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Research article

Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest

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Summary. We used microscopic pollen analysis to investigate the diversity and similarity of pollen diets of six colonies of stingless bees (Apidae; Meliponini) located within one monospecific (three colonies of *Trigona collina*) and one mixed nesting aggregation (one colony of *T. collina*, and one colony of each of the close relatives *T. melina* and *T. melanocephala*) in lowland tropical rain forest in Sabah, Malaysia. Samples of 20 corbicular loads, collected six times over a period of three months from each colony, contained a total of 74 different morphotypes of pollen grains with an average between 4.7 to 8.5 per sample for the different colonies. In an analysis on total diet composition intraspecific similarity was much greater than interspecific similarity. The focal colony of *Trigona collina* from the mixed aggregation distinctly clustered according to species rather than nest location, suggesting that some interspecific resource partitioning occurs. The sampling period was accompanied by a drastic increase in flowering activity as evidenced by data from a flower phenology transect. At times of limited flowering similarity of pollen diets was generally low, both within and between species. It is hypothesized that this is so because bees are forced to forage from scattered subsets of flower patches spread out over a large foraging range. In times of increased flowering pollen diet similarity significantly increased between colonies of the monospecific aggregation, presumably because colonies concentrated on more profitable sources in closer proximity. In contrast, similarity remained low within the mixed aggregation, suggesting that innate differences in foraging preferences precluded any effect of diet convergence.

Key words: Pollen foraging, resource partitioning, generalist forager, stratum preference, resource availability.

Introduction

Stingless bees (Apidae, Meliponini) live socially in perennial colonies of a few hundred up to several thousands of individuals (Wille, 1983). They are generally polylectic and forage on an array of food plants that provide some pollen and nectar over much of the year rather than being highly specialized flower visitors. On the population level some species are known to use floral resources from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms et al., 1996). Niche overlap between different stingless bee species was frequently found to be high in studies of flower visitation, although some selectivity has been reported, at least on the sub-tribal level (Heithaus, 1979; Ramalho, 1990; Wilms et al., 1996). Results from a study in Sarawak, Malaysia, using a canopy access system suggest that resource partitioning between species may be mediated by interspecific differences in foraging stratum preferences (Nagamitsu et al., 1999).

The analysis of colony pollen stores or forager pollen loads has proven to be a useful tool in assessing bee diet as it is independent of flower accessibility and allows for equally high resolution in the forest canopy and understory (Engel and Dingemans-Bakels, 1980; Sommeijer et al., 1983; Ramalho et al, 1989; Nagamitsu et al., 1999). Sommeijer et al. (1983) studied pollen loads of homing foragers of stingless bees in farmland in Trinidad and found that the variability of pollen spectra was greater between two species of *Melipona* than between colonies of the same species. Nagamitsu et al. (1999) found quite pronounced seasonal fluctuations of the between-species similarity of pollen diets of five species of stingless bees and speculated that the amount of resource partitioning may be related to general pollen resource availability. To our knowledge there has been no study so far that has linked pollen foraging and resource partitioning to floral resource availability in the habitat. We

report on our findings from a study on three closely related species of Southeast Asian *Trigona (Tetragonula)*. The study took advantage of the specific spatial arrangement of two aggregations of bee nests at our study site as well as of the continuous increase of flowering activity in the habitat during the course of the field season. We asked the following questions:

1. Is there species specificity of both qualitative and quantitative aspects of pollen resource diversity?
2. What is the relationship between flowering activity in the habitat and (i), the diversity of foraged pollen, and (ii), pollen resource overlap between colonies and species?

Material and methods

Study site

The study was carried out in the Deramakot Forest Reserve in central Sabah, Malaysia, northern Borneo (117°30′E, 5°19′N). The commercial forest reserve is covered by still large areas of old-growth (25 years since last major disturbance) slightly disturbed lowland mixed dipterocarp forest (*Parashorea tomentella/Eusideroxylon zwageri* type) (Chai and Amin, 1994). The climate is normally only slightly seasonal with reduced rainfall in March and April, but in early 1998 was heavily influenced by the onset of the local effect of the Pacific El Niño event that resulted in an exceptional dry spell in the whole of Southeast Asia. The particular flowering phenology observed during the study period from March until May 1998 was probably caused in part by this exceptional dry spell (see results).

Bees and bee nests

The study took advantage of the species composition and spatial arrangement of two aggregations of nests (see Fig. 1a): One (monospecific) aggregation consisted of three nests of *Trigona (Tetragonula) collina* Smith that were situated underneath the base of two large trees growing in close proximity (less than 5 m apart). The other (mixed) aggregation consisted of one nest of each of the following three species: *T. (Tetr.) collina*, *T. (Tetr.) melanocephala* Gribodo, *T. (Tetr.) melina* Gribodo. These nests were also situated underneath two large trees that were in close proximity (less than 30 m apart). The two aggregations were located in old secondary forest at a distance of approximately 250 m from each other. Due to the close proximity of the nests it was guaranteed that the colonies of each of the aggregations had widely overlapping foraging ranges and, at least potentially, were able to use overlapping sets of flowering plants. The species are small to medium-sized stingless bees that do not seem to exhibit any obvious morphological differences potentially related to pollen foraging. *T. collina* is the largest species (head width ~ 2.3 mm) followed by *T. melina* (~ 2.1 mm) and *T. melanocephala* (~ 2.0 mm).

Flowering phenology

In an attempt to quantify the floral resource availability in the habitat we repeatedly ran a 2 km flower phenology transect that criss-crossed through the bees' nesting area. We counted all flowering woody plants visible from the transect and collected specimens to assess species diversity. In the case of large trees binoculars were used for the confirmation of the presence of flowers and decayed flowers were collected from the forest floor. Assessment of flowering activity normally took place immediately following pollen sampling. Due to its limited scope and lack of canopy access the transect was likely to miss much of the actual flowering in the area. Therefore, the results should be regarded as an index of flowering intensity and diversity rather than a detailed survey of potential bee resources.

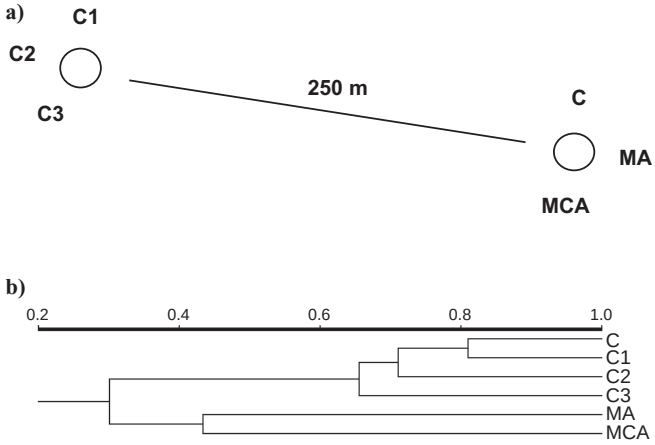

Figure 1. (a) Schematic view of the relative position of nests of two aggregations of stingless bees. The first aggregation is monospecific and consists of three colonies of *T. collina* (C 1-3), the second is mixed and has one colony of each of the three species: *T. collina* (C), *T. melina* (MA), and *T. melanocephala* (MCA). (b) Dendrogram based on qualitative similarity of all pollen types present in all samples of the respective colony over the entire study period. Distances are Sørensen-Index, clustering was done with UPGMA

Pollen samples

Returning pollen foragers were captured at the nest entrances using a hand-held exhaustor. For any given date pooled 20-forager samples were collected from each colony between 6:30 and 12:30 depending on weather conditions and foraging activity. Repeated samples were taken on six consecutive points in time during March, April, and May 1998 (12/13.3., 18.3., 1.4., 16./17.4., 29.4., and 7.5.). On 2.2., 17.2., 17.4., 8.5., and 9.5. we additionally collected individual samples from all three species (N = 53 (*T. collina*), N = 28 (*T. melina*), and N = 21 (*T. melanocephala*)) in order to assess individual within-foraging trip resource use.

Pollen treatment and analysis

Standard palynological protocols (KOH digestion, acetolysis, glycerin jelly mounting) were followed for slide making. The slides were then analyzed in a standardized way. First, the core area of each slide was thoroughly searched for pollen types and types were characterized by size, shape, number and shape of the apertures, and ornamentation. High resolution light micrographs were made from polar and equatorial views of all pollen types. For quantitative analysis pollen grains of all types encountered repeatedly in the core area were then counted within the boundaries of 14 quadrants situated along a transect across the cover slip. Particularly abundant grains were counted in the smaller subunits of various (suitable) sizes of the same quadrants and counts of all types were finally transformed into per-area densities. Density data were consecutively transformed into per-slide percentages for each pollen type by multiplying the densities with a type-specific volume correction factor inferred from size and shape of the respective grains. Grains represented with less than 0.5 volume-% were considered as contaminations and omitted from further analysis. Using this area- and volume-based approach allowed for a sufficiently high level of standardization between samples without the tedious task of counting thousands of minute grains situated among small numbers of giants (Biesmeijer and Sommeijer, 1992).

Taxonomic identifications of types to the level of plant family, genus or species (or taxonomic "type") wherever possible were done from micrographs by SvdK (see appendix).

To describe pollen type diversity of samples we used simple pollen type richness (number of types per sample) as well as Shannons J' (Pielou, 1966), a measure of the evenness of the quantitative representation of types in a sample. Effects of colony and time on sample richness and evenness were analyzed using ANCOVA with time as a covariate.

Between-sample similarity was calculated as the qualitative Sørensen-index that ranges between 1 (identical) and 0 (no match) (Magurran, 1988). For the comparison of within-aggregation similarity of samples in relation to time we selected a focal colony in each aggregation (in case of the mixed aggregation it was the *collina*-colony C) and calculated Sørensen-values between the focal colony and the two other colonies for each point in time. Means were used for Linear Regression Analysis with time as the independent variable.

Results

Individual pollen loads

Individual bees of all three species seemed to be highly constant pollen foragers. Samples were defined as pure if more than 95 volume-% of the sample consisted of the same pollen type. Based on this definition, all but two loads (from 102) were found to be pure, and even higher purity standards (e.g. 98 volume-%) would not significantly alter that result. Thus, the presence of a range of different pollen types in the pooled samples of a given colony described below is largely a result of different foragers specializing (at least temporarily) in different pollen plants.

Total between-colony similarity

A total of 74 different pollen types were recorded (see Appendix) in the pooled samples of all six stingless bee colonies, with the number of types being almost identical for all *T. collina* colonies (20 to 26) and *T. melanocephala* (25), and being slightly higher in *T. melina* (32). Figure 1b shows the results of a cluster analysis that was done on a qualitative presence/absence matrix (74 pollen types × 6 colonies) pooling all samples for each colony. It is evident that intraspecific similarity is much greater than interspecific similarity. The *collina*-nest C that is situated within the distant mixed aggregation is actually nested within the cluster of the three other *collina*-colonies.

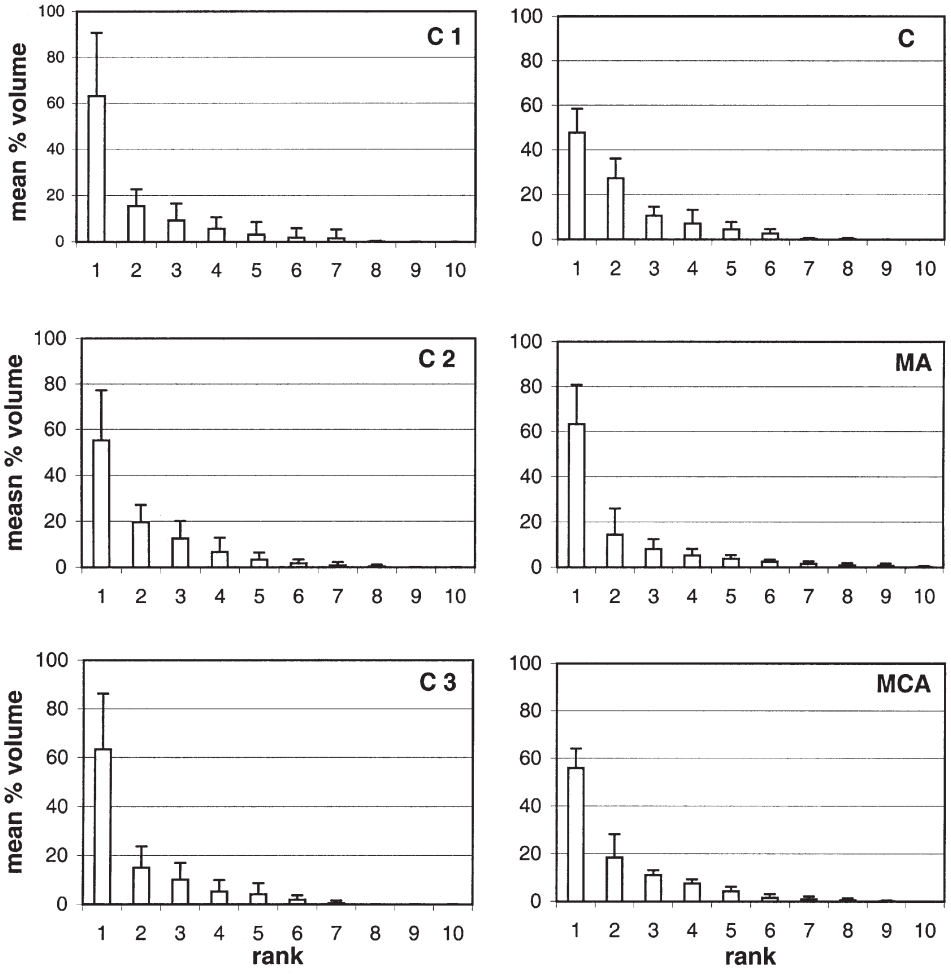

Figure 2. Mean rank-predominance distribution of volume-representation of pollen types in 20-forager samples of six colonies of stingless bees belonging to three different species: *T. collina* (C, C1-3), *T. melina* (MA), and *T. melanocephala* (MCA). Error bars are standard deviations.

Table 1. Summary of pollen analysis of 20-forager samples (N = 6) of six colonies of stingless bees

	mean no. pollen types/ 20 bees (std. deviation)	mean eveness (J´) of volume distribution (std. deviation)	total no. of pollen types
T. collina (**C1**)	4.67 (2.34)	0.61 (0.29)	20
T. collina (**C2**)	5.67 (2.25)	0.70 (0.18)	24
T. collina (**C3**)	5.34 (1.51)	0.60 (0.28)	26
T. collina (**C**)	5.83 (1.60)	0.77 (0.13)	22
T. melina (**MA**)	8.50 (1.05)	0.55 (0.18)	35
T. melanocephala (**MCA**)	6.67 (1.63)	0.69 (0.05)	25

Within-sample pollen diversity

At a given point in time 20-forager samples contained between 2 and 10 different types above the 0.5%-volume threshold. Tab. 1) summarizes the results of within sample diversity of pollen sources for all colonies. Between colonies there was significant variation in the number of pollen types per sample ($N = 36$; $df = 5$; $F = 3.15$; $p < 0.05$), a result that was almost entirely based on the slightly elevated numbers in the *T. melina* colony. No differences were apparent between different colonies of *T. collina*. There was no between-colony effect on the evenness of pollen type representation ($F = 1.11$; N.S.). Generally, the rank-predominance distributions of samples of different colonies were similar (Fig. 2).

Flowering activity and pollen diversity

Both species diversity and abundance of blooming plants significantly increased during the study period (Linear Regression with time as independent variable; species diversity: $R^2 = 0.86$, $F = 31.86$, $p < 0.01$; number of individuals: $R^2 = 0.68$, $F = 11.84$, $p < 0.05$) (Fig. 3d). This confirms our impression of a continuously increasing flowering activity accompanying the severe dry spell that was experienced by the whole Deramakot area from February until May 1998. Flowering involved all strata of the forest and finally, in the end of April, turned into a minor mass flowering event including several species of Dipterocarpaceae. This finding is contrasted with the lack of any change in the number of pollen types per sample over time ($R^2 = 0.030$; $F = 0.895$; N.S) (Fig. 3a). There was, however, an slight increase of sample evenness ($R^2 = 0.179$; $F = 6.33$; $p < 0.05$).

Within the two aggregations the similarity of pollen samples showed a strikingly different pattern over time. Whereas similarity significantly increased over time within the monospecific *collina*-aggregation ($R^2 = 0.90$; $F = 35.18$; $p < 0.01$) (Fig. 3b), there was no change of similarity at all between colonies in the mixed aggregation ($R^2 = 0.005$; $F = 0.02$; $p = 0.90$) (Fig. 3c).

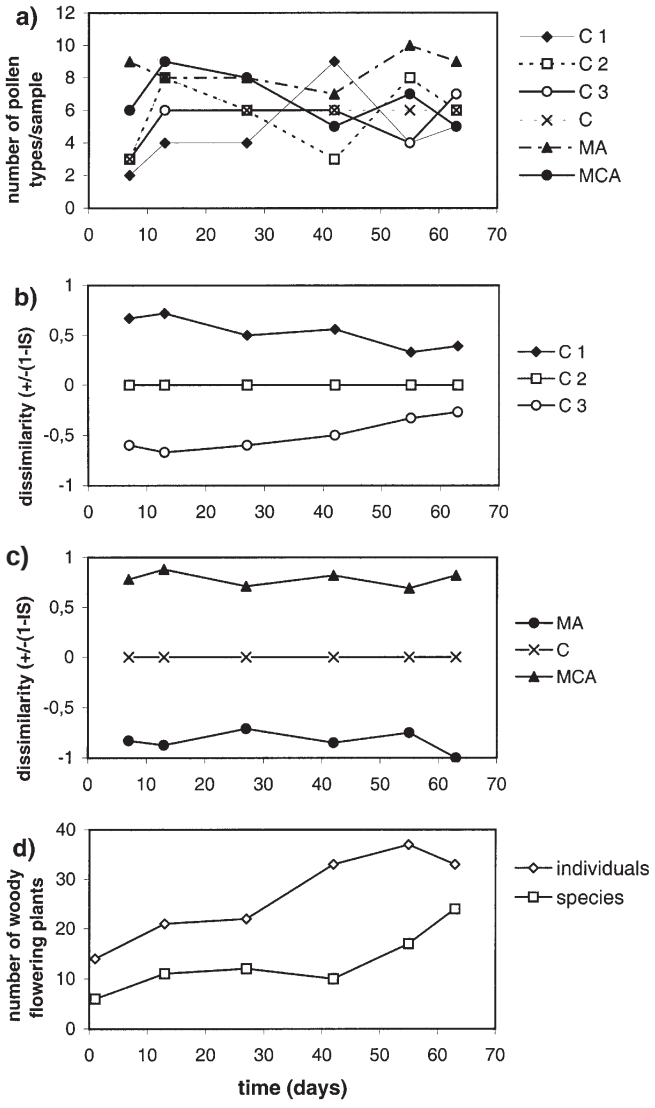

Figure 3. (a) Pollen type richness of samples between March and May 1998 for different colonies of stingless bees (C = *T. collina* (4 colonies); MA = *T. melina*; MCA=*T. melanocephala*), (b) dissimilarity of pollen samples within the monospecific *collina*-aggregation over time (dissimilarity is calculated as (1-Sørensen-Index) and plotted as positive and negative deviation from 0 (focal colony), (c) dissimilarity of pollen samples within the mixed aggregation, and (d) flowering activity as a function of time in the habitat

Discussion

Specificity of pollen sources

Our results suggest that some species specificity exists in pollen plant preferences of the *Trigona (Tetragonula)* species investigated. Judged by their pollen source plants all four colonies of *T. collina* were clustered according to their species rather than their spatial location and were clearly distinct from those of the colonies of *T. melanocephala* and *T. melina*. Our findings add strength to the view that some floral resource partitioning occurs even between closely related

species of social bees in tropical habitats (Sommeijer et al., 1983; Nagamitsu et al. 1999).

We can only speculate on the proximate causes of diverging floral preferences of the species investigated. As there seem to be no significant distinguishing morphological features that might lead to differential patterns of pollen collection between species, the causes are likely to be found in the context of flower search behavior and/or foraging strategy. Johnson (1983) distinguished solitary and group foragers among neotropical species of stingless bees, with solitarily foraging species exploiting resources scattered in space and time whereas group foragers concentrate on rich and clumped resources. These are only extremes of a range of strategies that are further specified through interspecific differences in aggressiveness and speed of recruitment (Johnson and Hubbell, 1975; Johnson, 1983). In our study the rather uniform rank-predominance distributions of pollen sources of all three species suggest that there are no drastic differences between species concerning diversity and degree of clumping of food patches. At any time, even during times of high flowering activity, the colonies were foraging on a relatively broad array of pollen plants, a finding that does not plead for the existence of an effective mass recruitment system like those present in other Meliponines (Hubbell and Johnson, 1978; Johnson, 1983). Possible interspecific differences in foraging behavior are revealed by studies using artificial feeder experiments (Nagamitsu and Inoue, 1997). In their study the authors report that *T. melanocephala* is relatively quick to arrive at fresh honey baits, whereas *T. melina* is significantly slower, and *T. collina* is generally reluctant to visit baits at all (Nagamitsu and Inoue, 1997). The speed of detecting new food resources may thus affect the choice of pollen sources.

Part of the differences in pollen sources between the species may result from foraging stratum preferences. Nagamitsu et al. (1999) studied flower visitation of 11 stingless bees in a rainforest in Sarawak with the help of a canopy observation system. Their findings suggest that, in contrast to all other species, *T. melanocephala* is foraging predominantly in the understory. Feeder experiments seem to confirm this view (Nagamitsu and Inoue, 1997). Our own results are difficult to interpret in this respect because most pollen identifications are not accurate enough to allow deduction of plant stratum. Typical understory taxa as Palmae are indeed present in *T. melanocephala*, but occur even more frequently in *T. melina*. On the other hand, the pollen diet of *T. melanocephala* also includes typical canopy taxa like Dipterocarpaceae and Bombacaceae (see Appendix), suggesting that possible stratum preferences are not exclusive.

Pollen foraging and general resource availability

Floral resource availability of bees is difficult to quantify in natural forest habitats due to the difficulty of judging the relative importance of certain flowering plant species to the bees in question. Acknowledging this we are nonetheless confident that our approach of relating general flowering activity to bee foraging is justified because (i) the bee species in question did obviously use a broad range of flowering plants, and (ii) because the evident increase of flowering equally concerned both abundance and diversity of woody plants in all strata of the forest. Thus, it seems justified to assume that pollen resource availability in the habitat did indeed vary accordingly for the three bee species.

In our study pollen resource overlap between colonies, conspecific or not, was generally low at the beginning of the study period when floral resources were scarce. Much of this effect is probably due to extrinsic factors such as a highly scattered distribution of food patches at the time. If flower patches are at low density in the habitat foragers will have to cover long distances to find them. The larger the diameter of the foraging range, the more likely are foraging bees from different colonies to forage at different sets of patches. In many cases this will also lead to exploitation of different plant taxa. This may explain why intra- and interspecific similarities of pollen diets were almost equally low at times of low food availability.

When resources became more available, however, foraging bees were probably capable of exerting significantly more active choice concerning their pollen diet. According to optimal foraging theory foragers are expected to consecutively drop non-profitable food items/patches from their diet in favor of more profitable ones (MacArthur and Pianka, 1966). In case of the conspecific colonies of *T. collina* this potential for choice may have led to the observed increase of pollen diet similarity as foragers settled on a selection of highly profitable and nearby flower patches. The same scenario is likely to have applied for the mixed aggregation as well, but with a somewhat different outcome. Here, innate differences in foraging preferences or floral choice (e. g. stratum preferences, color preferences, etc.) between species seem to have counteracted any effect of diet convergence.

In contrast to Nagamitsu et al. (1999) we did not find occasional sharp increases in diet overlap between different species, a difference that is likely to be related to the particular flowering characteristics present at the time and location of the respective studies. In our case, flowering diversity increased together with general flowering activity, thus creating a multitude of profitable foraging opportunities for bees to choose from. In a flowering situation that is more heavily biased in favor of one or a few overabundant plant taxa, diet overlap between bee species is bound to be more pronounced.

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Appendix. Pollen types represented by more than 0,5 volume-% in 20-forager samples of six colonies of stingless bees of three species: *T. collina* (C 1-3, C), *T. melina* (MA), and *T. melanocephala* (MCA)

no.	apertures	family	genus/type	C 1	C 2	C 3	C	MA	MCA
1	inaperturate	Euphorbiaceae	*Croton* type					x	
2	inaperturate	Euphorbiaceae	*Croton* type	x	x		x	x	x
3	inaperturate	Hernandiaceae			x				
4	inaperturate, tetrade	Mimosaceae	*Mimosa pudica* type	x		x	x		
5	inaperturate, polyade	Mimosaceae	*Accacia/Albizia* type			x			
6	inaperturate, tetrade			x	x	x	x		
7	inaperturate			x		x	x		
8	monocolpate	Palmae	*Cocos nucifera* type					x	x
9	monocolpate	Palmae	*Eugeissona* type					x	
10	monocolpate	Palmae ?						x	
11	monoporate	Palmae ?						x	
12	monocolpate							x	
13	monocolporate				x			x	x
14	monoporate	Pandanaceae	*Pandanus*					x	
15	monoporate	Typhaceae	*Typha* type					x	
16	dizonoporate	Moraceae						x	x
17	triaperturate	Passifloraceae		x	x	x	x		
18	triaperturate	Passifloraceae	*Passiflora*					x	
19	triaperturate	Passifloraceae	*Passiflora*	x	x	x	x	x	
20	trizonocolpate	Convolvulaceae	Merremia type						x
21	trizonocolpate	Dipterocarpaceae	*Shorea* type	x	x	x	x		x
22	trizonocolpate	Thecaceae		x	x	x	x		x
23	trizonocolpate				x	x	x		
24	trizonocolpate				x				
25	trizonocolporate	Anacardiaceae		x	x	x	x	x	x
26	trizonocolporate	Anacardiaceae				x			
27	trizonocolporate	Bombacaceae		x	x	x	x	x	x
28	trizonocolporate	Bombacaceae		x	x	x			
29	trizonocolporate	Bombacaceae						x	
30	trizonocolporate	Bombacaceae						x	
31	trizonocolporate	Bombacaceae		x		x	x		
32	trizonocolporate	Bombacaceae		x	x	x	x	x	
33	trizonocolporate	Euphorbiaceae	*Macaranga* type					x	
34	trizonocolporate	Euphorbiaceae	*Blumeodendron* type	x	x				
35	trizonocolporate	Euphorbiaceae	*Blumeodendron* type					x	x
36	trizonocolporate	Guttiferae	*Antidesma* type ?					x	
37	trizonocolporate	Leguminosae		x	x	x	x		
38	trizonocolporate	Leguminosae ?						x	
39	trizonocolporate	Loranthaceae							x
40	trizonocolporate	Rubiaceae		x	x	x	x	x	x
41	trizonocolporate	Rubiaceae ?				x			
42	trizonocolporate	Rubiaceae ?	*Ixora* ?						x
43	trizonocolporate	Sanzaniaceae ?	*Sanzania* ?						x
44	trizonocolporate	Sapindaceae ?						x	
45	trizonocolporate					x			
46	trizonocolporate							x	
47	trizonocolporate			x	x		x	x	x
48	trizonocolporate				x				
49	trizonocolporate							x	x
50	trizonocolporate								x
51	trizonocolporate							x	
52	trizonocolporate							x	x
53	trizonocolporate								x
54	trizonocolporate					x			
55	trizonocolporate				x				
56	trizonocolporate				x				
57	trizonocolporate			x	x	x	x	x	x
58	trizonocolporate								x
59	trizonocolporate			x		x			
60	trizonocolporate			x	x	x	x		
61	trizonocolporate								x
62	trizonocolporate						x		
63	trizonoporate	Loganiaceae	*Fagraea*				x		
64	trizonoporate	Loganiaceae ?	*Fagraea* ?			x			
65	trizonoporate	Moraceae						x	
66	trizonoporate	Sterculiaceae	*Pterospermum* type ?			x			
67	trizonosyncolporate	Myrthaceae	*Eugenia*					x	
68	tetrazonocolporate	Rutaceae			x		x		
69	tetrazonocolporate	Sapotaceae/Meliaceae					x	x	
70	tetrazonocolporate	Sapotaceae/Meliaceae						x	
71	tetrazonocolporate	Sapotaceae/Meliaceae							x
72	octozonocolporate	Polygalaceae	*Xanthophyllum* type						x
73	polypantoporate	Malvaceae	*Hibiscus* type			x			
74	?-aperturate							x	x

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