

**Chiropterophily and Ornithophily in *Freycinetia*  
(*Pandanaceae*) in Samoa**

By

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**Key Words:** Angiosperms, *Pandanaceae*, *Freycinetia reineckei*; *Pteropus samoensis*, *Aplonis atrifuscus*, *Columba vitiensis castaneiceps*.—Floral ecology, chiropterophily, ornithophily, pollination, dioecism.

**Abstract:** In Samoa, field observations, experiments, and SEM micrographs of hair and feather samples indicate the dioecious liana *Freycinetia reineckei* to be both chiropterophilous and ornithophilous with the principal pollinators being an endemic flying fox, *Pteropus samoensis*, and an endemic starling, *Aplonis atrifuscus*. Nutritional analysis of staminate and pistillate inflorescences indicate qualitative and quantitative differences between the rewards offered by the two sexes. No nectar is presented, the principal pollinator rewards being fleshy bracts and pollen. As a result, staminate and bisexual inflorescences sustain higher levels of pollinator damage, a factor which may tend to maintain dioecism within the population.

It is of some interest that the first reports of chiropterophily concerned megachiropteran visits to flowers. DE LA NUX (as quoted in JAEGER 1954) reported visits of *Pteropus niger* to an "umbelliferous" tree, while MOSELEY (1879) noted flying fox visits to red flowers in Tongatapu. Perhaps the most important account, however, was that of BURCK (1892), who reported flying fox pollination of *Freycinetia* at Buitenzorg. Although BURCK's account was initially accepted (BAILLON 1895, WARBURG 1900, KNUTH & LOEW 1904) it was discredited by both PORSCH (1915, 1923) and CAMMERLOHER (1923, 1928):

"An adaptation to the pollination by bats which has been put forth by BURCK and most recently by KNUTH is not true. The evidence against such an assumption is the odor of a typical ornithophilous display system, which in the nocturnal flight of the bat is invisible. The exact opposite is the case; bats are not the pollinators but the ravagers of

*Freycinetia*." (Translated from PORSCH 1915, pp. 305-306.) In this journal, however, PORSCH conceded that *Freycinetia* inflorescences can be pollinated by bats, but that this is a rare occurrence:

"With the rejection of the hypothesis, that the *Freycinetia* 'flower' is adapted to pollination by bats, I wish of course by no means to somehow deny that bats evidently consume the food bodies with even greater preference occasionally than the pollinators. In fact this is what they frequently do. And if they thereby do not break off the bloom, thus can their activity even cause fruit formation." (Translated from PORSCH 1923, p. 30.)

BURCK's work remained discredited, however, with JAEGER (1954) agreeing with PORSCH that megachiropterans cannot significantly function as pollinators but only as "ravageurs" due to their large size. Since that time, however, megachiropteran pollination has been reported for a variety of plant species (HEIDE 1927, JAEGER 1954, VAN DER PIJL 1956, BAKER & HARRIS 1957, HARRIS & BAKER 1958, BAKER & al.: 1971, START & MARSHALL 1976, GOULD 1978, FAEGRI & VAN DER PIJL 1979) and it seems unreasonable to continue to disregard BURCK's account on such *a priori* grounds.

In 1956 VAN DER PIJL suggested a possible resolution to the controversy: BURCK and PORSCH had in fact studied two different species of *Freycinetia*, one of which was chiropterophilous and the other ornithophilous. PORSCH (1923) and CAMMERLOHER (1923, 1928) studied the red-colored *Freycinetia funicularis*, while BURCK (1892) described the species he studied as having pink bracts. From this VAN DER PIJL (1956) suggested that BURCK had actually studied *Freycinetia insignis*, which VAN DER PIJL believed to be chiropterophilous. It is clear from the 1923 paper of PORSCH, however, that bats were in fact frequent visitors to the *F. funicularis* inflorescences he studied although he discounted their role as pollinators; is it possible that some species of *Freycinetia* can be both ornithophilous and chiropterophilous? *Freycinetia* inflorescences do appear to be attractive to a variety of vertebrates. A careful review of both the botanical and zoological literature reveals that *Freycinetia* inflorescences can be visited by a variety of vertebrates including bats (BURCK 1892, KNUTH & LOEW 1904, VAN DER PIJL 1956, DANIEL 1976), birds (CUNNINGHAM 1842, PERKINS 1902, GUPPY 1906, PORSCH 1915, 1923, CAMMERLOHER 1923, 1928, COX 1983 a), and squirrels (HEIDE 1923), although it appears that the account of DEGENER (1930) of rat visitation was based on conjecture only and not upon observation (DEGENER, pers. comm.).

I here report evidence that the Samoan species *Freycinetia reinecke* (WARBURG ex REINECKE (*Pandanaceae*)) is both ornithophilous and chiropterophilous. This finding is of interest not only because it suggests

that BURCK's account should be regarded more favorably, but also because it contradicts recent suggestions from workers in the neotropics (BAWA 1980, 1982) that vertebrates do not function as pollinators of dioecious plants.

#### Materials and Methods

The pollination ecology of *Freycinetia reineckeii* was studied in 1979, 1980, and 1981 in the Samoan islands (14° South 170° West) of the South Pacific. The principal study site was in the cloud forest of Tapatapao on the island of Upolu, Western Samoa, at an altitude of approximately 600 m. Inflorescences were collected by either climbing the trees upon which the lianas grew or with pruning hooks. Inflorescences were examined for signs of animal visitation such as claw marks on the outer leaves, teeth or beak marks on the fleshy inner bracts, or feces inside the involucre. Two exclusion experiments were performed; in one, six inflorescences were either bagged in coarse wire, double bagged in both mosquito net and coarse wire, or not bagged at all. In the other, access to an inflorescence was completely barred to non-flying vertebrates unless they entered a trap below the inflorescence. Extensive observations of the populations were made with field glasses from blinds. Two live individuals of *Pteropus samoensis* PEALE (*Pteropidae*, *Megachiroptera*), *Pteropus tonganus* QUOY & GAIMARD (*Pteropidae*, *Megachiroptera*), and a single individual of *Aplonis atrifuscus* PEALE (*Sturnidae*) were captured and presented with a variety of food items including staminate and pistillate inflorescences of *Freycinetia reineckeii* and their responses observed and photographed. Also a single individual each of *Pteropus samoensis* and *Aplonis atrifuscus* were shot in free flight. Hair and feather samples, respectively, from the head regions were coated with silver-gold-palladium amalgam and examined for pollen with scanning electron microscopy. The pollen found was compared to reference SEM photographs of *Freycinetia reineckeii* pollen.

A staminate and pistillate inflorescence of the same age were collected at anthesis (Cox 390 & Cox 391, UC) and analyzed chemically after drying. The results were compared to a variety of Samoan fruits known to be eaten by the flying fox *Pteropus samoensis* and the starling *Aplonis atrifuscus*. Sugar concentrations were calculated from dry subsamples by eluting under refrigeration for 24 hours in distilled water, adding PABA (para amino benzoic acid), and quantifying with a spectrophotometer at 470 nm by the method of BAKER (1979). Sugar compositions were determined through paper chromatography of spots of the elutions following BAKER & BAKER (1982). Amino acid concentrations were calculated by staining with ninhydrin and estimating proline concentrations with a spectrophotometer at 440 nm and other amino acid concentrations at 570 nm, in a modification of the technique of YEMM & COCKING (1955). Amino acid compositions were determined by dansylation and conducting two solvent liquid chromatography on Schleicher and Schuell micropolyamide sheets using the method of BAKER & BAKER (1976). Lipid concentrations were calculated by eluting under refrigeration for 5 hours weighed dry subsamples in a 2:1 mixture of chloroform and methanol in vials sealed with teflon tape. Aliquots of the elutions were spotted on small weighed disks of filter paper. After evaporation of the chloroform-methanol, the disks were reweighed and the change in weight corrected by a factor determined from the weight change of control disks spotted with pure chloroform-methanol; a Cahn electro-microbalance was used for these measurements. Concentration of

crude protein was estimated by determining the amount of total nitrogen through a microkjeldahl digestion (JENSEN 1962) of weighed subsamples with the liberated ammonia being determined by Nessler's reagent; the total nitrogen thus calculated was then multiplied by 6.25 to estimate crude protein. Presence of phenols was tested with Folin reagent and Ciocalteu reagent. Presence of cardiac glycosides was tested with the Kedde reaction (KREBS 1969). The presence of detectable heterocyclic nitrogen and the presence of starch was tested with Dragendorff's reagent (KREBS 1969).

Vouchers of all plant materials studied are on deposit at GH and UC. Vouchers of all megachiroptera and chiroptera studied are on deposit at the Museum of Comparative Zoology, Harvard University.

### Results

*Freycinetia reineckeii* inflorescences have a distinctive morphology which is directly related to their pollination ecology. They are produced at the termination of annual axes, with a renewal shoot developing from one bud in the axil of a leaf below the inflorescence; as a result only a single inflorescence per plant is produced in a single year since the axis remains unbranched. The large inflorescence, 50 cm in diameter, is borne in an erect position. The inflorescences of *Freycinetia* are usually a raceme of spikes telescoped by a reduction of internode length into a pseudoumbellate structure forming an involucre, exceptions being the species *F. angustifolia* and *F. jagorii*. Since each of the three or four spikes is subtended by a large fleshy bract (Fig. 1), this shortening of the internodes in the region of the inflorescence effectively clusters the bracts and spikes into a single anthecological unit which superficially resembles a huge flower. The true flowers are extremely tiny and congested on the spikes; the absence of perianth members and this congestion has made delimitation of flowers difficult without the study of early developmental stages (Cox 1981 a), in which perianth primordia and floral bracts are apparent in some species. The staminate spikes are yellow to orange in color, while the pistillate spikes are green. The fleshy orange bracts which terminate the inflorescence do not subtend spikes. Termed "Beköstigungskörper" by BURCK (1892), these together with the staminate spikes and the large fleshy bracts subtending the spikes serve as the major pollinator attractants. Nectar is not produced in any known species of *Freycinetia*.

In Samoa, claw marks were frequently seen on the leaves below the inflorescences, as were also teeth marks in the fleshy bracts. Staminate inflorescences suffered a particularly high rate of damage, with staminate spikes being eaten at a much higher rate than pistillate spikes (Cox 1982). Feces were also found inside the involucres. In the exclusion experiment in which access to a *F. reineckeii* inflorescence was denied to

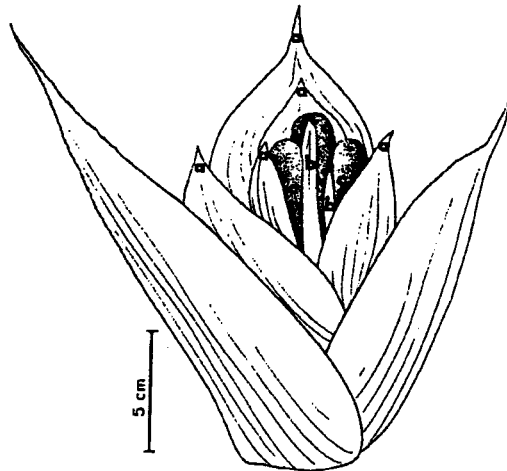


Fig. 1. A pistillate *Freycinetia reineckeii* inflorescence. *a* outer bracts; *b* inner bracts, food bodies, or Beköstigungskörper; *c* spikes

Table 1. Inflorescence destruction of *Freycinetia reineckeii* in exclusion experiment

| Replication | Treatment |                       |  |
|-------------|-----------|-----------------------|--|
|             | Unbagged  | Bagged in coarse wire | Double bagged in both mosquito net and coarse wire |
| 1           | 100%      | 0%                    | 0%   |
| 2           | 90%       | 5%                    | 0%   |

terrestrial visitors, the inflorescence was visited by an animal which ate the fleshy bracts but did not spring the trap, indicating the visitor to be a flying vertebrate. The bagged inflorescences exhibited no or little destruction, but the unbagged inflorescences exhibited severe destruction of the bracts indicating the causal agents to be vertebrates rather than insects small enough to fit through the coarse wire mesh bags (Table 2). Local informants indicated flying foxes to be the major pollinator of *F. reineckeii* and that Samoan starling (*fuia*) also visited the inflorescences. However, during an eight week period of nightly

Table 2. Comparative nutritional analysis of *Freycinetia reineckeii* with Samoan weight. ND = not detected; T = traces; \* = mean

| Sample                        | sugar<br>% | amino<br>acids<br>% | N<br>%         | crude<br>protein<br>% | lipid<br>% |
|-------------------------------|------------|---------------------|----------------|-----------------------|------------|
| <i>Freycinetia reineckeii</i> |            |                     |                |                       |            |
| ♀ spikes                      | 0.195      | 0.414               | 0.339          | 2.119                 | 8.0        |
| ♂ spikes                      | 0.404      | 0.648               | 4.135          | 25.844                | 23.8       |
| ♀ bracts                      | 0.229      | 0.104               | 0.207          | 1.294                 | 8.25*      |
| ♂ bracts                      | 1.349      | 0.096               | 0.180          | 1.125                 | 7.14       |
| mature fruit (Cox 352)        | 1.378      | 0.400               | — <sup>b</sup> | —                     | —          |
| <i>Dysoxylum samoense</i>     |            |                     |                |                       |            |
| fruit (Cox 343)               | 0.080      | 0.720               | —              | —                     | —          |
| <i>Cupaniopsis samoense</i>   |            |                     |                |                       |            |
| fruit (Cox 261)               | 2.948      | 0.360               | —              | —                     | —          |
| seed (Cox 261)                | 0.113      | 3.730               | —              | —                     | —          |
| <i>Ficus graeffii</i>         |            |                     |                |                       |            |
| fruit (Cox 258)               | 0.479      | 0.73                | —              | —                     | —          |
| <i>Collospermum samoense</i>  |            |                     |                |                       |            |
| fruit (Cox 264)               | 0.161      | 0.08                | —              | —                     | —          |

observation of the *F. reineckeii* population at Tapatapaō, no nocturnal visitors were observed, although one evening at 1845 an individual of *Pteropus samoensis* was seen in the population. The flying fox *Pteropus tonganus*, which is almost strictly nocturnal in its habits (Cox 1983 b), thus appeared to not be a significant pollinator of *F. reineckeii* at Tapatapaō. This conclusion is supported by the results of the feeding trials with captive individuals of *Pteropus tonganus*: although they accepted a variety of native and cultivated fruits, they would not eat *F. reineckeii* inflorescences. Their apparent aversion to *F. reineckeii* inflorescences may be a consequence of their foraging ecology; *P. tonganus* forages in villages (on *Ceiba pentandra* and *Syzygium jambos* flowers) and in disturbed, secondary forests but rarely penetrates primary forests to which *F. reineckeii* is confined (Cox 1983 b).

Further consultation with Samoan informants confirmed the existence of two ecologically distinct species of *Pteropus* in Samoa: *Pe'a fai taulaga pe'a* (*Pteropus tonganus*) and *pe'a vao*, the diurnal flying fox *Pteropus samoensis*. The informants indicated *P. samoensis* to be the primary pollinator of *F. reineckeii*. Subsequent daytime observations confirmed the veracity of this report. At 1330 on 31 March 1979 I

fruits eaten by *Pteropus samoensis*; concentrations given in percentage of six samples. S.D.: 4.24; b = not studied

| Sugar proportions |     |     |     |     | Amino acid composition |           |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |   |
|-------------------|-----|-----|-----|-----|------------------------|-----------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|
| SUC               | GLU | FRU | MAL | MEL | SUC                    | GLU + FRU | Ala | Arg | Asp | Asn | Cys | Glu | Gly | His | Ile | Leu | Lys | Met | Phe | Pro | Ser | Thr | Tyr | Val |   |
| .24               | .24 | .41 | .11 | ND  | .369                   |           | +   | +   |     |     | +   | +   | ?   | +   | +   |     |     |     | +   | +   | +   |     |     |     | + |
| ND                | .30 | .55 | .15 | ND  | low                    |           | +   | +   | +   | ?   | +   | +   | +   | ?   | +   | +   | +   | T   | +   | +   | +   | +   | +   | +   | + |
| ND                | .52 | .34 | .14 | ND  | low                    |           | +   |     |     |     |     | +   | +   | +   | +   | +   | +   | +   | +   | +   | ?   |     |     |     | + |
| .11               | .29 | .53 | .07 | ND  | .126                   |           | +   |     |     |     | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |     |     |     |     | + |
| .20               | .59 | .21 | ND  | ND  | .251                   |           | +   | +   | ?   |     | +   | +   | +   | +   | +   | +   |     |     | +   | +   | +   | +   | +   | +   | + |
| .15               | .34 | .49 | .01 | ND  | .182                   |           | +   |     |     |     | +   |     |     |     | ?   | ?   | +   |     | ?   | +   |     |     |     |     |   |
| —                 | —   | —   | —   | —   | —                      |           | +   |     |     |     |     | +   |     |     | +   |     |     |     | +   |     |     |     |     |     |   |
| —                 | —   | —   | —   | —   | —                      |           | +   | ?   |     | ?   |     |     |     |     | +   |     |     |     | +   |     |     |     |     |     |   |
| .20               | .44 | .36 | ND  | ND  | .252                   |           | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | —   | — |
| ND                | T   | ND  | ND  | ND  | —                      |           | ++  |     |     |     | +   | +   | +   | +   | +   | +   |     |     | +   | +   |     |     | ?   | ++  |   |

witnessed visitation to an *F. reineckeii* inflorescence by *P. samoensis*. *P. samoensis* is an extremely large flying fox with wing spans frequently exceeding 1.7 m (PEALE 1848). It is unusual in its behavior in that it is almost strictly diurnal (PEALE 1848, NICOLL 1909), territorial, and confined to undisturbed primary forests although it can often be seen in the afternoon soaring above the forest canopy (COX 1983 b). The hypothesis that *P. samoensis* functions as a pollinator of *F. reineckeii* was supported by the results of feeding experiments with captive *P. samoensis* individuals. Presented with a variety of cultivated and native fruits and *F. reineckeii* inflorescences, both individuals were found to respond almost immediately to the *F. reineckeii* inflorescences but reject the cultivated fruits offered to them. In eating the *F. reineckeii* inflorescences, the bats would consume first the outer fleshy bracts and inner "Beköstigungskörper", in the process placing their heads between the spikes and getting large quantities of the sticky yellow pollen on their head if the inflorescence was staminate. In pistillate inflorescences, the pollen load would be transferred to the sessile stigmata of the spikes in the same manner, since the position of the outer bracts and the inner *Beköstigungskörper* forces the head of the animal feeding on them to

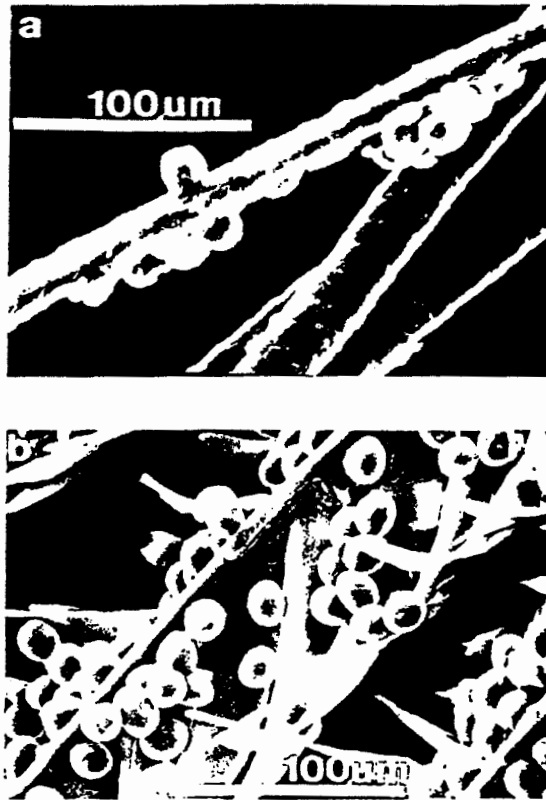


Fig. 2. Scanning electron micrographs of *Freycinetia reinckei* pollen on hair and feather samples of native pollinators shot in free flight. a *Pteropus samoensis* facial hair. b *Aplonis atrifusca* head feather

come in contact with the outer and inner surfaces of the spikes, respectively. If the inflorescence was staminate or bisexual (Cox 1981) the bats would also eat the pollen-bearing spikes, biting them off at the base and licking the pollen. They would not, however, eat pistillate spikes. While eating staminate spikes their heads would become visibly discolored from the yellow, waxy pollen.

At the initiation of the 1981 field session in Samoa it was found that the *P. samoensis* population at Tapatapaō had suffered a significant decline due to indiscriminate logging of the forest for swidden agriculture and poaching of flying foxes by local residents (flying fox

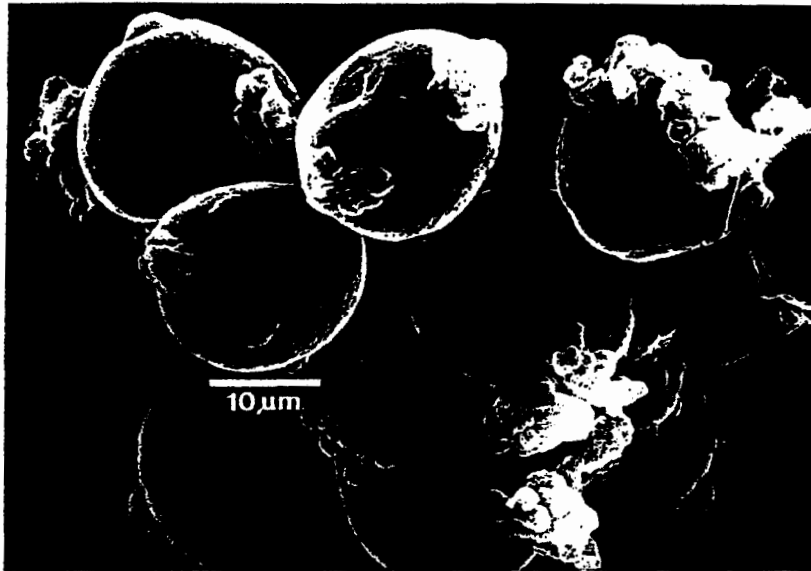


Fig. 3. Scanning electron micrograph of *Freycinetia reineckei* pollen. Note waxy granules adhering to pollen surfaces

meat is considered a great delicacy in Samoa). Observations were therefore directed towards the small pockets of remaining forest. During five weeks of field studies, 19 visits of the Samoan starling *Aplonis atrifusca* to *F. reineckei* inflorescences were recorded and one visit of the fiani fruit pigeon *Columba vitiensis castaneiceps* PEALE. The mean *A. atrifusca* visit had a duration of 5 min 12 sec ( $n = 15$ , s.d. = 4 min 54 sec) with the peak period of visitation between 1300 and 1500. The birds foraged on the inflorescences in a manner quite similar to the way flying foxes foraged. Both birds and bats would fly in to the tree near the top and descend to the erect *Freycinetia* inflorescences by hopping from branch to branch (birds) or climbing down the tree using the curved nail of the first digit (thumb) of each hand to grasp the bole of the tree and various lianas on it (flying foxes). Both would then position themselves within or directly beneath the erect inflorescence and eat the bracts. While feeding, their heads would become discolored with pollen. Position of the pollen load on the head of *A. atrifusca* was similar to the position of the pollen load on *P. samoensis*. A captive individual of *A. atrifusca* was found to consume any *F. reineckei* inflorescence placed in its cage.

Feather and hair samples obtained from the heads of *Pteropus samoensis* and *Aplonis atrifuscus* shot in free flight revealed through SEM study dense pollen loads of *F. reineckeii* pollen, which was the only pollen type found on them (Fig. 2). The pollen was identified by comparison with a reference SEM photograph of *F. reineckeii* pollen (Fig. 3). The SEM study revealed *F. reineckeii* pollen to be small, about 18  $\mu\text{m}$  in diameter, but to be covered with a waxy substance which serves to adhere the pollen to flying fox facial hair and starling head feathers.

Analysis of sugar concentrations in *F. reineckeii* bracts revealed a significant sexual dimorphism: staminate bracts have almost six times the sugar concentration per unit dry weight of pistillate bracts (Table 2). This dimorphism may contribute to the higher rate of destruction of staminate bracts in controlled field experiments (Cox 1982). A sexual difference in pollinator rewards is also found in the spikes: staminate spikes have double the sugar concentration of pistillate spikes. These concentrations of sugars are well within the observed range of sugar concentrations found in native fruits commonly eaten by *Pteropus samoensis* and *Aplonis atrifuscus* and it seems reasonable to assume that *Freycinetia* bracts are perceived by these animals as a fruit. Analysis of sugar compositions reveal the inflorescences to be hexose rich (Table 2), as are most nectars of plants pollinated by bats and passerine birds (BAKER & BAKER 1982), and, incidentally, as are also most bat and bird dispersed fruits (I. BAKER, pers. comm.). The amino acid concentrations of *F. reineckeii* inflorescences also fall into the observed range for indigenous fruits (Table 2), with staminate spikes having the highest concentrations. Staminate bracts have a total of 8 different amino acids detected, pistillate bracts have 8, pistillate spikes have 10, and staminate spikes have 18 as compared to an average of 6.2 amino acids for the Samoan fruits surveyed. Clearly the inflorescences of *F. reineckeii* offer visitors a more diverse assortment of amino acids than those found in the fruits surveyed.

Sexual dimorphisms were also found in *F. reineckeii* inflorescences in the concentrations of lipids, nitrogen, and crude protein. Staminate and pistillate bracts were found to be roughly equivalent, but staminate spikes were found to have almost 26% of their dry weight in crude protein, and 24% of their dry weight composed of lipids (Table 2), an increase by a factor of 13 and 4, respectively, over the levels found in pistillate spikes. The high lipid content of staminate spikes may be due to the waxy matrix in which the pollen grains are imbedded (Fig. 3) which appears to serve the dual purpose of providing a high-quality pollinator reward and adhering the pollen to the pollinator. The superior reward offered by staminate spikes is undoubtedly a cause of their attractiveness to pollinators as observed in controlled field trials (Cox

1982). Although the *Pandanaceae* have long been believed to be dioecious, true bisexual spikes have recently been discovered (COX 1981 b). Since bisexual spikes also produce the pollen-wax matrix and are also eaten by the pollinators, they have a lowered fitness contribution since their investment in gynoecial structures is forfeited. Since pistillate spikes are not eaten and transmit their genes via ovules, and staminate spikes transmit their genes via pollen on the pollinator's face, even though they are eaten, bisexual inflorescences are at a reproductive disadvantage. Thus vertebrate pollination may act as a mechanism that maintains dioecism (COX 1982) in *Freycinetia* populations.

All samples of inflorescences and fruits possessed phenols, but cardiac glycosides, heterocyclic nitrogen, and starch could not be detected in *F. reineckeii* inflorescences; the fruits were not tested for these compounds.

#### Discussion

*Freycinetia* is one of a few plant taxa that offer only solid rewards to vertebrate pollinators and do not produce nectar, the principal rewards being the fleshy bracts and the waxy pollen matrix from staminate spikes. Other taxa which present only solid rewards to pollinators include species of *Osmoxylon* in Malaysia, where pigeons feed on sterile flowers resembling fruits (BECCARI 1878), *Eugenia cauliflora*, where bats eat the fleshy petals (although VAN DER PIJL [1956] questions the nectarless condition of the flowers), *Calceolaria uniflora*, where birds are attracted to appendages on the corolla lip (VOGEL 1974) and nectarless flowers of *Madhuca (longifolia?)* which FAEGRI & VAN DER PIJL (1979) regard as being attractive to bats. The striking similarity in nutritional content of *Freycinetia reineckeii* bracts with both *F. reineckeii* fruits and other Samoan fruits lends credence to speculations that ornithophily and chiropterophily originally evolved from frugivory by birds and bats respectively. If this is true, however, the paucity of taxa that offer only solid rewards remains a mystery, although certainly the intermediate evolutionary step of offering both solid rewards and nectar is well represented in flowering plant taxa. For example, in *Acca*, both petals and nectar are consumed by birds (KNUTH & LOEW 1904), in *Ceiba acuminata*, bats feed on both pollen and nectar (BAKER & al. 1971) and in *Protea humiflora*, rodents feed on nectar, and possibly bracts as well (ROURKE & WIENS 1977).

The evidence gathered during this study does, however, support the hypothesis that *Freycinetia reineckeii* is both ornithophilous and chiropterophilous, being principally visited by large birds of the

*Sturnidae* and large flying foxes of the *Pteropidae*. The lack of plant-pollinator coevolution is most striking though, particularly since plant-pollinator relationships are so frequently interpreted as being *de post facto* evidences of coevolution. Although clearly the inflorescence of *F. reineckeii* is well-adapted for visitation by vertebrates, I can detect no specific adaptation to the plant by the vertebrate pollinators, who opportunistically feed on *F. reineckeii* inflorescences during the flowering season (March through May), but feed on a variety of other fruits and possibly flowers during the rest of the year. Opportunistic pollination does not appear to be maladaptive for *Freycinetia* and may in fact represent a distinct advantage in the ability to colonize new islands where any particular component of the vertebrate fauna may be absent. It has, for example, allowed the Hawaiian *Freycinetia arborea* to survive an extinction of the native birds that once pollinated it; *F. arborea* is now pollinated primarily by the introduced Japanese white-eye, *Zosterops japonica* (COX 1983 a). For a genus ranging from Sri Lanka to Tahiti and from Vietnam to New Zealand the advantages in such an opportunistic pollination system are apparent.

Ornithophily and chiropterophily in *Freycinetia* are of interest since recent workers in the neotropics (BAWA 1980) have suggested that vertebrates do not pollinate dioecious plants. It appears that most of the 185 species of *Freycinetia* of the paleotropics are pollinated by vertebrates, and there is strong circumstantial evidence (DANIEL 1976) that species of the dioecious epiphyte genus *Collospermum* are pollinated by vertebrates as well. Generalizations based on studies from the neotropics may have to be altered as more information on dystropic pollination systems from the paleotropics becomes available, particularly systems involving large megachiropterans or passerine birds. Dystropic pollination systems are unlikely to be coevolved, and indeed the attractiveness of *Freycinetia* inflorescences to a variety of vertebrates is a strong indication of an opportunistic rather than a coevolutionary pollination system. For example, I have found the Hawaiian *Freycinetia arborea* GAUDICHAUD to be visited by organisms ranging in size from the small white-eye *Zosterops japonica* which is about 11 cm long, to the large Hawaiian crow, *Corvus tropicus*, which exceeds 51 cm in length (COX 1983 a). This openness of the inflorescence and its availability to a variety of vertebrate pollinators was missed by PORSCH (1923) in his attack on BURCK (1892) in this journal sixty years ago. PORSCH was correct in diagnosing ornithophily in *Freycinetia* but was wrong in discrediting BURCK's account of chiropterophily. The occurrence of both bird and bat pollination in *Freycinetia reineckeii* suggests that both BURCK and PORSCH were right, and that BURCK's contribution and his achievement in being the first botanist to report

chiropterophily in plants should receive, as suggested by VAN DER PIJL (1956), acknowledgement by the scientific community.

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