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Melittophily and Ornithophily of Long-tubed Flowers in Zingiberaceae and Gesneriaceae in West Sumatra

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Abstract Pollination of seven zingiberaceous and two gesneriaceous species was studied in natural forests at various altitudes in West Sumatra, Indonesia. Terrestrial, red, long-tubed flowers of *Achasma macrocheilos* were visited by a large, remarkably long-tongued anthophorine bee, *Amegilla elephas*. The swiftly-flying bees showed traplining foraging behavior just like euglossine bees in the Neotropics. This bee species was oligolectic to the plant species and almost the only pollinator of it. Yellow (rarely white), long-tubed flowers of *Zingiber puberulum*, *Grobba aurantiaca*, *Amomum aculeatum* and *Cyrtandra pendula* were pollinated by median-sized, shade-loving, traplining, long-tongued anthophorine bees in the genera *Amegilla* and *Elaphropoda*. White, short-tubed flowers of *Amomum uliginosum* and *Cyrtandra* aff. *grandiflora* were pollinated by traplining halictid bees in the genus *Nomia*. Long-tubed flowers borne on red stout spikes of *Hornstedtia* aff. *conica* and *Phaeomeria fulgens* were pollinated by a long-billed sunbird, *Arachnothera longirostra*. These ornithophilous flowers produced significantly more nectar of lower sugar concentration than the melittophilous flowers.

According to the proboscis lengths, long-tongued bees were classified into three groups, which corresponded to the three pollination guilds of the melittophilous flowers. Among species in a bee guild, convergence of proboscis lengths was detected, and the floral hosts of the bee species were sometimes overlapping. Twenty-five percent of melittophilous species were visited by more than one bee species, but nonetheless most individual plants were visited by only a single bee species. At higher altitudes more than 1400 m, anthophorine bees were displaced by bumblebees and the guild structure of long-tongued bees was simpler than at lower altitudes.

Key Words: pollination / Zingiberaceae / Gesneriaceae / Anthophorinae / sunbird / traplining / Sumatra

Bee communities on many flowers in tropical rain forests are dominated in abundance by stingless bees in the Neotropics (Heithaus, 1979; Roubik, 1989) and by honeybees and stingless bees in the Palaeotropics (Inoue *et al.*, 1991). These eusocial, relatively short-tongued bees are generalists and especially abundant on flowers at sunny habitats and on flowers of canopy and subcanopy tree species. In contrast, at forest floor, there are many plant species with long-tubed flowers which are pollinated by solitary, long-tongued bee species. For example in the Neotropics, flowers of Apocynaceae, Bignoniaceae, Gesneriaceae, Rubiaceae, Verbenaceae, Marantaceae and Zingiberaceae are mainly pollinated by traplining, long-tongued euglossine bees (Janzen, 1971; Dressler, 1982; Schemske, 1984;

Ackerman, 1985). In the Palaeotropics, although ecological information is far less than in the Neotropics, some long-tubed flowers of Balsaminaceae, Gesneriaceae, Marantaceae and Zingiberaceae are reported to be visited by long-tongued anthophorine bees (Lieftinck, 1944, 1956; Stone & Willmer, 1989), which are rare, shade-loving, swiftly-flying trapliners ecologically just like euglossine bees.

Pollination biology of long-tubed flowers in the Palaeotropics was studied only on Balsaminaceae (Kato *et al.*, 1991) and Musaceae (Itino *et al.*, 1991). We focused our attention on the pollination of Zingiberaceae and Gesneriaceae, because these two families were the most diverse among long-tubed flower families in Southeast Asia. For example, 150 species in Zingiberaceae and 160 species in Gesneriaceae have been recorded from Malay Peninsula (Ridley, 1924a, b; Holttum, 1950). Zingiberaceae is characterized by the specialized, zygophilous, long-tubed flowers and this morphological characteristics should have coevolved with some long-tongued animals, e.g., bees, moths, birds and bats. Some related families in Zingiberales such as Musaceae, Heliconiaceae and Strelitziaceae are ornithophilous or chiropterophilous (Stiles, 1975; Frost & Frost, 1981; Itino *et al.*, 1991). Persistent observations on the pollination of Zingiberaceae might clarify the early diversification process of Zingiberaceae and Zingiberales.

In order to detect pollination syndrome of long-tubed flowers in the Palaeotropics, we conducted a fieldwork on the pollination of seven zingiberaceous and two gesneriaceous species in natural forests at various altitudes in West Sumatra, Indonesia. In this paper, first we describe anthecological properties and pollinators of nine plant species and show that two zingiberaceous species are ornithophilous and the other seven are melittophilous. Secondly, we compare the proboscis lengths of long-tongued bee species, and show how the bee guild structure was characterized by clear inter-guild character displacement and by intra-guild convergence. Finally, we analyze the pattern of niche segregation among bee species and among plant species and discuss the evolutionary process of pollination system at forest floor in the Palaeotropics.

MATERIALS AND METHODS

Fieldwork was conducted at ten sites at various altitudes in West Sumatra, Indonesia (Table 1). The vegetation of the sites changed along the altitudinal gradient from lowland tropical rain

Table 1. Locations and altitudes of ten study sites in West Sumatra.

Code	Site	Longitude	Latitude	Altitude (m)
A	Sungaidareh, Sijunjung	0°59'S	101°32'E	80
B	Ulugadut, Padang	0°55'S	100°28'E	220
C	Bukitsabalah, Sijunjung	0°47'S	101°09'E	450
D	Mukomuko, Bukittingi	0°21'S	100°07'E	550
E	Airsirah, Padang	0°58'S	100°31'E	920
F	Sungaishirah, Payakumbuh	0°02'S	100°42'E	950
G	Kayujao, Alahanpanjang	1°04'S	100°37'E	1280
H	Danau Talang, Alahanpanjang	1°03'S	100°40'E	1580
I	Gunung Gadut, Padang	0°54'S	100°33'E	1750
J	Gunung Rasam, Alahanpanjang	1°09'S	100°42'E	2200

forests via evergreen oak-dominated mountain forests to *Vaccinium*-dominated shrubby alpine forests. All these sites were covered at least partly with natural forests.

Persistent observations of pollinator visits to long-tubed flowers were made on the forest floor of the ten sites from Dec. 3, 1987 to Jan. 28, 1988 and from Dec. 28, 1991 to Jan. 19, 1992. Main targets of this study were the following seven zingiberaceous and two gesneriaceous plant species: Zingiberaceae: *Achasma macrocheilos* Griffith, *Zingiber puberulum* Ridley, *Grobba aurantiaca* Miquel, *Amomum aculeatum* Roxburg, *Amomum uliginosum* Koenig, *Hornstedtia* aff. *conica* Ridley, *Phaeomeria fulgens* (Ridley); Gesneriaceae: *Cyrtandra pendula* Blume, *Cyrtandra* aff. *grandiflora* Ridley. Other long-tubed flowers in Balsaminaceae and other families were also studied. Herbarium specimens and ethanol-fixed flowers of these species are deposited in Biological Laboratory, Yoshida College, Kyoto University.

The time periods of the observation varied with plant species, ranging from one to 25 hours. Since the bees were very wary and sensitive to the slightest motion of observers, the greatest caution was taken not to bother the bees. Some flower-visitors were collected to measure their forewing lengths (WL) and proboscis lengths (PL). Volume and sugar concentration of floral nectar of flowers were measured with microcapillary tubes and a pocket refractometer, respectively. The measurements were done four times at an interval of 2-3 hours in *Achasma macrocheilos*, but only once in the daytime in other plant species.

Pollen loads on a corbicula of each bee were taken, put in a microtube and diffused in water. Samples including zingiberaceous pollen were treated only by KOH, but other samples by a series of acetolysis treatments. A drop of the suspension was transferred to a slide, stained with basic fuchsin and mounted in glycerin jelly. From each slide a series of random microscope fields were examined until > 100 grains were counted and identified, some to species, to genus and still others only to family. By estimating the volume of pollen grain, the composition of pollen load in number was converted to percentage of volume.

RESULTS

Pollination of seven zingiberaceous species

(1) *Achasma macrocheilos* Griff.

A capitate inflorescence was borne on a short erect stalk from a subterranean rhizome, and red flowers with yellow nectar guide in the center of large labellum were radially arranged on the ground. Corolla tube was very long (Fig. 1B) and the mean depth was 65.5 mm (s.d. = 9.5, n = 4). The plants forming dense bush were mainly distributed in the secondary forests beside streams (sites B and C, Table 3), and the density of inflorescences was about 6 per hectare at site B.

Flower visitors were an anthophorine bee, *Amegilla elephas*, and a hesperiid skipper, *Ancistroides nigrita*, at site B. Only once, we glanced at a sunbird, *Arachnothera longirostris*, visiting a flower of unidentified *Achasma* species at site C. *Amegilla elephas* was the longest-tongued bee in Sumatra (Table 2, Fig. 2D). The bee was attracted to red color as well as to red flowers on the ground. The bee flew swiftly near the ground in the bush of *Achasma*. On arriving at an inflorescence, a female hovered above the flowers (Fig. 2A). Just before landing on labellum of the flower, it set its long galea free from the underside of the body (Fig. 2B) and extended it downward, then it landed on labellum inserting its

Table 2. Long-billed bird and long-tongued bee species recorded on long-tubed flowers at forest floor in West Sumatra, with the mean forewing length (WL), the mean proboscis length (PL) and the ratio PL/WL.

Class	Family	Code	Species	Sites Recorded	Mean Forewing Length (mm)	Mean Bill/ Proboscis Length (mm)	PL/WL
Aves	Nectariniidae	1	*Arachnothera longirostra*	A,B,C,F,G	64.6	38.5	0.60
Insecta	Halictidae	2	*Thrinchostoma asianum*	E	11.7	14.9	1.27
		3	*Nomia* aff. *combusta*	C	10.0	6.3	0.63
		4	*Nomia* aff. *elliotii*	D	9.6	5.1	0.53
	Anthophoridae	5	*Elaphropoda impatiens*	G	10.3	16.5	1.60
		6	*Amegilla (Grossamegilla) elephas*	B,C	13.4	33.9	2.53
		7	*Am. (G.) sumatrana*	E,G	10.7	16.4	1.53
		8	*Am. (G.) pendleburyi*	A,B,C,D	11.2	15.6	1.39
		9	*Am. (Zonamegilla) andrewsi**	A,B,C,E,G	10.3	9.4	0.91
	Apidae	10	*Bombus (Senexibombus) senex*	I, J	22.0	12.4**	0.56
		11	*B. (Rufipedibombus) rufipes*	H,I,J	15.3	8.2**	0.53

* sun-loving bees
** PL of workers

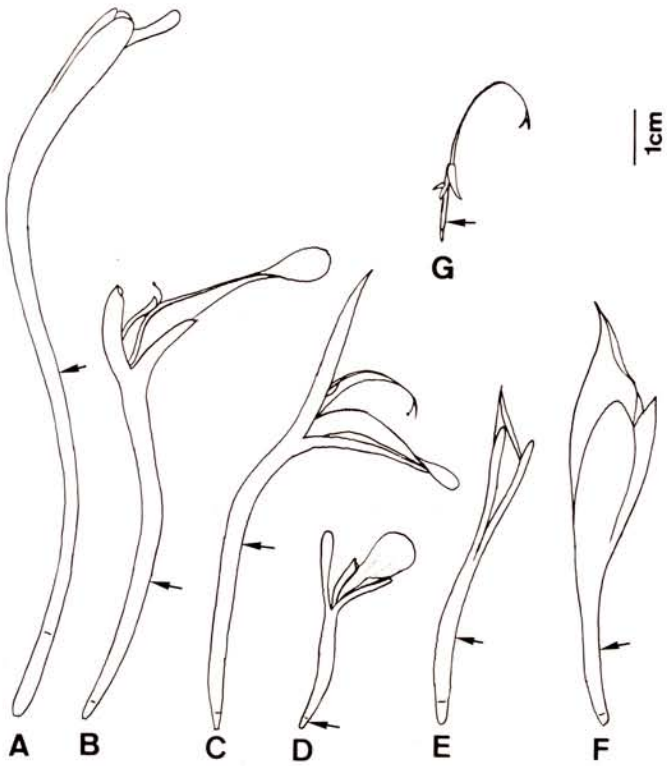

Fig. 1. Lateral views of studied zingiberaceous flowers with outer corolla tubes removed.
A, *Hornstedtia* aff. *conica*, B, *Achasma macrocheilos*; C, *Zingiber puberulum*; D, *Amomum uliginosum*; E, *Phaeomeria fulgens*; F, *Amomum aculeatum*; G, *Grobba aurantiaca*. Arrows show the mean nectar levels of flowers in the daytime.

Fig. 2. Studied zingiberaceous flowers and flower visitors. A-C, terrestrial *Achasma macrocheilos* flowers visited by an *Amegilla elephas* female; D, lateral and ventral views of *Amegilla elephas* males with proboscis extended and folded, respectively, scale = 1 mm; E, flower head of *Phaeomeria fulgens*; F, a spike with two flowers of *Zingiber puberulum*; G, flowers of *Amomum aculeatum*; H, flowers of *Amomum uliginosum*; I, a flower borne on a spike of *Hornstedtia* aff. *conica*.

proboscis into corolla tube (Fig. 2C). Another female bee not only ingested nectar but also collected pollen, and the mean period of its staying on a flower was 5.9 seconds (s.d. = 6.7, n = 31). After taking off, it again hovered above the flower, not flying away soon. When hovering, it scrubbed its mid tibiae with hind tibiae probably to transport pollen grains to

scopa of hind tibiae. After about 12-41 seconds of hovering, it again landed on another flower, never on the same one. A bee landed on some but not all flowers, and flew away. They appeared to be traplining although tracing them in the field was incomplete.

Male bees swiftly flying near the ground were also attracted to flowers and hovered above the flowers for about only one second, but then flew away. Males also appeared to be traplining. Although a male bees rarely landed on flowers, when landing on a flower it stayed there for 35 seconds inserting its proboscis into the corolla tube. Females visited flowers mainly in early morning and males mainly in the daytime at site B (Fig. 3). The mean nectar volume was less in the morning than in the afternoon. This suggests that the decrease of nectar volume was brought about by female bees' nectar-ingestion in early morning. Mean sugar concentration of nectar was 27.4 % (s.d. = 2.2, n = 7).

(2) *Zingiber puberulum* Ridley

A narrowly fusiform spike was borne on a short scape at a height of 10-30 cm above the ground (Fig. 2F). Corolla tube was slender and adnate to dorsal erect cream lobe and to cream labellum. Anther was connective to a prolonged, slender curved beak-like appendage (Fig. 1C). Stigma was protruding just below the apex of the appendage.

Flower visitor was an anthophorine species, *Elaphropoda impatiens*. Six bees (probably five males and one female) visited the flower in a 4.5-hour observation at site G (1015 - 1545 h, Jan.17, 1992), and landed on flowers only twice. The pollen load of a female collected on the flower was composed of pollen of only this plant species. Mean nectar volume was 2.7 m l (n = 2; 2.06, 3.40) and mean sugar concentration of nectar was 38.5 % (n = 2; 38, 39).

(3) *Grobba aurantiaca* Miquel

Yellow flowers were borne on erect slender inflorescences with a few crowded branches.

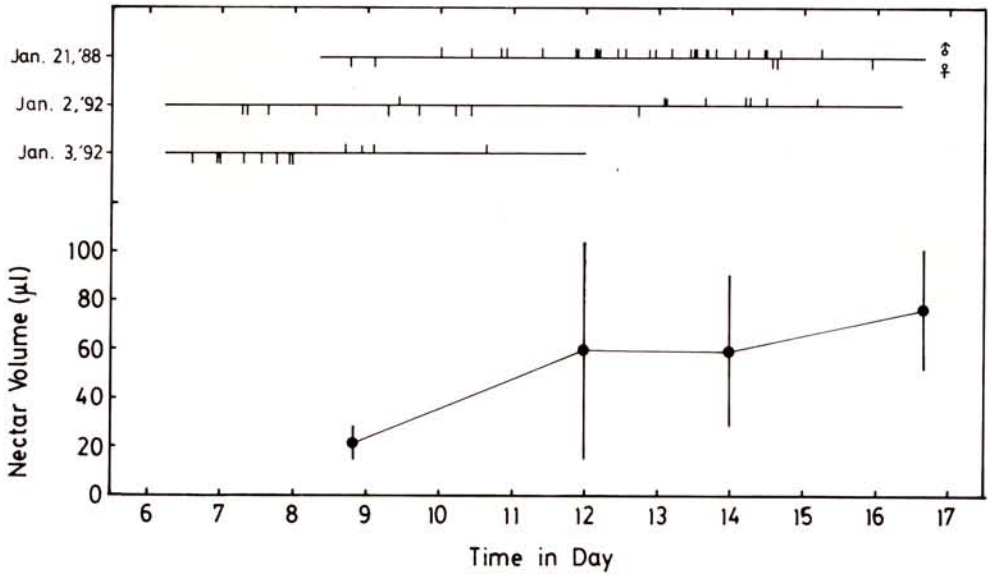

Fig. 3. Time records of *Amegilla elephas* visits to an inflorescence of *Achasma macrocheilos* (upper) and the mean nectar volume (ml) of flowers (lower) on Jan. 2-3, 1992. Vertical bar = standard deviation.

Labellum and filament were small and united for some distance above the junction of the corolla-lobes. Anther and stigma was far protruded beyond corolla tube and decurved (Fig. 1G).

Flower visitor was an anthophorine bee, *Elaphropoda impatiens*. The bees visited two times in a one-hour observation at site G (1430 - 1530 h, Jan. 14, 1988). When a bee landed on the labellum, the protruded anther and stigma touched the posterior portion of bee's abdomen. Observation on floral nectar was not made.

(4) *Amomum aculeatum* Roxb.

A short, round spike with base in the ground bore 3-6 erect, radially arranged yellow flowers, which were far extended from bracts, the whole of the flower parts forming a narrow cup (Fig. 1F, Fig. 2G).

Flower visitor was a long-tongued anthophorine bee, *Amegilla pendleburyi*. One female and two males visited the flower in a 4.2-hour observation at site C (0920 - 1330 h, Jan. 8, 1992). The pollen load of a flower-visiting female was composed of two zingiberaceous plant species: *Amomum aculeatum* (47 % in number and 39 % in volume) and *Zingiber* sp. (53 % in number and 61 % in volume). Mean nectar volume of flowers was 9.0 ml (s.d. = 1.24, n = 4) and mean sugar concentration of nectar was 40.0 % (s.d. = 0.1, n = 4).

(5) *Amomum uliginosum* Koenig

A globose spike borne on a subterranean rhyzome had 1-3 erect flowers on the ground (Fig. 2H). Corolla tube was short and labellum was boat-shaped and white with a yellow tip (Fig. 1D). Flower visitor was a halictid bee, *Nomia* aff. *combusta*. Hind tibiae of males were enlarged like those of *Elaphropoda* and euglossine bees. Males were traplining around the flowers without landing on flowers. Two females visited flowers in a one hour's observation at site C (0930 - 1030 h, Jan. 7, 1992). No pollen was collected by the bees. None of 15 flowers contained floral nectar.

(6) *Hornstedtia* aff. *conica* Ridl.

Fusiform spikes were borne on stout peduncles at a height of 30-70 cm above the ground and were tightly covered with large red bracts (Fig. 2I). One or two flowers were borne on a spike. Corolla tube was very long and curved (Fig. 1A). A flower lasted for only a day. When life span of a flower was terminated, the flower was pushed out from the spike.

Flower visitor was a long-billed sunbird, *Arachnothera longirostra*. Two birds visited the flowers in a three-hour observation at site E (1130 - 1430 h, Jan. 12, 1992). No bees were observed visiting flowers. The entrance of corolla tube was so tightly blocked up by stamen and stigma that insertion of bee's proboscis appeared to be impossible. Mean nectar volume was 60.3 ml (s.d. = 31.1, n = 3), and mean sugar concentration of floral nectar was 24.3 % (s.d. = 0.4, n = 4).

(7) *Phaeomeria fulgens* (Ridl.)

Heads of inflorescences were borne on long scapes at a height of 30-50 cm above the ground. Flowers were scarcely protruded from the head and only yellow erect labellum and red calyces were seen from above (Fig. 2E). Corolla tube was slender (Fig. 1E). Entrance of corolla tube was so tightly blocked up by stamen and stigma that insertion of bee's proboscis

appeared to be impossible.

Flower visitor was a long-billed sunbird, *Arachnothera longirostra*. In a 1.5-hour observation at site G (1030 - 1200 h, Jan. 17, 1992), it visited the flowers two times. Mean nectar volume was 13.3 ml (s.d. = 0.4, n = 3) and mean sugar concentration of nectar was 26.2 % (s.d. = 1.1, n = 3).

Pollination of two gesneriaceous species

(1) *Cyrtandra pendula* Bl.

Flowers were borne in a head on a decurved scape just on the ground surface. Corolla was white and long-tubed with a narrow base. Flower visitor was a long-tongued anthophorine, *Amegilla pendleburyi*. Male bees were traplining the flowers at sites A and B. Eleven bees (probably two females and nine males) visited the flowers in a four-hour observation at site B (0600 - 1000 h, Jan. 22, 1988) and nine males did in a one-hour observation at site A (1200 - 1300 h, Jan. 6, 1992). Mean nectar volume was 2.4 ml (n = 2; 1.67, 3.13) and mean sugar concentration of nectar was 34.0 % (n = 2; 32, 36) at site D.

(2) *Cyrtandra* aff. *grandiflora* Ridl.

Small inflorescences were borne from the axils of leaves. Corolla tube was white and short. The flower visitor was a halictid bee, *Nomia* aff. *elliotii*. Males were swiftly traplining around the flowers. Six males visited and only one landed on a flower in a 1.5-hour observation at site D (1115 -1245 h, Jan. 14, 1992). Mean nectar volume was 1.0 ml (s.d. = 0.8, n = 3) and mean sugar concentration of nectar was 26.3 % (s.d. = 0.4, n = 3).

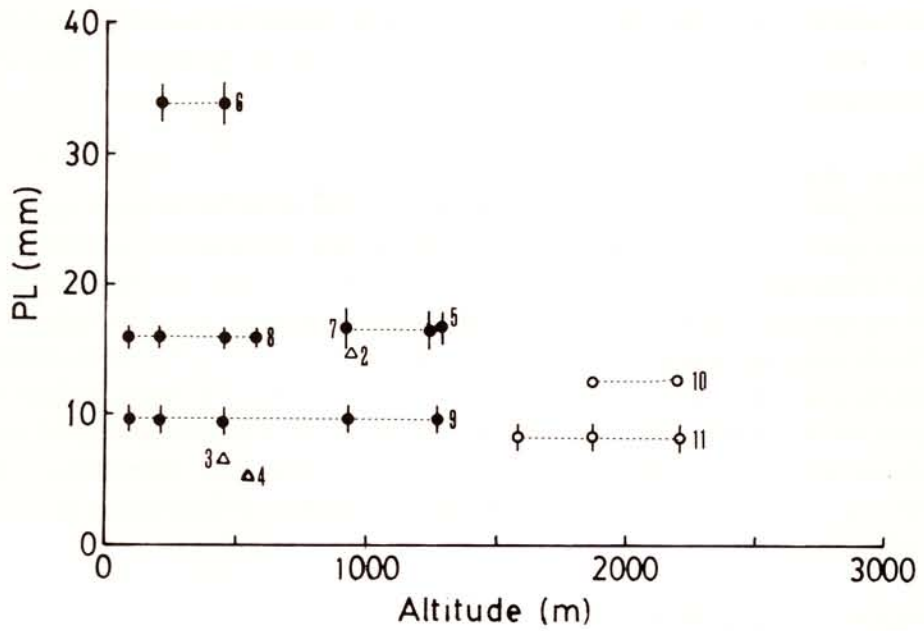

Fig. 4. Proboscis lengths of sympatric long-tongued bee species at various altitudes in West Sumatra (vertical bar = standard deviation). Open triangle, Halictidae; solid circle, Anthophorinae; open circle, Bombinae (workers). Numbers in the graph refer to bee species codes in Table 2.

Table 3. Morphological and anthecological characters of long-tubed flowers and their pollinators at forest floors in West Sumatra. Codes of study sites and pollinators are shown in Tables 1 and 2, respectively.

Family	Code	Species	Flower Color	Mean Corolla Tube Length (mm)	Mean Nectar Vol. (ml)	Mean Sugar Concent-ration (%)	Study Site	Pollinators										
								Aves	Halictid.			Anthophorid.					Apid.	
								1	2	3	4	5	6	7	8	9	10	11
Zingiberaceae																		
	1	*Achasma macrocheilos*	red	65.5	60.0	27.4	B, C						+					
	2	*Zingiber puberulum*	cream	57.3	2.7	38.5	G					+						
	3	*Grobba aurantiaca*	yellow	12.5	-	-	G					+						
	4	*Amomum aculeatum*	yellow	27.6	9.0	40.0	C								+			
	5	*Amomum uliginosum*	white	18.8	0.0	-	C			+								
	6	*Hornstedtia* aff. *coninca*	red	11.5	60.3	24.3	F	+										
	7	*Phaeomeria fulgens*	yellow	47.0	13.3	26.2	G	+										
Gesneriaceae																		
	8	*Cyrtandra pendula*	white	31.4	2.4	34.0	A, B								+			
	9	*Cyrtandra* aff. *grandiflora*	white	12.0	1.0	26.3	D				+							
Balsaminaceae																		
	10	*Impatiens korthalsii*	yellow	21.7	1.0	37.9	E,G		+					+		+		
	11	*I. talangensis*	yellow	22.9	1.2	33.8	G					+						
	12	*I. eubotrya*	yellow	24.0	1.5	39.4	G					+		+		+		
	13	*I. junghuhnii*	yellow	18.2	-	-	D								+			
	14	*I. gadutensis*	yellow	17.0	1.93	1.4	I										?	+

Guild structure of long-tongued bees

Eleven long-tongued bee species were recorded to visit the long-tubed flower species at forest floor in West Sumatra (Table 2). Three halictid bee species comprised a long-tongued *Thrinchostoma* and two less long-tongued *Nomia* spp. These species were "shade-loving bees", which usually flew swiftly at forest floor and very rarely came to sunny habitats. The collected anthophorine bee species belonged to two genera, *Elaphropoda* (one species) and *Amegilla* (three species of subgenus *Grossamegilla* and one of *Zonamegilla*). All these species of *Elaphropoda* and *Grossamegilla* were also shade-loving bees. *Amegilla (Zonamegilla) andrewsi* was a sun-loving bee but rarely visited flowers at forest floors. The ratio of proboscis length to the forewing length (PL/WL) was highest in the largest species *Am. elephas*, and followed by four species (*El. impatiens, Am. sumatrana, Am. pendleburyi* and *Th. asianum*, Table 2)

Long-tongued bee guild structure changed as an altitudinal gradient (Fig. 4). At lower altitudes less than 1400 m, the shade-loving long-tongued bees can be classified into three PL classes: PL > 32 mm (I); 14 < PL < 17 mm (II); 5 < PL < 7 mm (III). The PL classes corresponded to the PL/WL ratio classes above mentioned. Contrasting with the character displacement of PL among the three guilds, character convergence of PL was detected among species of PL class II. All PL classes were present at low altitudes less than 500 m, and PL class I disappeared at altitudes over 500 m. At altitudes between 700 and 800 m, the lowland bee species of PL class II were displaced by hill species. A drastic change of guild structure was observed at altitudes between 1400 and 1500 m. Above this altitude, halictid and anthophorine long-tongued bees disappeared and in turn bumblebees appeared. In the high mountains in West Sumatra, there were two bumblebee species with different PL

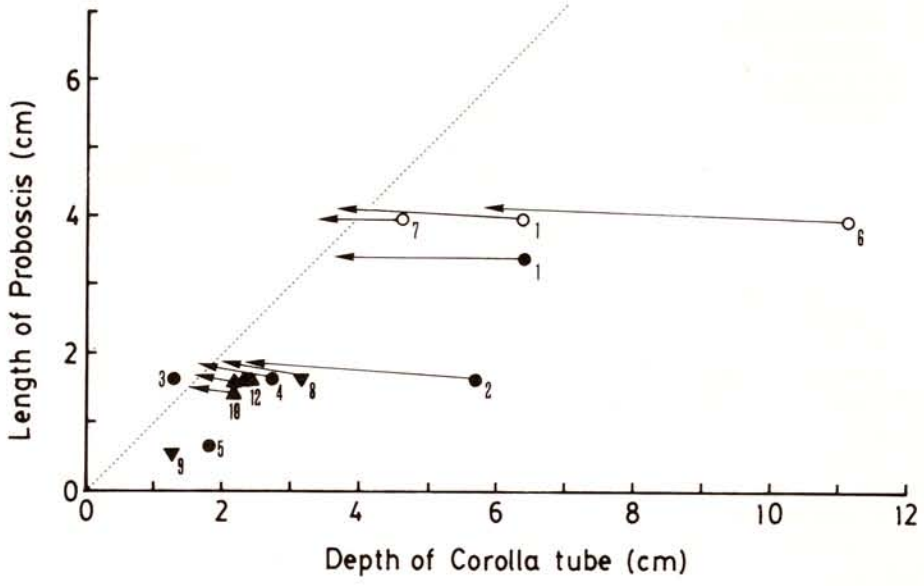

Fig. 5. Relationship between the depth of corolla tube and the proboscis length of pollinator. Circles, triangles and inverse triangles refer to Zingiberaceae, Balsaminaceae and Gesneriaceae, respectively. Open and solid symbols refer to ornithophily and melittophily, respectively. Length of arrows show the mean depth of nectar in corolla tubes. Numbers in the graph refer to plant species codes shown in Table 3.

values.

Table 3 compares the flower visitors of long-tubed flower species in Zingiberaceae and Gesneriaceae with those in Balsaminaceae studied by Kato *et al.* (1991). Flower species were divided into ornithophilous and melittophilous types, and the latter was further divided into three subtypes: deepest flowers, medially deep flowers and short-tubed flowers. Pollinators of these three groups corresponded to the PL classes above mentioned. There were significant differences in nectar volume and sugar concentration between ornithophilous flowers and medially deep melittophilous flowers (by ANOVA, d.f. = 6, $F = 8.91$, $p < 0.05$; d.f. = 6, $F = 33.8$, $p < 0.001$, respectively). Some medially deep flower species shared common bee pollinators of the same PL class. For example, *Amomum aculeatum, Cyrtandra pendula* and *Impatiens junghuhnii* were pollinated by *Am. pendleburyi*. Although three *Impatiens* species were visited by more than one bee species, nine plant species (75 % of melittophilous plant species in Table 3) were visited by a single bee species. At individual level, each individual plant was usually visited by only a single bee species.

Figure 5 shows the relationship between the corolla depth in plant species and PL in their corresponding pollinators. PL was generally shorter than corolla tube except in *Grobba aurantiaca*, which impose bees to bend backward in order to attach the tip of protruded stamen and stigma on bee's hind abdomen. When considering mean nectar level in corolla tube, the depth from flower entrance to mean nectar level was largely just smaller than PL (see arrows in Fig. 5). This means that flower nectar is practically depleted by pollinators.

DISCUSSION

Of nine long-tubed flower species in Zingiberaceae and Gesneriaceae, seven were viewed as melittophilous and two as ornithophilous. The melittophilous plant species can be classified into three pollination guilds corresponding to three PL classes of pollinating bees. The first guild comprises flower species with the deepest corolla exemplified by *Achasma macrocheilos* pollinated by *Amegilla elephas*. The flowers had the following anthecological characteristics: (1) red flowers on the ground, (2) long corolla tube, (3) high nectar production rate and (4) low sugar concentration of floral nectar (28 %). This syndrome resembles that of ornithophily and these plants might occasionally be pollinated by sunbirds. Janzen (1971) reported traplining foraging behavior of euglossine bees in the Neotropics. *Amegilla elephas* having a remarkably long proboscis is also a rare, shade-loving, swiftly-flying trapliner, and this is an example of inter-continental behavioral convergence at similar environments of extremely low flower density.

The second guild comprises medially deep flower species exemplified by *Zingiber puberulum, Grobba aurantiaca, Amomum aculeatum, Cyrtandra pendula* and *Impatiens* spp. Cardamon (*Elettaria cardamomum*) studied in Papua New Guinia by Stone and Willmer (1989) might also be a member of this guild. These flowers had the following anthecological characteristics: (1) yellow or white flowers on or above the ground, (2) long corolla tube, (3) not so high nectar production rate, (4) high sugar concentration of floral nectar (32-40 %). Their pollinators were one *Elaphropoda*, two *Amegilla (Grossamegilla)* and one *Thrinchostoma* species and all were also trapliners. *Grossamegilla* is a subgenus most diverse in Southeast Asia and characterized by a relatively long PL (Brooks, 1988). This diversity of *Grossamegilla* is attributed to the diversity of long-tubed flowers at forest floor in Southeast Asia. At higher altitudes higher than 1400 m, these bees were displaced by bumblebees, and the pollination syndrome would be modified there.

The third guild comprises white, shortly tubular flower species exemplified by *Amomum uliginosum* and *Cyrtandra* aff. *grandiflora*. These species were pollinated by shade-loving *Nomia* spp. Congeneric plant species usually belong to the same pollination guild, but not always as in *Amomum* and *Cyrtandra*. Traplining behavior of shade-loving *Nomia* can be regarded as behavioral convergence with *Amegilla, Elaphropoda* and euglossine bees.

Pollination syndrome of ornithophilous flower species was detected as follows: (1) red corolla or calyces or bracts of spikes, (2) long, stout corolla tube, (3) tightly imbricated spike with stout, long peduncle, (4) high nectar production rate, (5) low sugar concentration of floral nectar (24 - 26 %; Table 3). These properties are comparable with those of an ornithophilous wild banana, *Musa salaccensis* (Itino *et al.*, 1991).

Zingiberaceae characterized by zygomorphic flowers is the family in which specialized melittophily is thought to have originated during Campanian in Cretaceous (Friis, 1988). Although fossil records of solitary bees are lacking in Cretaceous, the appearance of them is thought to precede the end of Cretaceous because a fossil of more specialized *Trigona* (Apidae) is found from a Cretaceous formation (Michener and Crimaldi, 1988). Birds also originate in Cretaceous. Accordingly, both anthophorine bees and birds are candidates of original pollinators of Zingiberaceae. Kress (1990) presented the parsimonious phylogeny of Zingiberales as follows ((Musaceae (Strelitziaceae (Lowiaceae (Heliconiaceae ((Zingiberaceae, Costaceae) (Cannaceae, Marantaceae)). Ornithophily is reported in

Musaceae (Itino *et al.*, 1991), Strelitziaceae (Frost & Frost, 1981), Heliconiaceae (Stiles, 1975) and only a part of Zingiberaceae (this study). The distribution of ornithophily in the cladogram of Zingiberales suggests that ornithophily is an apomorphic condition but that ornithophily in Zingiberaceae secondarily derived from melittophily.

Most but not all species in Gesneriaceae have long-tubed flowers. Whereas the studied species were melittophilous, there are ornithophilous species such as *Aeschynanthus* spp. which are epiphytes with red, long-tubed flowers (McClure, 1966). No long-tongued bee species flying in the subcanopy stratum have not been found in the Palaeotropics unlike in the Neotropics. More persistent observations of many species in various habitats are necessary to discuss the evolutionary process of pollination system in Gesneriaceae.

Finally, we discuss the guild structure of long-tongued bee species in Sumatra. Our pollinator sampling was so incomplete that there would be more species. For example, we collected only three of the seven *Grossamegilla* species recorded from Sumatra (Lieftinck, 1954). However, in total no more than 20 bee species with a long tongue would occur, and naturally the number of long-tubed flower species would exceed this number. This means that many long-tongued flowers share common pollinators. This prediction was partly supported by our study. For example, at species level, *Am. pendleburyi* visited three flower species, and at individual level a bee visited only one plant species but another visited two, judging from composition of pollen in bee's pollen load. Viewing from plants, 75 % of studied plant species were each visited by only a single bee species. Considering the rarity of bees and traplining foraging behavior, individual plant appeared to be mainly visited by a single bee species even if there would be some sympatric species with similar PLs at a habitat. The observations that the partnership is constructed not between species (i.e., one plant species vs. one bee species) but between individuals (i.e., one individual plant vs. one individual bee) might explain the convergence of PL among bee species in a bee guild.

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加藤　真，市野隆雄，永光輝義　　西スマトラの熱帯雨林の林床に分布するショウガ科とイワタバコ科の長筒花におけるハナバチ媒と鳥媒

インドネシア，西スマトラ州のさまざまな標高の自然林で，ショウガ科7種とイワタバコ科2種の送粉について調査した。地表に咲く *Achasma macrocheilos* の赤い長筒花に，極めて長舌の大型のコシブトハナバチ属の1種 *Amegilla elephas* が訪花した。このハチは地表近くを極めて速く飛翔し，新熱帯のシタバチで見られるような巡回採餌行動をみせた。このハチはこのショウガ科植物のみに花粉と花蜜を依存しており，またこの植物はほとんどこのハチのみによって送粉されていた。ショウガ科3種 (*Zingiber puberulum, Grobba aurantiaca, Amomum aculeatum*) とイワタバコ科1種 *Cyrtandra pendula* の黄色 (または白) の長筒花は，見回り採餌をする好樹陰性で中型・長舌のケブカハナバチ亜科のハナバチ (コシブトハナバチ属 *Amegilla* とモモブトコシブトハナバチ属 *Elaphropoda*) によって送粉されていた。短い筒状花をつける *Amomum uliginosum* と *Cyrtandra* aff. *grandifolia* は巡回採餌をするアオスジコハナバチ属 *Nomia* のハナバチによって送粉されていた。ショウガ科の2種，*Hornstedtia* aff. *conica* と *Phaeomeria fulgens* は，赤い苞に包まれた堅固な花序に，極めて伸長した長筒花をつける。これらの花は長いくちばしをもったタイヨウチョウ科の鳥，コクモカリドリ *Arachnothera longirostra* によって送粉されていた。これら鳥媒の花は，ハナバチ媒の花よりも糖度の有意に低い花蜜を有意に多量に生産していた。

これらの長舌のハナバチ類は舌の長さによって3つのグループに分けられ，それらはハナバチ媒の花の3つの送粉ギルドに対応していた。それぞれのギルド内では舌の長さの形質置換は見られなかった。ハナバチ媒の種の25%は2種以上のハナバチによって訪花されていたが，それにもかかわらず，ほとんどの植物個体は1種のハナバチによって訪花されていた。1400 mを越える標高では，マルハナバチがケブカハナバチ亜科のハチに置き代わり，長舌ハナバチの群集構造は単純になっていた。