネシア国スマトラの熱帯山地多雨林において, 同所的に生育するツリフネソウ属 (*Impatiens*, ツリフネソウ科) 4種の開花様式と送粉様式を比較した. *Impatiens platypetala*の淡紅紫色の花は, 細長く垂れ下がった距に糖分26%の花蜜を昼夜にわたって分泌し, 薄暮活動性のスズメガ (*Macroglossum corythus*) によって送粉されていた. *Impatiens korthalsii*, *I. talangensis*, *I. eubotrya*の黄色の花は, 先細りの距に34-37%の糖を含有する花蜜を主に昼間に分泌し, 特殊化した長舌のコシブトハナバチの2種と異常に長舌になったコハナバチの1種によって送粉されていた. 花の距の形態は, 送粉者が花蜜への到達できるかどうかを決定していた. ハナバチ媒の3種の *Impatiens* は3種のハナバチを一部共有していたが, ハナバチの体表の花粉付着場所を違えることによって送粉者を使い分けていた. 4種の *Impatiens* は開花期間の延長によって, 送粉者の低い訪花率を補っていた. 盗蜜が東南アジアで初めてケブカハナバチ科の2種で観察された.