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Ecological and Phytochemical Diversity of Arillate Seeds in Aglaia (Meliaceae): A Study of Vertebrate Dispersal in Tropical Trees

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ECOLOGICAL AND PHYTOCHEMICAL DIVERSITY OF ARILLATE SEEDS IN *AGLAIA* (MELIACEAE): A STUDY OF VERTEBRATE DISPERSAL IN TROPICAL TREES

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The dispersal of ten species of equatorial rainforest tree, belonging to the genus *Aglaia*, was studied in Malaysia and Indonesia. In three of these (*Aglaia* species 2, *A. oligocarpa* and *A. teysmanniana*) the fruits are dehiscent capsules and the red-skinned arillate seeds are dispersed by birds. Nine species of bird, belonging to six families (Bucerotidae, Capitonidae, Corvidae, Eurylaimidae, Pycnonotidae and Sturnidae), were observed to swallow the seeds. The fruits of the remaining species are indehiscent and the seeds have a white, yellow or translucent aril. The seeds of five species (*A. elliptica*, *A. odoratissima*, *A. speciosa*, *A. korthalsii* and *A. ganggo*) are dispersed by primates (including *Pongo pygmaeus*, *Hylobates lar*, *Presbytis melalophus* and *Macaca fasicularis*) and one species (*A.* aff. *elaeagnoidea*) by a civet (*Paradoxurus hermaphroditus*). Several species of squirrel feed on the seeds, but are thought not to be important dispersers. Published accounts suggest that pigeons (Columbidae) in West Malesia, and birds of paradise (Paradisaeidae) and cassowaries (Casuariidae) in Australasia, are also dispersal agents.

The arils of six of these *Aglaia* species and four species belonging to other genera (*Tabernaemontana macrocarpa*, *Zingiber* sp., *Lansium domesticum* and *Durio zibethinus*) were analysed for lipids, carbohydrates and amino acids. A high lipid content (27–60% dry mass) was found in arils of the bird-dispersed *Aglaia* seeds; those of primate-dispersed species were lower in lipids and higher in free carbohydrates (reducing sugars and sucrose).

1. Introduction

Aglaia, with more than one hundred species, is the largest genus in the pantropical mahogany family. The family has been the subject of monographic study since 1960; existing publications deal with the morphology and taxonomy (see, for example, White & Styles 1963; Pennington & Styles 1975; Mabberley 1979; Pennington 1981) and with chromosome cytology (see, for example, Styles & Vosa 1971). From the beginning, however, it 'was intended, so far as possible, to study in the field the functional significance of the floral and fruit characters used in the classification' (White, in Pennington & Styles 1975, p. 422). *Aglaia* is the first genus in the family to be the subject of a study of this kind.

The genus *Aglaia* is confined to the eastern tropics and extends from India to Samoa and from China southwards to Queensland. The present paper combines observations by C.M.P. of dispersal in the genus *Aglaia* with phytochemical analyses, by M.J.K., of arils of six species of *Aglaia* and those of four other Sumatran plants for comparison. The field work was carried out during four visits to Peninsular Malaysia and one to Sumatra (Indonesia), a total of two years in the field. It forms part of a wider study of taxonomy and reproductive biology in the genus, which includes consideration of the diversity of size and architecture of the trees belonging to different species, their pollination, seed dispersal, phenology, seedling recruitment and survival (Pannell 1980). Accounts of those species that occur in Peninsular Malaysia have been written (Pannell 1980, 1987) and a taxonomic monograph of the genus was begun in 1981.

Most species of *Aglaia* are small or medium-sized trees of lowland and hill tropical rainforest up to about 1800 m above sea level. They are rarely an important constituent of the canopy in tall forests; several species are shade-tolerant. The present study is confined to rainforest species. In the Malay Peninsula, Sumatra and Borneo, up to twelve species of *Aglaia* may occur together in a single forest site. At least 45 species are recorded from Peninsular Malaysia, but few of these are endemic.

All known species of *Aglaia* are dioecious. The inflorescence is usually borne in the axil of a leaf, but a few species are ramiflorous. The fruits are spherical or ovoid in shape; in some species, they are dehiscent, and in others indehiscent. Each of the one to four locules in the fruit contains either a single seed or none at all. In most species of *Aglaia*, the seed is completely surrounded by a fleshy layer. This layer is derived from the seed, but the exact ontogeny is not known for any species of *Aglaia*. In the absence of developmental studies, the narrow morphological definition of the aril as a free funincular growth seems inappropriate and, for this reason, 'aril' is used here in a general sense for all species. A similarly wide use of the term for all fleshy seed coats was adopted by Corner in his earlier works (for example, 1954) and more recently by White in Pennington & Styles (1975); the morphological case for doing this is presented by Kapil *et al.* (1980).

2. Methods

(*a*) *Forest sites and species studied*

Field work was carried out in primary lowland rainforest at elevations below 500 m. The study began with one year (1978) spent in Peninsular Malaysia, where several different forest sites were visited before the main study area at Kuala Lompat (3° 40′ N, 102° 20′ E) in Krau Game Reserve, Pahang, was selected. This site is part of a large tract of forest at the foot of the mountain Gunong Benom. Five species of primate are resident in the forest near Kuala Lompat and at least twelve species of *Aglaia* occur there, half of which are common. There is a system of trails; these make movement and observation relatively easy. Some observations were made in Pasoh Forest Reserve (2° 58′ N, 102° 17′ E), Negri Sembilan, but primate sightings were fewer, and *Aglaia* trees more sparsely scattered, than at Kuala Lompat. Further visits to Kuala Lompat and Pasoh were made in August and September 1979 and July–September 1981 and to Kuala Lompat in November 1983. During six months spent in Sumatra (May–October 1983), Ketambe (3° 40′ N, 97° 40′ E), in Gunong Leuser National Park, was visited at a time when two species, *Aglaia korthalsii* and *A. speciosa*, were coming to the end of their fruiting seasons. This is the site of Rijksen's study (1978) of the ecology of *Pongo pygmaeus abelii*, the orang utan. Fruiting trees of *Aglaia* species 2, *A. elliptica* and *A. odoratissima* were studied in 1978, of *A. elliptica*, *A. odoratissima* and *A. teysmanniana* in 1979, and of *A. elliptica*, *A. teysmanniana* and *A. oligocarpa* in 1981. For part of the time in 1981, T. J. Stowe (address: R.S.P.B., Sandy, Bedfordshire SG19 2DL, U.K.) assisted with observations of *A. teysmanniana* and *A. oligocarpa* and the identification of birds visiting them.

Kuala Lompat has been the site of a number of studies of primate behaviour and feeding habits (see Chivers 1980*a*). In most cases, no collections of food plants have been preserved, but it has been possible to make use of some of the records of primate food plants by translation of the vernacular names provided by Kalang bin Tot, who has been employed as a local assistant to nearly all the scientists who have worked in the area. Some of his names are specific to individual species of *Aglaia*, but many refer to several species of tree which belong to different genera and even different families. The primates at Kuala Lompat are difficult to observe without long periods of habituation of individual groups. Far more information on seed dispersal would be available if more specimens of food trees had been collected and preserved by the primatologists who made detailed observations on the behaviour of these primates. Kalang's knowledge of the primates meant that he was able to provide reliable information on dispersal of some of the species of *Aglaia* which did not bear fruits during the study period or for which observations on fruiting trees failed to produce results.

The work of Rijksen (1978) on the ecology of *Pongo pygmaeus* is supported by herbarium collections of all food trees. His collections are deposited in the Rijksherbarium, Leiden, the Netherlands, where they are available for study by botanists. By examining Rijksen's collections and visiting his study area, it was possible to incorporate his observations of *P. pygmaeus* and *Aglaia* into the present account.

(*b*) *Field observations and collecting methods*

Whenever trees of *Aglaia* were found with ripe fruits they were watched daily, from first light, for animals taking the seeds. Special attention was paid to the way in which the visiting animals handled the seeds, particularly whether they damaged the embryo and whether they carried seeds away from the tree or dropped them beneath it. Appendix 1 gives methods of collecting botanical specimens for identification, retention as permanent reference collections and phytochemical analysis.

Some of the flowering and fruiting times given were recorded by C. M. P. and the rest by Kalang bin Tot (personal communication).

(*c*) *Phytochemical analyses*

The arils of bird- or primate-dispersed species of *Aglaia* were analysed for protein, amino acids, lipid, fatty acids and carbohydrate. Appendix 2 gives details of the methods of analysis used, because these are likely to have affected the results obtained and the interpretation of some published analyses is made difficult for lack of this kind of information.

(*d*) *Nomenclature*

For most species from the Malay Peninsula, the nomenclature of birds follows Medway & Wells (1976), of mammals, Medway (1983) and of *Aglaia*, Pannell (1987). Other names are taken from the works cited. With the exception of the birds, the same sources provided the figures from which the sizes (average lengths) of the vertebrates observed were estimated. Bird sizes (lengths) were taken from King *et al.* (1975).

Appendix 3 lists all the plants referred to in the text, with the authorities and, wherever possible, citation of herbarium specimens. Appendix 4 lists vertebrate names with authorities and the family to which they belong.

3. Results

(*a*) *Field observations*

The fruit and seed characters of and vertebrate visitors to ten species of *Aglaia* are described below and summarized in tables 1–3.

(i) *Species dispersed principally by birds*

Table 2 gives a summary of animal visitors to trees of these species and their feeding behaviour. Notes on the periods of observation, fruit and seed structure and other remarks follow.

(1) *Aglaia* species 2

One tree of *Aglaia* species 2 in the Pasoh Forest Reserve bore a large crop of fruits in April 1978. This species forms a canopy tree about 35 m high with large fruits, up to 10 cm diameter.

TABLE 1. FRUIT AND SEED CHARACTERS OF TEN SPECIES OF *AGLAIA*, WITH THEIR AGENTS OF DISPERSAL

	Aglaia species 2	*A. oligocarpa*	*A. teysmanniana*	*A. elliptica*	*A. korthalsii*	*A. speciosa*	*A. odoratissima*	*A. ganggo*	*A. rufibarbis*	*Ag.* aff. *elaeagnoidea*
number of seeds in fully developed fruits	3	3 (4)	3	2	2	1 (2)	1 (2)	(1) 2 (3)	1	1 (2)
seed arillate	+	+	+	+	+	+	+	+	—	+
fruit dehiscent	+	+	+	—	—	—	—	—	—	—
arils red, high in lipid, not adhering to testa	+	+	+	—	—	—	—	—	—	—
outer pericarp brick red	+	—	—	—	—	—	—	—	—	—
outer pericarp pink	—	+	+	—	—	—	—	—	—	—
seeds dispersed by birds	+	+	+	—	—	—	—	—	—	—
fruit indehiscent	—	—	—	+	+	+	+	?	+	?
aril gelatinous, sweet, adhering to testa	—	—	—	+	+	+	+	?	—	?
outer pericarp orange	—	—	—	+	+	+	+	?	—	?
outer pericarp brown	—	—	—	—	—	—	—	—	+	—
seeds dispersed by primates	—	—	—	+	+	+	+	+	?	—
seeds dispersed by civets	—	—	—	—	—	—	—	—	—	+
seeds and/or arils eaten by squirrels	+	+	+	+	?	?	+	?	+	?

TABLE 2. FIELD OBSERVATIONS OF ANIMALS VISITING FRUITING *AGLAIA* TREES BELONGING TO SPECIES DISPERSED PRINCIPALLY BY BIRDS

plant	animal	approx. length/cm	no. of visitors	feeding without damage to mature seed	comments
Aglaia sp. 2	*Anthracoceros malayanus*	76	1–2, frequently	occasionally removed arillate seeds from dehisced fruits	did not attempt to break into unripe fruits
	Treron olax or *capellei*	20/35	1 bird seen once	took no seeds	chased away by *Callosciurus prevostii*
	Callosciurus prevostii	body 25 tail 23	1–2, frequently	removed seeds from dehisced fruits, remained in *Aglaia* tree or moved to adjacent tree. Ate the aril and dropped rest of seed unharmed	sometimes destroyed a seed by eating a large part of the embryo
	Callosciurus notatus	body 20 tail 18	—	—	more active than *Calliosciurus prevostii*. Took young fruits, gnawed the pericarp, sometimes removed a seed, sometimes dropped fruit with seeds intact. Gnawed at attached fruits by hanging upside down from the branches
	Ratufa affinis	body 33 tail 40	—	—	characteristically looped itself over a branch, held a young fruit with its fore-feet and gnawed at the pericarp. Sometimes moved to another tree carrying the fruit
Aglaia oligocarpa and *Aglaia teysmanniana*	*Anthracoceros malayanus*	76	occasional visits by individual birds	apparently took dehisced fruits and swallowed them whole	only seen visiting *A. oligocarpa* trees
	Megalaima mystacophanus	23	at least one individual on most days of observation	removed arillate seeds from dehisced fruits and swallowed them. If it broke off the entire fruit, the bird carried this to another branch and attempted to extract the arillate seeds	only seen visiting *A. oligocarpa* trees
	Calorhamphus fuliginosus	18	1–7 birds, daily	ingested arillate seeds	chased bulbuls out of the trees and showed signs of aggression towards a larger bird, *Gracula religiosa*
	Eurylaimus ochromalus	16	occasional visits by individuals or small groups	removed arillate seeds from the dehisced fruits in flight. If an entire fruit became detached, the bird landed on a branch, removed the seeds and swallowed them	only seen visiting *A. oligocarpa* trees chased bulbuls out of the trees

Aglaia oligocarpa and *Aglaia teysmanniana*	*Calyptomena viridis*	19	frequent visitor, daily	ingested more seeds and arils than the last three species and rarely dropped a fruit once it had removed one from a branch	dislodged large numbers of fruits when moving in the *A. oligocarpa* trees
	Pycnonotus zeylanicus	29			all three species visited the *A. oligocarpa* trees, but none was seen taking seeds. The first two are forest dwellers and the third is a bird of cultivated land, scrub and forest edge
	P. melanoleucos	18			
	P. finlaysonii	19			
	Pycnonotus brunneus	19	the most frequent visitors and often accompanied by young birds	both species were seen feeding on seeds in these trees, but it was often not possible to distinguish between them. The adults took arillate seeds from dehisced fruits and either swallowed them or fed them to the young. On one occasion an adult was seen leaving the tree with a seed in its bill	movement of birds to and from adjacent trees of other species was frequent
	P. erythropthalmus	18			
	Criniger bres	22	occasional visitor	took and swallowed arillate seeds from dehisced fruits	only seen visiting *A. oligocarpa* trees
	Aegithina viridissima	14		—	both species visited only the *A. oligocarpa* trees and were not seen ingesting the seeds
	Dicaeum chrysorrheum	10			
	Gracula religiosa		1–2 birds, daily	took fruits and swallowed them whole or occasionally, took arillate seeds from dehisced fruits	frequently dislodged fruits while moving in *A. oligocarpa* trees. Showed signs of aggression towards *Calorhamphus fuliginosus*; was observed regurgitating seeds without the aril (and possibly pieces of pericarp) from a perch near the top of a tree 25 m high, 150 m from one of the *A. oligocarpa* trees and 25 m from the *A. teysmanniana* tree
	Platysmurus leucopterus	40	1–2 birds, occasionally	took whole dehisced fruits, moved to a larger branch, transferred the fruit from its bill to a position between the branch and one foot and removed two or three arillate seeds from the fruit. These birds ingested large numbers of seeds in this way	only seen visiting *A. oligocarpa* trees

Table 2 (*cont.*)

plant	animal	approx. length/cm	no. of visitors	feeding without damage to mature seed	comments
Aglaia oligocarpa and *Aglaia teysmanniana*	*Phaenicophaeus chlorophaeus*	33, 19	including tail	—	an insectivorous species (Fogden 1972), only seen visiting one of the *A. oligocarpa* trees, and not observed feeding. It was chased out of the tree by *Callosciurus notatus*
	Ratufa bicolor	body 35 tail 44	occasional visitor	looped itself over a branch when feeding (cf. *R. affinis* in *Aglaia* species 2) and sometimes reached fruits by hanging from a branch by its hind legs. It removed one of the seeds from dehisced fruits, dropped the the rest of the fruit, removed and ingested the aril and discarded the seed without damaging the embryo	only seen visiting one of the *A. oligocarpa* trees
	Callosciurus prevostii	body 25 tail 23	occasional visitor	took dehisced fruits, removed one of the seeds and ate only the aril	only seen visiting one of the *A. oligocarpa* trees
	Callosciurus notatus	body 20 tail 18	1–2 daily	searched for ripe fruits with darting movements up and down the branches. On finding a ripe fruit it removed one of the seeds, dropped the rest and held the seed between its front feet to strip off and ingest the aril, discarding the cleaned seed. This was done either while sitting on a branch or hanging by the hind legs from a branch or the trunk of the tree	
	Tupaia glis	body 17 tail 16	occasional visitor		only seen visiting *A. teysmanniana* tree. Ate all or part of the seed, thereby destroying the embryo

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TABLE 3. VERTEBRATE VISITORS TO FRUITING TREES OF TEN SPECIES OF *AGLAIA*

(Abbreviations: v, visited a tree with ripe fruits; i, ingested seeds, with arils intact; a, removed and ingested aril only; d, ate all or part of seed and usually thereby destroyed the embryo; c, carried seeds away with arils intact. Parentheses indicate published or unpublished reports from observers other than C. M. P.)

	Aglaia sp. 2	*A. olig-ocarpa*	*A. teys-manniana*	*A. ell-iptica*	*A. kor-thalsii*	*A. spec-iosa*	*A. odor-atissima*	*A. ganggo*	*A. ruf-ibarbis*	*A.* aff. *elaeag-noidea*
Birds										
Anthracoceros malayanus	vc	vi	—	—	—	—	—	—	—	—
Aegithina viridissima	—	v	—	—	—	—	—	—	—	—
Calorhamphus fuliginosus	—	vi	vi	—	—	—	—	—	—	—
Megalaima mystacophanus	—	vi	—	—	—	—	—	—	—	—
Treron capellei/olax	v	—	—	—	—	—	—	—	—	—
Platysmurus leucopterus	—	vi	—	—	—	—	—	—	—	—
Phaenicophaeus chlorophaeus	—	v	—	—	—	—	—	—	—	—
Dicaeum chrysorrheum	—	v	—	—	—	—	—	—	—	—
Eurylaimus ochromalus	—	vi	—	—	—	—	—	—	—	—
Calyptomena viridis	—	vi	vi	—	—	—	—	—	—	—
Criniger bres	—	v	—	—	—	—	—	—	—	
Pycnonotus brunneus	—	vi	vi	—	—	—	—	—	—	—
P. erythrophthalmus	—	vi	vi	—	—	—	—	—	—	—
P. finlaysoni	—	v	—	—	—	—	—	—	—	—
P. melanoleucos	—	v	—	—	—	—	—	—	—	—
P. simplex	—	v	—	—	—	—	—	—	—	—
P. zeylanicus	—	v	—	—	—	—	—	—	—	—
Gracula religiosa	—	vi	vi	—	—	—	—	—	—	—
Primates										
Macaca fasicularis	—	—	—	—	—	(vi)	(vi)	(va)	(vd)	—
Presbytis melalophus	—	—	—	vi	—	(vi)	(vi)	(va)	—	—
Hylobates lar	—	—	—	—	va	—	—	(vi)	—	—
H. syndactylus	—	—	—	—	—	—	—	(va)	—	—
Pongo pygmaeus	—	—	—	—	(vi)	(vi)	—	—	—	—
Tree shrews										
Tupaia glis	—	—	vd	—	—	—	—	—	—	—
Squirrels										
Callosciurus notatus	vd	va	va	—	—	—	—	—	—	—
C. prevostii	vadc	va	—	—	—	—	—	—	—	—
Ratufa bicolor	—	va	—	—	—	—	—	—	—	—
R. affinis	vdc	—	—	—	—	—	—	—	—	—
Civets										
Paradoxurus hermaphroditus	—	—	—	—	—	—	—	—	—	(vi)

The pericarp is brick-red in colour on the outside and white inside. There are three locules, two or three of which contain one seed each. The seeds are up to 50 mm long and 25 mm wide and have a shiny orange–red aril, which is hard and oily and can easily be detached from the rest of the seed, revealing a shiny chestnut-brown testa. When ripe, the fruit dehisces along three longitudinal lines. The white inner pericarp contrasts with the outer pericarp and the arils, making the dehisced fruits conspicuous.

Observations were made on 4–6 April 1978. Immediately after dawn and occasionally during the day, birds and squirrels visited the tree and removed all the seeds from dehisced fruits. The squirrels frequently gnawed through the pericarp of undehisced fruits and took immature seeds. Damaged pericarp exuded latex, which was white at first, but soon turned brown, concealing the wound and making the unripe fruit inconspicuous again. Some of the seeds were destroyed on the tree by insect larvae, similar to those mentioned under *A. elliptica* below.

When seeds fall to the ground with all or part of the orange-red aril attached, they are conspicuous and soon disappear, probably eaten by ground birds and rodents. One afternoon, several *Rollulus rouloul*, crested wood partridge (25 cm), which may have been eating the fallen seeds, were disturbed beneath the tree.

When a seed is dropped after the aril has been removed, the brown seed coat makes it so inconspicuous on the ground that it is almost impossible for a human being to find. A number of seedlings germinated near the tree later in 1978, indicating that some seeds had escaped being eaten.

(2) *Aglaia oligocarpa*

Two trees, 12 m and 15 m tall, near Kuala Lompat, were fruiting abundantly at the end of August and during the first half of September 1981. They were in an area of forest where much of the undergrowth and many small trees had been removed by domesticated elephants, formerly tethered there. On 25 August, the number of fruits on one of these trees was estimated to be between 5000 and 10000. The fruits are up to 25 mm in diameter and are borne singly or in small infructescences with two to four fruits. They have three to four locules and one to four seeds. The pericarp is pink on the outer surface, with a dense covering of peltate scales, and white inside. The 1–2 mm thick aril has a bright red outer skin and milky, white flesh. With the aril removed, the seed measures approximately 14 mm × 7 mm × 6 mm; its shiny brown testa makes it inconspicuous on the ground when the aril has been removed. The contrast between the outer and inner pericparp, and between the latter and the arils, makes the seeds conspicuous in the dehisced fruits.

Fruits dehisced before dawn and birds began to visit the tree soon after first light, when it was often not possible to identify them. Frequent visits continued until 10h00 or 11h00 and after that were intermittent for the rest of the day, even though some dehisced fruits containing seeds remained.

The ripe fruits were easily detached; many were dislodged by the birds as they moved in the tree and they frequently pulled off the entire fruit when attempting to remove a seed. Because the entire fruit was too large for the small birds to swallow whole, they shook it to remove the one seed held in the beak, while the rest of the fruit, which often still contained one or two seeds, fell to the ground. If a bird failed to extract the seed in this way, it discarded the whole fruit. It was not possible to see whether the larger birds also extracted individual seeds or whether they swallowed the complete fruits. All the birds observed feeding on the seeds swallowed them whole, with the aril attached.

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Although these trees were in slightly disturbed forest, all the birds observed feeding in them belong to species that frequent primary forest.

(3) *Aglaia teysmanniana*

One tree, 15 m high, was fruiting in the forest at Kuala Lompat in 1979, but the density of the surrounding canopy made it impossible to observe visitors either from the ground or by climbing a nearby tree. In July and August 1981 another tree, about 8 m high, near the two trees of *Aglaia oligocarpa*, bore a large crop of fruits. The infructescences and fruits are similar in morphology and size to those of *A. oligocarpa* except that the number of locules appears not to exceed three and the indumentum is of stellate hairs rather than peltate scales.

On one occasion, two individuals of *Ptilinopus jambu*, the Jambu fruit dove (27 cm), were seen perching on the branches of the dead tree in which *Gracula religiosa* perched to regurgitate seeds. They may have come to feed in the *A. teysmanniana* tree, which was adjacent to the dead tree, but were not seen to do so and it is possible that these rather shy birds were frightened by the presence of an observer.

Observations were made at the beginning and end of the fruiting period and are not, therefore, strictly comparable with those for *A. oligocarpa*, which were made during the peak of fruiting. Fewer fruits dehisced each day in the *A. teysmanniana* tree than in *A. oligocarpa* and visiting birds did not knock off fruits or detach entire fruits when attempting to remove a seed; they removed all the seeds from dehisced fruits before midday. The large numbers of fruits dislodged in the *A. oligocarpa* trees may have been a result of the fruits' becoming over-ripe when not all the seeds were removed on the day of dehiscence.

(ii) *Species dispersed principally by mammals*

(1) *Aglaia elliptica*

Aglaia elliptica is a common canopy tree, to 20 m high, at Kuala Lompat. In this site, it usually grows within 30 m of a river (and rarely more than 100 m away), where the average canopy height is lower than on higher ground. In Sumatra, *A. elliptica* was found in forest on limestone with no river nearby, but the canopy there was also rather low. The fruits are borne in large infructescences, usually with 100 or more fruits packed tightly together; there may be as many as 100 or 200 infructescences on a single tree. All the fruits in an infructescence ripen at about the same time, but different infructescences on the same tree mature at different times over a period of several weeks. The fruits have two locules and one or two seeds with a 2–3 mm thick, pale orange, gelatinous aril; the average seed size is 25 mm × 12 mm. At Kuala Lompat this species produced flowers and fruits in each of the years 1978, 1979 and 1980, and ripe fruits were present for six months from May to October.

No animals were seen feeding in the tree, although movements of squirrels were heard occasionally and at such times pieces of pericarp were seen falling to the ground. Some seeds collected in raised quadrats beneath the trees bore the tooth marks of squirrels. Chivers (1980*b*, p. 325) reports that the fruit pulp of Pelir Tupai (the local name for this species) is eaten by *Presbytis melalophus*, the banded leaf monkey (body 50 cm; tail 75 cm). According to Rijksen (1978), the fruits are ignored by *Pongo pygmaeus*, but are taken by *Ratufa bicolor*. This information, however, has not been confirmed from Rijksen's herbarium collection.

In each fruit crop, a number of seeds of *A. elliptica* were destroyed by insect larvae. These have been examined and identified by Dr. M. Speight of the Department of Zoology, Oxford. They include larvae of moths (Heterocera), flies (Diptera) and at least two families of beetles (Coleoptera), one of these being the weevil family (Curculionidae).

(2) *Aglaia korthalsii* and (3) *Aglaia speciosa*

The commonest *Aglaia* trees at Ketambe, in Gunong Leuser National Park, Sumatra, are provisionally assigned to two species: *A. korthalsii* (local name, Setur Gajah) and *A. speciosa* (local name, Setur Padi). Both are medium-sized trees, to 30 m in height. The fruit of *A. korthalsii* is about the same size as that of *A. elliptica*, but the pericarp is thicker and its two seeds are slightly smaller (approximately 18 mm × 12 mm × 8 mm). That of *A. speciosa* is similar to but larger than *A. odoratissima* (see below) and contains one or two seeds (approximately 16 mm × 13 mm × 8 mm). In both species, the aril is about 2 mm thick. There are also vegetative differences between these two species and these are correlated with the differences in the fruits.

The taxonomic treatment of these species is, however, incomplete; further work may result in a different name for the trees assigned here to *A. korthalsii*. Alternatively, it may be that intermediates between these plants and *A. speciosa* will be found, in which case the division into two species could not be maintained.

Rijksen (1978) apparently grouped both under one name, *A. speciosa* (local name, Setur). When these trees were fruiting during the four months from October 1973 to January 1974, the arils were one of the principal foods of *Pongo pygmaeus* and seeds without their arils were found in many of the *P. pygmaeus* faeces examined by Rijksen (1978). He attributes the unusually high density of *A. speciosa* in his study area (11.49% of all the trees over 15 cm in diameter at breast height) to dispersal by this ape. He also describes the different ways in which different individuals feed on large seeds with firmly adhering flesh; some swallow the whole seeds, whereas others carefully remove as much flesh as possible and discard the rest of the seed. Food is sometimes collected in a pouch formed inside the lower lip and it is therefore possible that even those individuals that do not swallow the seeds do carry some away from the parent tree before processing them.

In July 1983, two individuals of *Hylobates lar*, the white-handed gibbon (46 cm), were seen (by C.M.P.) taking seeds from ripe fruits of *A. korthalsii* at Ketambe; they removed much of the aril and dropped the rest of the seed beneath the tree.

(4) *Aglaia odoratissima*

A. odoratissima is a small tree, to 10 m high, and is common in the forest at Kuala Lompat. Fruits ripen a few at a time, so that there are rarely more than twenty ripe fruits on a tree at once. The pericarp is pinkish-orange and indehiscent; the one seed (rarely two) (approximately 13 mm × 10 mm × 6 mm) has a gelatinous yellow aril. In 1978, 1979 and 1980, flowers and fruits were produced annually and ripe fruits were present for three or four months between June and October.

No animals were observed visiting fruiting trees by C.M.P., but Kalang (personal communication) has seen *Macaca fasicularis*, the long-tailed macaque (body 40 cm; tail 48 cm), and *Presbytis melalophus*, ingesting the arillate seeds.

(5) *Aglaia ganggo*

A canopy tree in the forest at Kuala Lompat, *A. ganggo* was not seen fruiting. Dried seeds measure approximately 12 mm × 7 mm × 6 mm. However, new seedlings regularly appear at some distance from adult trees, some at least having germinated from seeds contained in the faeces of *Hylobates lar* (Kalang, personal communication). According to Chivers (1980*b*, p. 325) *Hylobates syndactylus*, the siamang (83 cm), *Hylobates lar*, *Presbytis melalophus*, *Macaca fasicularis* and an unidentified squirrel eat the fruit pulp of Pemanis Gading (the local name given to this species). Raemakers (1977) lists it among the top 50 plant foods of *Hylobates syndactylus*.

(6) *Aglaia rufibarbis*

This is a small tree, to 10 m high, and is common at Kuala Lompat, where there are as many as 40 trees per hectare in some parts of the forest. Fruits are borne singly and have a dense covering of stellate hairs forming a layer 4 mm thick. In 1978, 1979 and 1980, individuals of this species flowered annually; they failed to set fruit in 1978, but a few trees produced ripe fruits in August 1979 and October 1980.

There is no line of dehiscence, but the pericarp is easily removed to expose one large seed (approximately 18 mm in diameter) which has no aril and only a thin seed coat protecting the two green cotyledons. The seeds are eaten by *Macaca fasicularis* and squirrels (Kalang, personal communication).

(7) *Aglaia* aff. *elaeagnoidea*

Seeds of a species of *Aglaia* related to *A. elaeagnoidea* were found by Schmutz (notes with herbarium specimen no. 3596 (Leiden)) in the faeces of *Paradoxurus hermaphroditus*, the musang or common palm civet, (body 54 cm; tail 49 cm) on Flores, Lesser Sunda Islands. The dried seeds measure approximately 10 mm × 6 mm × 3 mm. From the dried specimens, fruit morphology seems to resemble that of *A. odoratissima*, but neither fresh nor spirit material was available for examination.

(*b*) *The species analysed for comparison with Aglaia*

The arils of four plant species from lowland Sumatra, which belong to genera other than *Aglaia* and are known or thought to be dispersed by vertebrates, were analysed for nutrients.

Lansium domesticum (Meliaceae), the langsat, which is related to *Aglaia*, and *Durio zibethinus* (Bombacaceae), the durian, are both cultivated for their fruits in tropical Asia, where the arils are eaten by the local people. The seeds of *Lansium domesticum* have a sweet, white aril; those of *Durio zibethinus* have a strong-smelling, mucilaginous, yellow aril. The seeds of *L. domesticum* in the samples used for analysis measured approximately 13 mm × 6 mm; those of *D. zibethinus* were approximately 30 mm × 40 mm.

Each half of the double fruits of *Tabernaemontana macrocarpa* (Apocynaceae) has a thick (15–20 mm), yellow, latex-containing pericarp and one locule with about 20 seeds (10 mm × 7 mm × 5 mm), each of which is surrounded by a pinkish-red aril, 1–2 mm thick. The morphology of the fruit resembles that of *Stemmadenia donell-smithii* (also Apocynaceae), which is dispersed by birds (McDiarmid *et al.* 1977). In the unidentified species of *Zingiber* (Zingiberaceae), a wild ginger, used for analysis, the ground-level infructescence contains numerous small black seeds (7 mm × 5 mm × 3 mm), each with a white aril, which is less than 1 mm thick and laciniate at the distal end.

(c) *Phytochemical analyses*

The results of the nutritional analyses of the aril samples for ten species, listing the various components on the basis of percentage of dry mass, are presented in table 4. 'Residue' was determined as the difference between 100% and the total of the percentages of the other components, which were assayed directly.

TABLE 4. SUMMARY OF THE NUTRIENTS (PERCENTAGE BY DRY MASS) IN THE ARILS OF THE TEN SPECIES ANALYSED

	reducing sugars	oligo-sacch-arides	total sugars	starch	total sugars + starch	lipids	protein (Kjeldahl N × 6.25)	residue
arils high in lipids								
Aglaia species 2	8.8	1.4	10.2	4.9	15.1	37.7	0.7	46.5
A. oligocarpa	7.4	2.3	9.7	3.9	13.6	60.6	0.6	25.2
A. teysmanniana	11.4	1.7	13.1	9.7	22.8	27.6	5.1	44.5
Zingiber sp.	3.3	2.1	5.4	1.4	6.8	23.7	20.6	48.9
Tabernaemontana macrocarpa	14.5	2.0	16.5	< 0.1	16.6	32.1	13.2	38.1
arils sweet								
Aglaia elliptica	25.4	1.0	26.4	6.2	32.6	2.8	1.2	63.4
A. korthalsii	23.6	0.9	24.5	5.2	29.7	12.8	4.8	52.7
A. speciosa	15.3	0.2	15.5	5.8	21.3	11.0	2.1	65.6
Lansium domesticum	24.3	8.4	32.7	3.4	36.1	11.5	1.9	50.5
Durio zibethinus	6.2	24.1	30.3	6.6	36.9	8.1	2.8	52.2

Gas–liquid chromatographic analysis of the neutral fraction carbohydrates demonstrated an absence of pentose sugars in all species; fructose and glucose were the major hexose sugars detected, with galactose and mannose occurring in minor amounts. Sucrose was the major disaccharide detected, although trace amounts of maltose and other unidentified disaccharides were found in *Aglaia oligocarpa*, *Lansium domesticum*, *Tabernaemontana macrocarpa* and *Durio zibethinus*; the last two species also showed trace amounts of unidentified trisaccharides. The values listed in table 4 under the column 'oligosaccharides' may therefore be reasonably interpreted as estimates of sucrose in the arils.

The bird-dispersed species contain a higher percentage dry mass of lipid than the primate-dispersed ones (table 4). Gas–liquid chromatographic analysis of the saponified lipid fraction (table 5) showed that all the *Aglaia* species contained hexadecanoic (palmitic), *cis*-9-octadecenoic (oleic) and octadecanoic (stearic) acids as the major fatty acids. *A. teysmanniana* also showed a major peak late in the chromatogram which may be either a triterpenoid or a sterol. Minor amounts of *cis*-11-eicosanoic acid were detected in *Aglaia* species 2. Of the remaining five species, only *Durio zibethinus* and *Tabernaemontana macrocarpa* synthesized hexadecanoic, *cis*-9-octadecenoic and octadecanoic acids in major amounts. *Lansium domesticum* and *Zingiber* sp. contained hexadecanoic and *cis*-9-octadecenoic acids as the major fatty acids with only minor amounts of octadecanoic acid present. Although the percentage dry mass of lipid in the arils may distinguish the primate-dispersed from the bird-dispersed species, there are no consistent differences in the synthesis of specific fatty acids.

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Table 5. Fatty acids and other lipophilic compounds present in the arils of the ten species analysed

(Symbols: ●, major component (peak area ⩾ 15% of total chromatogram area); ○, minor component (peak area < 15% of total chromatogram area).

	hexadecanoic (palmitic)	*cis*-9-octadecanoic (oleic)	octadecanoic	unknown (triterpenoid or sterol)	sitosterol	*cis*-11-eicosanoic	*cis*-9-hexadecenoic
arils high in lipids							
Aglaia species 2	●	●	●	—	○	○	—
A. oligocarpa	●	●	●	—	○	—	—
A. teysmanniana	●	●	●	●	○	—	—
Zingiber sp.	●	●	○	—	○	—	—
Tabernaemontana macrocarpa	●	●	●	—	○	●	—
arils sweet							
Aglaia elliptica	●	●	●	—	○	—	—
A. korthalsii	●	●	●	—	○	—	—
A. speciosa	●	●	●	—	○	—	—
Lansium domesticum	●	●	○	—	—	—	—
Durio zibethinus	●	●	●	—	○	—	○

The results of the gas chromatographic analysis of the amino acid content of the aril samples are given in table 6, where the amino acids and unknown metabolites are listed in their order of elution. The absence of molar response factors for each amino acid with respect to the internal standard precludes any estimation of their standing amounts. However, relative values may be determined from the formula:

$$\text{Relative concentration} = \frac{\text{peak area of amino acid}}{\text{peak area of internal standard} \times \text{dry mass of aril sample extracted}}.$$

The resulting figure may be used for a valid comparison of the relative amounts of a particular amino acid among the ten species. The chromatographic analysis cannot distinguish between asparagine and aspartic acid, nor between glutamine and glutamic acid, because the amides break down to the corresponding acids during derivatization. Histidine was not detected in any of the species assayed. Of phytochemical interest in the large number of unknown compounds detected in the extracts, some in rather large relative amounts, as in *Tabernaemontana macrocarpa* (u-7, 10–16 and 19). Most of the primate-dispersed species have high relative amounts of alanine, γ-aminobutyric acid, glycine and asparagine or aspartic acid. These are sweet-tasting amino acids, which may provide supplementary sweetness in addition to that provided by the large amounts of sugars found in the arils of the primate-dispersed species.

(*d*) *Summary of the results*

We have found that, among the West Malesian species of *Aglaia*, there are two main types of fruit, in which a number of morphological and phytochemical features are correlated with their principal dispersal agents, birds for one type and mammals, chiefly primates, for the other.

Except for *A.* aff. *elaeagnoidea*, all the observations considered are from localities west of

Table 6. Relative contents of amino acids and other nitrogenous compounds in the arils of the ten species analysed

(u-, Unknown.)

	arils high in lipid					arils sweet				
	Aglaia sp. 2	*A. oligocarpa*	*A. teysmanniana*	*Zingiber* sp.	*Tabernaemontana macrocarpa*	*Aglaia elliptica*	*A. hexandra*	*A. speciosa*	*Lansium domesticum*	*Durio zibethinus*
alanine	8	30	56	135	97	25	194	204	107	940
glycine	—	—	—	173	—	19	24	28	—	54
u-1	—	—	—	—	—	—	60	46	—	62
valine	—	9	—	26	72	—	26	21	—	55
threonine	—	—	—	78	106	—	87	54	—	10
serine	—	—	12	238	120	29	139	118	666	52
leucine	—	8	15	55	167	—	23	—	—	52
isoleucine	—	5	—	29	709	—	35	—	—	39
γ-aminobutyric acid	—	33	—	34	—	53	479	1130	110	279
proline	2201	535	7677	21	570	57	2333	4603	2672	69
u-2	—	—	9449	—	—	—	—	—	—	—
u-3	—	—	—	—	—	—	—	13	77	—
cysteine is (pipecolic acid)	—	—	1085	—	223	124	—	—	—	—
hydroxyproline	11	—	40	4	—	142	66	101	—	98
methionine	—	—	202	22	349	—	—	60	—	102
u-4	896	—	—	—	—	—	—	—	-	—
asparagine aspartic acid	52	25	123	546	2154	349	2520	931	813	853
u-5	425	—	—	57	—	135	100	34	—	—
phenylalanine	—	8	13	60	—	—	22	29	—	52
ornithine	58	—	100	—	—	—	28	18	—	—
glutamine glutamic acid	25	20	56	300	175	48	469	607	—	731
lysine	—	—	9	51	—	33	—	—	—	20
tyrosine	—	—	10	111	2361	23	39	28	—	74
u-6	—	—	—	—	—	—	—	—	112	—
arginine	—	—	—	6	—	—	—	—	90	—
histidine	—	—	—	—	—	—	—	—	—	—
u-7	—	—	—	—	1053	48	120	69	—	—
u-8	—	—	16	—	—	103	623	358	—	—
tryptophan	—	8	—	17	—	—	—	23	141	—
u-9	—	—	—	—	—	329	—	—	—	—
u-10	9	—	18	—	64084	802	762	434	122	130
u-11	12	—	—	—	18103	34	—	—	—	—
u-12	—	6	—	—	11662	—	—	—	—	—
u-13	—	—	—	—	15350	—	111	—	—	—
u-14	—	—	—	—	4298	—	—	—	—	—
u-15	—	—	—	—	5063	—	—	—	—	—
u-16	—	—	—	—	2143	—	—	—	—	—
u-17	22	—	370	—	—	—	—	22	—	—
u-18	—	—	—	—	—	—	—	—	129	—
cystine	—	—	—	47	—	—	—	—	—	36
u-19	18	19	20	—	1318	—	—	—	—	—

Wallace's line, on the Sunda continental shelf. Little is known about the dispersal of *Aglaia* in Australasia. Beehler (1983) includes, in error, the arillate seeds of *Aglaia* species† with dehiscent capsules among the plant foods of *Parotia lawesii*, Lawe's six-wired bird of paradise, and *Paradisaea raggiana*, the Raggiana bird of paradise, in New Guinea; the fallen fruits of an *Amoora* species (*Amoora* is now included in *Aglaia* (Pennington & Styles 1975; Pannell 1982)) are included in the diet of *Casuarius casuarius*, the cassowary, in Queensland (Stocker & Irvine 1983).

The bird-dispersed *Aglaia* fruit in West Malesia is a dehiscent capsule with a thick, fibrous, latex-containing pericarp, brick-red or pink on the outside and white inside. The pericarp dehisces loculicidally along three or four lines and each seed is surrounded by an aril with a red skin and milky or granular flesh, which is high in liquid (27–60% dry mass). The aril can be scraped or peeled away from the rest of the seed; this probably means that it is easily removed by the action of the gizzard or gut of the birds that swallow the seeds. The contrast in colours of the outer and inner pericarp of the fruits and the red seeds makes the dehisced, seed-containing fruits conspicuous on the tree. Although it is generally accepted that diurnal birds have colour vision, its details and mechanisms remain largely unresolved (Jacobs, 1981, p. 109). The experiments of Turček (1963), however, suggest that red is a particularly attractive colour to fruit-eating birds.

The primate-dispersed *Aglaia* fruit is indehiscent, but dehiscence lines are present in some species. The pericarp is fibrous, leathery or brittle, and orange, pinkish-orange or brown in colour. The white, yellow or orange translucent aril is low in lipid and high in free carbohydrates (reducing sugars and sucrose) and sweet-tasting amino acids (such as alanine, glycine and proline). Primates break open or peel away the pericarp and either swallow the seeds whole or suck off some of the aril and discard the seed. The aril adheres firmly to the testa, making it difficult to remove; this, together with its gelatinous nature, seems to encourage primates to swallow the entire seed with the aril.

It is the aril in *Aglaia* which is digested by dispersing animals, while the rest of the seed is rejected, regurgitated or passed unharmed. Analyses of the seeds of *Aglaia* for chemical defences, which might protect them from mastication and digestion by these animals, have not yet been made. If such defences are present, then physiological adaptations which overcome their effects have apparently evolved in certain destructive feeders, such as squirrels. The chemical defences of *Aglaia* are likely to be limonoids, a group of oxidized triterpenes, which are known to be widespread in the Meliaceae and certain related families (see Taylor (1983, 1984) for reviews). They have been found in the heartwood, foliage and seeds, but the majority of investigations have been made on timber samples. Limonoids taste bitter to man; their presence in meliaceous seeds is almost certainly why these seeds are not usually eaten by their animal dispersers (D. A. H. Taylor, personal communication 1984). Among the few analyses of Meliaceae seeds made, limonoids have been extracted from the seeds of *Chisocheton cumingianus* (as *C. paniculatus* in Connolly *et al.* (1979) and Saikia *et al.* (1978)) and *Aphanamixis polystachya* (Brown & Taylor 1978; King & Taylor 1983).

† A photograph of the fruits referred to here has been made available to C.M.P. by Dr Beehler; these fruits do not belong to *Aglaia*, but almost certainly to *Dysoxylum* (also Meliaceae).

4. Discussion

(a) *Quantitative field studies*

Quantitative assessments of the numbers of seeds removed from fruiting trees by different species of birds and mammals have been made in the past by Howe (1977, 1980, 1981), Howe & De Steven (1979), Howe & Primack (1975), Howe & Vande Kerckhove (1979, 1980, 1981) and McDiarmid *et al.* (1977). Such an approach is of value, in that it allows estimates to be made of the proportion of seeds taken by different potential dispersers in the season being considered, and may indicate which species of animal is likely to have been the disperser of the greatest number of seeds during that season. We, however, consider it to be unwise to extrapolate from such information to produce a hypothesis suggesting the coevolution of a specific disperser or dispersers with a species of tree throughout its life and throughout its range. The investigation of the dispersal of a number of closely related species of *Aglaia*, together with other aspects of their life histories and their distributions and morphological variation, suggests that an approach that aims to characterize the general types of dispersal may be more valuable. The exact agents of dispersal are almost certain to be different in different parts of the range of widespread species and in different seasons during the life of an individual tree. A tree may produce thousands or millions of diaspores during its lifetime, but, on average, only one or a few of these will survive and grow to reproduce successfully. It is highly unlikely that the dispersal agent of the successful one or few seeds could be identified with certainty.

In primary forests of the type where this study was carried out, it is not possible to collect accurate data on the numbers of seeds removed by animals feeding in the trees. An attempt was made to obtain approximate figures for *Aglaia oligocarpa*, where two trees with large crops of fruits were studied in an area of forest where some of the undergrowth had been cleared and one or two sides of the crown were visible. Visibility at dawn was too poor to identify small birds to species, and mists often persisted and made identification unsatisfactory for a further one or two hours after dawn. Although, for *A. oligocarpa*, two people were available to make observations, each one could only watch one visiting animal at a time and even that was usually concealed by leaves and branches for at least part of the time it spent in the tree. In addition to those considerations, F. Dowsett-Lemaire (personal communication) emphasizes that such methods are likely to underestimate or miss completely the visits of nocturnal animals and animals that will not tolerate the presence of a human observer.

(b) *Dispersal of Aglaia seeds by birds*

(i) *Which birds disperse Aglaia seeds?*

The observations of visits by birds to fruiting trees of *Aglaia* suggest that hornbills may be the principal dispersers of large-seeded species and that hornbills and several smaller bird species are involved in the dispersal of smaller-seeded species. It may be that other bird species, especially fruit pigeons (see p. 313), are also effective dispersers. *Aglaia ridleyi* (as *Amoora* aff. *ridleyi*) has fruits and seeds like those of *Aglaia* species 2 and is thought to have been dispersed to the island of Jarak in the Straits of Malacca by *Ducula bicolor*, the pied imperial pigeon (Wyatt Smith 1953 *a,b*). The seeds of some species of *Dysoxylum*, also with dehiscent fruits, in Australia, are ingested by two species of *Ptilinopus* (Crome 1975).

Some species of hornbill and pigeon are known to fly distances of 100 km or more (McClure 1974; Medway & Wells 1976; M. Leighton & D. R. Leighton 1983); these birds could be important in the dispersal of *Aglaia* seeds over longer distances. Some of the smaller birds, such as bulbuls, seen visiting *Aglaia* trees, are wasteful when feeding; the little that is known of their movements suggests that they do not travel long distances (McClure 1974) and seed-retention times are likely to be short (see, for example, Herrera 1981). They are therefore usually only likely to effect local dispersal of seeds. Although occasional dispersal over longer distances may result in the colonization of new areas and may bring together genotypes from different parts of the range of a species, local dispersal is necessary for the maintenance of a population in any one area. Both types of dispersal are likely to be important in the long-term survival and evolution of a species.

(ii) *Seed size and nutrient content of the aril and specialization in the diets of dispersal agents*

Of the three bird-dispersed species of *Aglaia* considered here, *A. oligocarpa* and *A. teysmanniana* are similar in fruit size and morphology; they occur at the same site, their fruiting times overlapped in 1981 and similar species of birds and other vertebrates fed on the arils. The major difference to emerge between the two species is in the chemical composition of the aril. In *A. oligocarpa* the aril tissue is 60% (dry mass) lipid, whereas in *A. teysmanniana* it is only 28%. Although we cannot explain why, it is interesting to note that a major component of the lipid fraction in *A. teysmanniana* is an unidentified compound (triterpenoid or sterol?) which was not found in *A. oligocarpa*, nor in any of the other species analysed (table 5).

The third bird-dispersed *Aglaia* (*A.* species 2) is a tree taller than the last two species and has much larger seeds; this size restricts the number of animals able to feed on them. These are either birds with a gape wide enough to swallow the entire seed with the aril intact, or mammals, such as squirrels, which can hold the fruits and seeds and remove the hard aril without ingesting the seed whole. The small birds observed feeding on *A. oligocarpa* and *A. teysmanniana* would be unable to swallow the arillate seeds of *A.* species 2; the only bird seen taking them was *Anthracoceros malayanus*, which was also observed ingesting the seeds of *A. oligocarpa*. Becker & Wong (1985) similarly concluded that *Aglaia* species 2 (as *Aglaia* sp.) at Pasoh was dispersed primarily by *Anthracoceros malayanus* during the period of their study of this species.

Snow (1971) and McKey (1975) have suggested that there are two main types of fruit-eating bird, which 'digest only the pericarp or other soft parts of the fruit and void the seeds intact, either by regurgitation or defecation' (Snow 1981). They are the specialized frugivores, which

Table 7. Seed size and the percentage dry mass of lipid in the arils of some tropical plants

	approximate seed size/mm	percentage lipid	source
Aglaia sp. 2	50 × 25	38	this paper
Virola surinamensis	19 × 15	53–75	Howe & Vande Kerckhove (1980, 1981)
V. sebifera	14 × 10	54	Howe (1981)
A. oligocarpa	14 × 7	61	this paper
A. teysmanniana	14 × 7	28	this paper
Tabernaemontana macrocarpa	10 × 7	32	this paper
Trichilia prieuriana	10 × 7	73	Hladik (1977*a*)
* *T. cuneata*	9 × 6	60	Foster & McDiarmid (1983)
Strelitzia nicolai	9 × 6	67	Frost (1980)
Stemmadenia donell-smithii	8 × 3.5	64	McDiarmid, Ricklefs & Foster (1977)

* *Trichilia martiana*; see Pennington (1981).

feed on fruits with large seeds and a relatively small amount of lipid-rich flesh, and the unspecialized or opportunistic species, which feed on small fruits with watery flesh, containing mainly carbohydrates. Our own and some other published analyses (table 7) show that, for species with bird-dispersed arillate seeds, the relation between seed size and the quality of the aril does not always follow this pattern.

It seems that the degree of dependence of a particular fruit-eater on fruits has sometimes been confused with its importance as a disperser of the seeds of the species on which it feeds. Snow (1971) contrasted the specialized tropical fruit-eating birds, whose diets consist entirely or almost entirely of fruits, with unspecialized fruit-eating birds of temperate latitudes, where the absence of fruits at certain times of the year means that birds are unable to become specialized for a diet of fruits alone. The concept of quality of dispersal was introduced to this theme by McKey (1975), who suggested that 'the evolution of adaptations to specialized frugivory have resulted in generally increased dispersal quality' and 'the quality of dispersal by specialized frugivores is higher than that performed by birds eating fruits opportunistically'. From the botanical point of view, however, this is an oversimplification. *Steatornis caripensis* (the oilbird), for example, is referred to as a specialized fruit-eater, which is true in that it has not been observed to eat anything other than fruits in the wild (Snow 1961, 1962). Nevertheless, most of the seeds from the fruits on which it feeds are regurgitated in the caves where the bird nests and roosts and, unless they are carried out into the open by some secondary agent, are lost in terms of reproduction for the plants from which they came. Although the arils of some bird-dispersed species of *Aglaia* have a high (dry-mass) lipid content, none of the birds that feed on them can strictly be classified as 'specialized fruit-eaters' in the sense used above. With the exception of *Calyptomena viridis*, there are records of the adults of all the species which were observed ingesting *Aglaia* seeds in Peninsular Malaysia (see table 2) eating some animal food, usually small invertebrates such as insects and snails (Madoc 1976; Smythies 1981; Medway & Wells 1976; M. Leighton & D. R. Leighton 1983). In captivity, *Anthracoceros malayanus* has been recorded eating small vertebrates (Smythies 1981). Even *C. viridis*, which apparently feeds exclusively on fruits as an adult, has been observed to take large numbers of insects to its young (Fogden 1972). The genus *Aglaia* and many of its species are, however, widespread in tropical Asia and have clearly been effectively dispersed. At least some of the animals observed in this study have almost certainly played a part in this dispersal; it seems unlikely that the effectiveness of dispersal has been influenced by a lack of complete specialization on a diet of fruits by these dispersers. Times of passage of seeds through the guts and ranging habits of the dispersers are likely to have been more important.

(*c*) *Dispersal of Aglaia seeds by primates*

Three species of ape and at least two species of monkey ingest the arils and seeds of *Aglaia* in the areas where the study was carried out. They are *Pongo pygmaeus*, *Hylobates syndactylus*, *H. lar*, *Presbytis melalophus* and *Macaca fascicularis*. Fruits figure prominently in the diet of each of these species. The actual proportion in the diet is difficult to quantify, but Chivers (1974), J. R. Mackinnon & K. S. Mackinnon (1978) and Rijksen (1978) all found that, for much of the year, fruits were taken in more than 50%, and sometimes over 90%, of the feeding acts observed in the primates they were studying. There is considerable overlap in diet between sympatric species. J. R. MacKinnon (1977), J. R. Mackinnon & K. S. MacKinnon (1978, 1980) and Rijksen (1978) discuss the features of the habitats of each of these species, diurnal activity, territory size and specific composition of the diet, which appear to allow them to live together in spite of the apparent competition for similar food sources.

The daily distance travelled by the primates that eat the seeds of *Aglaia* is usually no more than a few hundred metres (Chivers 1974; J. R. Mackinnon & K. S. Mackinnon 1978; M. Leighton & D. R. Leighton 1983). There is, however, some evidence that *Pongo pygmaeus* occasionally ranges over a much wider area (Rijksen 1978; M. Leighton & D. R. Leighton 1983); it may, therefore, occasionally carry seeds as far as several kilometres away from the parent plant, and this may also be true for other primates.

These primates usually swallow and pass or spit out large seeds without damaging them, although *Presbytis* and *Macaca* species sometimes gnaw into seeds and destroy the embryo (D. J. Chivers, personal communication). *P. pygmaeus* has peculiar dentition, which is efficient at scraping flesh from seeds, usually without damaging them (J. R. Mackinnon, personal communication). This ape does, however, chew and destroy the unripe seeds of certain *Durio* species and sometimes thereby destroys the majority of the crop (J. R. Mackinnon, personal communication).

Rijksen (1978) found that individuals of *Pongo pygmaeus* differ in the way they handle large seeds: some swallow them whole, with the flesh intact, whereas others carefully remove the flesh and throw away the rest of the seed. *Hylobates lar* swallows the seeds of *Aglaia ganggo* and may deposit them in its faeces some distance from the parent tree. However, the same species of gibbon at the end of the day was seen (by C. M. P.) sucking the flesh from the seed of *A. korthalsii* and dropping the rest of the seed beneath the tree. When considering the dispersal of *Parkia* (a pantropical genus of Leguminosae) seeds in Africa, Hopkins (1983) drew attention to observations made by Nissen (1931) on the differences in behaviour of *Pan troglodytes* when eating *Parkia* fruits, depending upon the intensity of their hunger. Early in a feeding bout, when they are particularly hungry, they swallow the seeds of *Parkia biglobosa* along with the nutritious pulp; after they have fed in this way, undamaged seeds appear in their faeces. As the intensity of hunger subsides, however, they discard the seeds near the parent tree and eat only the pulp. Although *P. troglodytes* has powerful mandibles with which it often damages or crushes seeds, large seeds belonging to a variety of species are still frequently found intact in its faeces (J. R. Mackinnon, personal communication). Such variation in the way that individual primates handle arillate seeds means that it may not always be easy to assess their importance as dispersers. As in the bird-dispersed species, the arils of the seeds eaten by primates are usually low in protein; the diets of these primates also include leaves, shoots and flowers, all of which are usually higher in protein than fruit flesh, and some animal protein, such as insects and birds' eggs (Chivers 1974; J. R. MacKinnon & K. S. MacKinnon 1978; Rijksen 1978). *P. troglodytes*, with its multi-male social groups, hunts small vertebrates, but those make up only a small proportion of the animal protein which it eats (Hladik 1977*a*).

The arils of primate-dispersed species of *Aglaia* were found to be high in reducing sugars and sweet-tasting amino acids. The lipid content is lower than in the bird-dispersed species. Sweetness is probably important in attracting primates to eat these arils. Primates, such as *Macaca fuscata*, the Japanese macaque, have been shown to respond positively, both behaviourally and neurally (impulse discharges from chorda tympani fibres), to substances that taste sweet to man (Sato 1975; Sato *et al.* 1977); their behaviour is summarized by Hellekant *et al.* (1980), in the words 'Most primates have, like man, a sweet tooth'. Among those amino acids found in large relative amounts in *Aglaia korthalsii*, *A. speciosa* and *Lansium domesticum*, alanine, glycine and proline taste sweet to man (Schiffman 1980). It would, therefore, be of interest to determine the standing concentrations and sweetness of these amino acids in the aril samples on the hypothesis that they play a supportive role in making the aril attractive to primates.

With the exception of nectar-feeding species, sugar preference in birds is uncertain. Electrophysiological studies show little or no response to sucrose as an applied stimulus (Duncan 1960; Pfaffmann 1975). However, in preference tests with glucose and sucrose solutions, Duncan (1960) found that *Columba livia*, the feral pigeon, showed a slight preference for sucrose at concentrations around 150 g l^{-1}; this proved to be statistically significant.

There are some records of primates ingesting red, arillate seeds from dehiscent fruits; Hladik (1977*a*) includes the arils of *Trichilia prieuriana* (Meliaceae) in a list of important foods eaten by *Pan troglodytes* in Gabon. *Hylobates syndactylus* at Kuala Lompat ingests the arils and seeds of *Knema* aff. *oblongifolia* (Myristicaceae) (C. M. P., personal observation) and *Pongo pygmaeus* at Ketambe ingests the arils and seeds of *Knema conferta* (Rijksen 1978).

(*d*) *Dispersal by vertebrates other than birds and primates*

The faeces of some species of Viverridae, the civet family, frequently contain large undamaged seeds (C. M. P., personal observations); Schmutz found the seeds of *Aglaia* aff. *elaeagnoidea* in the faeces of *Paradoxurus hermaphroditus* (see p. 315). M. Leighton & D. R. Leighton (1983) made limited observations, on civets, which suggested that they eat ripe fruits similar in morphology to primate fruits.

No animals were observed feeding on the fallen arillate seeds of *Aglaia* in this study, but ground feeders could be important dispersers in some parts of the range of the genus. Other animals which might be agents of dispersal include some ground-feeding birds, deer, rodents and other vertebrates, such as pigs (M. Leighton & D. R. Leighton 1983; Stocker & Irvine 1983) and (for some species of *Durio*, at least) even tigers, elephants and bears (Corner 1949; Rijksen 1978; van der Pijl 1969). There is no evidence so far for dispersal of *Aglaia* seeds by bats, but the fruit and infructescence morphology of a few species suggests that this is a possibility.

Squirrels are probably rarely effective as dispersers of fleshy fruits and seeds because they usually either destroy the embryo, by gnawing into the seed, or strip off the aril and drop the rest of the seed beneath the parent tree. They do, however, sometimes carry seeds away and may drop them unharmed at some distance from the tree. M. Leighton & D. R. Leighton (1983) found that *Callosciurus prevostii* usually only consumes the fleshy parts of both bird- and primate-eaten fruits, but it does eat the embryo of some seeds. Four other squirrels in their study, including *Ratufa affinis* and *Callosciurus notatus*, destroy the seeds. Some squirrels in the Far East are scatter-hoarders, for example *Sundasciurus hippurus* (M. Leighton & D. R. Leighton 1983); although they are largely destructive, these squirrels could occasionally disperse intact seeds.

It would appear that *Aglaia rufibarbis* is dispersed by animals that usually destroy the seed. The seed has no aril; squirrels and *Macaca fasicularis* probably act as dispersal agents. It is therefore interesting to note that *A. rufibarbis* is not widespread; it seems to be confined to a small number of localities in Peninsular Malaysia, although it is locally common at Kuala Lompat.

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5. Conclusion

Some species of *Aglaia* from West Malesia, studied for dispersal agents and biochemical composition of the aril tissue which surrounds their seeds and is digested by dispersing animals, fell into two major groups. The seeds of those with dehiscent fruits, and with red-skinned and lipid-rich arils, were dispersed by birds, and of those with indehiscent fruits and with gelatinous, sweet arils were dispersed by primates.

We conclude that the ways in which animals handle seeds when feeding in fruiting *Aglaia* trees, the length of time of passage of an undamaged seed through the gut, the distances travelled by dispersers and other aspects of their behaviour and ecology, along with a study of distribution of plant species and the different faunal zones in which they occur, are important factors when considering dispersal. Investigations of these matters may lead to an improved understanding of rainforest regeneration and of evolutionary divergence within large genera of rainforest trees.

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Appendix 1. Collection and preservation of botanical specimens for identification and phytochemical analysis

Shoots bearing mature leaves were pressed and dried, and ripe fruits for subsequent morphological and taxonomic study were preserved in 'spirit' (a solution of equal quantities of industrial methylated spirit and distilled water, to every 3 l of which were added 25 ml formaldehyde and 25 ml glycerol). These have been or will be deposited in the herbaria of Bogor (BO), Forest Research Institute, Kepong, Malaysia (FRI), Leiden (L) and Oxford (FHO).

Samples of arils were preserved for phytochemical analysis in one of two ways. Some were dried, either in the sun or over gentle heat (60–80 °C) for two or more days; the length of time required for drying varied with the relative humidity of the surrounding atmosphere. Temperatures above 80 °C were not used, because this could result in the flesh's becoming too hard to prepare for analysis. There was no need to remove arils from the seeds before drying, except when they became so firmly attached to the seed on drying that they could no longer be separated from the seed. The dried samples were sealed in plastic containers with sachets of silica gel. The alternative to drying was to place the aril samples in 70 % aqueous ethanol on the day of collection. Because some substances may have leached from the arils into the ethanol solution in which they were preserved, this solution was retained with the arils for analysis.

When a high degree of accuracy in the analyses of sugars, amino acids, and fatty acids is required, the seeds should be immersed in boiling 96 % ethanol immediately after collection; this kills living tissue rapidly and reduces enzymic activity during death to a minimum (see Hladik 1977*b*).

Of the species analysed, the arils of *Aglaia oligocarpa*, *Lansium domesticum* and *Durio zibethinus* were dried and those of *Aglaia korthalsii* and *A. speciosa* were preserved in 70 % aqueous ethanol. The fruits of *Aglaia teysmanniana*, *A.* species 2, and *Tabernaemontana macrocarpa* had not originally been collected for the purpose of making phytochemical analyses and the material used had been preserved in the 'spirit' solution described above.

Appendix 2. Phytochemical analysis of aril tissue

Preliminary treatment of preserved material

In the laboratory, the dried aril samples were transferred to a vacuum desiccator and stored over silica gel for one week before analysis. Samples received in 70 % (by volume) aqueous ethanol were transferred to flasks; the ethanol was removed *in vacuo* (at less than 40 °C) with a rotary-film evaporator, and the remaining aqueous phase together with the arils was quick-frozen and then freeze-dried. Freeze-dried samples were stored in a vacuum desiccator over silica gel until analysis.

The high lipid content of most of the arils precluded milling or pulverizing the samples, so all samples were ground with a mortar and pestle. This produced an oily paste, of which 1 g was taken for analysis. The 1 g samples were extracted sequentially with: (i) chloroform: methanol (2:1 by volume) to remove lipophilic material; (ii) 85 % (by volume) aqueous ethanol to remove mono- and oligosaccharides, organic and amino acids; and (iii) boiling distilled water to remove starch.

Lipids

The lipid content of the aril samples was sufficiently high to be determined gravimetrically. The chloroform: methanol extracts were evaporated to dryness *in vacuo* (at less than 40 °C) with a rotary-film evaporator. The residue was then redissolved in chloroform and extracted twice with distilled water, retaining the aqueous phases for combining with the ethanolic extracts. The chloroform phases were transferred to pre-weighed flasks, evaporated to dryness *in vacuo* (at less than 40 °C) and stored in a vacuum desiccator over silica gel for 72 hours before reweighing.

For gas–liquid chromatographic analysis, samples of the extracted lipid material were saponified at 100 °C for 3 h with alcoholic KOH (100 g l^{-1} in 90% aqueous ethanol) then neutralized with HCl and evaporated to dryness. The residues were then treated at 100 °C for 1 h with a solution of methoxyamine hydrochloride, 20 g l^{-1} in pyridine, to form the methoxime derivatives of any ketoacids that might be present. After evaporation to near dryness, the samples were treated at 100 °C for 1 h with *N*,*O*-bis-(trimethylsilyl)-trifluoroacetamide (BSTFA) containing 1% trimethylchlorosilane to form the trimethylsilyl (TMS) derivatives. Samples were chromatographed with a Pye Unicam Series 204 gas–liquid chromatograph fitted with a flame ionization detector and a 50 m fused silica open tubular (FSOT) capillary column coated with OV-1. From these chromatograms, selected peaks were identified by means of a Finnigan 1020 gas chromatograph–mass spectrometer, by comparing the spectra of sample peaks with a data file and with a retention-time index.

Ethanol-soluble metabolites

The 85% aqueous ethanol extracts were combined with the water extracts of the chloroform-soluble fraction (see above), and the ethanol removed *in vacuo* (at less than 40 °C) by means of a rotary-film evaporator. The extracts were then brought to 5 ml final volume, from which 1 ml was removed from a colorimetric analysis of carbohydrates, 2 ml was removed for ion-exchange chromatography, and the remaining 2 ml was used for Kjeldahl nitrogen analysis.

Colorimetric analysis of carbohydrate

The 1 ml aliquot was treated with 1 ml of 100 g l^{-1} $ZnSO_4$ followed by 1 ml of 0.5 M NaOH to precipitate any proteins present. After centrifugation, the supernatant fractions were diluted to bring the carbohydrate concentrations within the range of the colorimetric method. Reducing sugar concentrations were determined by using a modification (Kozioł 1981) of the *para*-hydroxybenzoic acid hydrazide procedure of Lever (1972). The reaction mixture contained 0.05 ml of diluted sample, 0.1 ml of 0.05 M ammonium oxalate, 0.85 ml of distilled water and 2 ml of chromogen, prepared freshly by mixing equal volumes of 3 M NaOH with a solution of 2% (by mass) *para*-hydroxybenzoic acid hydrazide in 0.5 M HCl. After mixing, the reaction mixture was heated in a boiling water bath for five minutes, cooled in an ice–water bath for 30 s and absorbance read to 410 nm; the sensitivity range of the method was 1–16 μg reducing sugar per millilitre of sample.

Total free carbohydrates were estimated by hydrolysing an aliquot of the deproteinized sample. The hydrolysis mixture contained: 0.05 ml sample, 0.1 ml of 0.05 M ammonium oxalate, 0.1 ml 2.5 M H_2SO_4 and 1.65 ml distilled water. Samples were heated in a boiling water bath for 15 min. After cooling, 0.1 ml 5 M NaOH was added, the sample was mixed and the volume adjusted to 2 ml if necessary. A 1 ml portion of the hydrolysed sample was withdrawn and reacted with the *para*-hydroxybenzoic acid hydrazide chromogen. Di- and oligosaccharides were determined as the difference between the hydrolysed and unhydrolysed samples. The values obtained may not, however, be accurate estimates of the mono- and oligosaccharides present in the fresh fruits. The method used for preservation of the arils killed the tissues slowly, and enzymic hydrolysis of oligosaccharides to monosaccharides may have taken place during that time.

Ion-exchange chromatography

Neutral-fraction carbohydrates, organic and amino acids were separated by passing the samples (2 ml) from the ethanolic extracts first through a column containing 2 ml Dowex 50W-X8 (H^+, 100/200 mesh) and then through a column containing 2 ml Dowex 21 K (Cl^-,

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100/200 mesh). The columns were rinsed four times with 2 ml distilled water, adding the rinses to the eluate, which contained the neutral-fraction carbohydrates. A previous study had demonstrated the absence of any hydrolysis of sucrose on these strongly acidic and basic resins (Kozioł & Cowling 1980). Amino acids were eluted from Dowex 50 W-X8 resin with 10 ml of 2 M HCl. All eluates were collected in pear-shaped flasks for freeze-drying. Carbohydrate residues were redissolved in 1.0 ml 90% (by volume) aqueous ethanol and 0.5 ml portions were transferred to conical-ended test tubes containing D-glucoheptose as an internal standard for gas chromatographic analysis. The solutions were evaporated to a thick syrup at 70 °C under a stream of dry N_2. Amino acid residues were redissolved in 1.0 ml 0.5 M HCl and 0.5 ml portions transferred to conical-ended test tubes containing DL-pipecolic acid as an internal standard for chromatographic analysis. The amino acid solutions were then freeze-dried.

Carbohydrate analysis by gas chromatography

The neutral-fraction carbohydrates were silylated by means of a solution of trimethylsilyl-imidazole (TSIM) in pyridine (3:2 by volume) and heating the samples at 100 °C for 1 h. TMS-derivatized samples were analysed with the gas-chromatography system described above. Sugars were identified by co-chromatography and by their retention times.

Amino acid analysis by gas chromatography

Amino acids were analysed as their *O*-isobutyl, *N*-heptafluorobutyryl derivatives. Samples were esterified by adding 0.2 ml freshly-prepared isobutanol hydrochloride (made by mixing 0.4 ml acetyl chloride with 2 ml isobutanol at 0 °C) to each test tube and heating at 100 °C for 20 min. After the samples had been dried at 100 °C under a stream of dry N_2, 0.1 ml of heptafluorobutyric anhydride was added to each test tube and the samples heated at 100 °C for 20 min. The samples were then evaporated to near dryness at 60 °C under a stream of dry N_2, and redissolved in 0.3 ml ethyl acetate: acetic anhydride (2:1 by volume). All derivatization reactions were performed in test tubes sealed with PTFE-line caps.

Kjeldahl nitrogen determination

The 2 ml portions reserved for nitrogen determinations were transferred to 50 ml Kjeldahl flasks, frozen and freeze-dried. The residue was then digested with 3 ml concentrated H_2SO_4 with a titanium catalyst (as titanium catalyst tablets, BDH Chemicals Ltd, Poole, England). After steam distillation, the ammonia liberated was assayed by titration with HCl (Allen 1974).

Starch

Starch content was estimated gravimetrically. The boiling water extracts were reduced to 10 ml final volume in a rotary-film evaporator, and starch was precipitated by the addition of absolute ethanol. The starch was collected on pre-weighed filter papers. After collection, the starch and papers were oven-dried at 80 °C for 24 h and then transferred to a desiccator for 72 h before reweighing.

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Appendix 3. Scientific names of plants mentioned in the text, with authorities and, where available, citation of voucher specimens

All Pannell numbers are deposited in the Forest Herbarium, Oxford (FHO); for other specimens cited, the herbarium follows in parentheses.

Apocynaceae	
Stemmadenia donell-smithii (Rose) Woodson	
Tabernaemontana macrocarpa Jack	Pannell no. 1868, Sumatra (determined by A. J. M. Leeuwenberg, Wageningen)
Bombacaceae	
Durio zibethinus Murray	Pannell, fruit only, from market, Bukittinggi, Sumatra
Leguminosae	
Parkia biglobosa (Jacquin) R. Brown ex G. Don fil.	
Meliaceae	
Aglaia aff. *elaeagnoidea* (A. Jussieu) Bentham	Schmutz no. 3596, Flores, Lesser Sunda Islands (L)
A. elliptica Blume	Pannell no. 1242 (for field observations) Pannell no. 1871, Sumatra (for aril analysis)
A. ganggo Miquel	Pannell no. 1321, Malaysia (male flowers only)
A. korthalsii Miquel	Pannell no. 1972, Sumatra (for aril analysis). Rijksen nos 210574 and 20973
A. oligocarpa Miquel	Pannell nos 1575 and 1622 (for field observations), 1622 (for analysis), Peninsular Malaysia
A. odoratissima Blume	Pannell no. 1270, Peninsular Malaysia
A. ridleyi (King) Pannell	Wyatt Smith, Kep, 71015, Jarak Island (FRI)
A. rufibarbis Ridley	Pannell no. 1415, Peninsular Malaysia
A. speciosa Blume	Pannell no. 1993, Sumatra
A. teysmanniana Miquel	Pannell no. 1574, Peninsular Malaysia
A. species 2	Pannell no. 1175, FRI no. 25506 (FRI) (from same tree), Peninsular Malaysia
Aphanamixis polystachya (Wallich) R. N. Parker	
Chisocheton cumingianus (C. de Candolle) Harms	As *C. paniculatus* Hiern in Connolly *et al.* (1979) and Saikia *et al.* (1978)
Lansium domesticum Correa	Pannell, fruit only from market, Bukittinggi, Sumatra
Trichilia martiana C. de Candolle	as *T. cuneata* Radlkofer, in Foster & McDiarmid (1983)
T. prieuriana A. Jussieu	
Myristicaceae	
Knema conferta (King) Warburg	

K. aff. *oblongifolia* (King) Warburg	Pannell no. 1157, Peninsular Malaysia (determined by D. Philcox, Kew)
Virola sebifera Aublet	
V. surinamensis (Rolander) Warburg	
Strelitziaceae	
Strelitzia nicolai Regel & Koernicke	
Zingiberaceae	
Zingiber sp.	Pannell no. 1870B, Sumatra.

Appendix 4. Scientific names of vertebrates mentioned in the text, with authorities, the families to which they belong and common names

AVES: birds	
Bucerotidae	
Anthracoceros malayanus (Raffles)	black hornbill
Chloropseidae	
Aegithina viridissima (Bonoparte)	green iora
Capitonidae	
Calorhamphus fuliginosus (Temminck)	brown barbet
Megalaima mystacophanus (Temminck)	gaudy barbet
Casuariidae	
Casuarius casuarius (Linnaeus)	double-wattled cassowary
Columbidae	
Columba livia Gmelin	feral pigeon
Ducula bicolor Scopoli	pied imperial pigeon
Ptilinopus jambu (Gmelin)	Jambu fruit dove
Treron capellei (Temminck)	large green pigeon
Treron olax (Temminck)	little green pigeon
Corvidae	
Platysmurus leucopterus (Temminck)	black magpie
Cuculidae	
Phaenicophaeus chlorophaeus (Raffles)	Raffles malkoha
Dicaeidae	
Dicaeum chrysorrheum Temminck & Laugier	yellow-vented flowerpecker
Eurylaimidae	
Eurylaimus ochromalus Raffles	black and yellow broadbill
Calyptomena viridis Raffles	green broadbill
Paradisaeidae	
Paradisaea raggiana Sclater	Raggiana bird of paradise
Parotia lawesii Ramsay	Lawes' six-wired bird of paradise
Phasianidae	
Rollulus rouloul (Scopoli)	crested wood partridge
Pycnonotidae	
Criniger bres (Lesson)	scrub bulbul
Pycnonotus brunneus Blyth	red-eyed brown bulbul

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P. erythropthalmus (Hume)	lesser brown bulbul
P. finlaysoni (Strickland)	stripe-throated bulbul
P. melanoleucos (Eyton)	black and white bulbul
P. simplex Lesson	white-eyed brown bulbul
P. zeylanicus Gmelin	yellow-crowned-bulbul
Steatornithidae	
Steatornis caripensis Humboldt	oilbird
Sturnidae	
Gracula religiosa Linnaeus	hill myna
MAMMALIA: mammals	
Cercopithecidae: monkeys	
Macaca fasicularis (Raffles)	long-tailed or crab macaque
M. fuscata Blyth	Japanese macaque
Presbytis melalophus (Raffles)	banded leaf monkey
Hylobatidae: gibbons	
Hylobates lar (Linnaeus)	white-handed or Lar gibbon
Hylobates syndactylus (Raffles)	siamang
Pongidae: great apes	
Pan troglodytes troglodytes (Blumenbach)	chimpanzee
Pongo pygmaeus abelii Lesson	orang utan
Sciuridae: squirrels	
Callosciurus notatus (Boddaert)	plantain squirrel
C. prevostii (Desmarest)	Prevost's squirrel
Ratufa bicolor (Sparrmann)	black giant squirrel
R. affinis (Raffles)	cream-coloured or common giant squirrel
Sundasciurus hippurus (Geoffroy)	horse-tailed squirrel
Tupaiidae: tree shrews	
Tupaia glis (Diard)	common tree shrew
Viverridae: civets	
Paradoxurus hermaphroditus (Pallas)	common palm civet