Fruit characters in Malesian Euphorbiaceae

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Abstract

Esser, H.-J. (Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138, USA; current address: University of Hamburg, Institute of General Botany, Ohnhorststrasse 18, 22609 Hamburg, Germany). 2003. Fruit characters in Malesian Euphorbiaceae. Telopea *10 (1): 169–177.* It is argued that zoochory is more abundant in Malesian Euphorbiaceae than in any other tropical area, and probably played a more significant role in the diversification of the family in Malesia than elsewhere.

Introduction

The Euphorbiaceae are among the larger families of flowering plants with c. 300 genera and 8000 species (Webster 1994, Radcliffe-Smith 2001). They are usually recognised by their unisexual flowers and typical fruits, although a phylogenetic diagnosis with morphological characters is still difficult. Recent studies, using molecular characters, indeed indicate that they may not be monophyletic (Savolainen et al. 2000, among others).

For many anatomical and morphological characters, comparative studies have been published covering the whole family or at least some of the five subfamilies, summarised with detailed references by Webster (1994). This includes vegetative, floral and seed characters. The fruits, however, never received much attention, and were hardly discussed by Webster.

These fruits are superior, three-locular, dry schizocarps, dehiscing violently along the septa into three mericarps (‘cocci’); the mericarps consist of pericarp and two septal parts, and contain one or two dry seeds each, the seeds with or without a caruncle. The dispersal of Euphorbiaceae is usually considered to be autochorous by explosion of the ballistic fruits, and diplochorous in combination with myrmechory (Berg 1975 a, b).

It is often implied that fruits are quite uniform within the family (e.g., Dilcher & Manchester 1988). Nevertheless Berg (1975b) published the only detailed anatomical and morphological analysis of euphorbiaceous fruits. He found structures unique in flowering plants. They could be a strong argument for the possible monophyly of Euphorbiaceae. Unfortunately comparative studies throughout the family have never been published.

Fruit diversity

Fruit diversity can be studied under various viewpoints. There are clearly historical, phylogenetic aspects, such as the distinction in bi-ovulate and uni-ovulate Euphorbiaceae. Another aspect is the occurrence of fleshy or indehiscent fruits. The Philippine *Balakata luzonica* (Vidal) Esser, for instance, has one-seeded berry-like drupes and was originally described as a species of *Myrica* (Myricaceae), and was later re-described as Icacinaceae (Esser 1999).

The aim of this contribution is a comparison of the occurrence of fleshy diaspores between various tropical areas. In some Euphorbiaceae, the whole fruit becomes fleshy

and will attract animals (e.g., in *Antidesma* Burm. ex L.), whereas in others the dry fruit wall falls off easily, exposing fleshy and attractively coloured seeds (e.g., in *Sapium* Jacq. and *Triadica* Lour.). For the purpose of this study I will distinguish between 'typical' fruits of Euphorbiaceae (i.e., dry seeds and fruits, and most probably autochorous), and probable adaptations to zoochory (including fleshy or indehiscent fruits as well as fleshy seeds). In most cases, dispersers will probably be birds (ornithochory), but this will not be distinguished here.

The recognition of zoochory is sometimes difficult from herbarium collections alone, and it is also not strictly distinguished in nature. Several Euphorbiaceae have basically dry and woody fruits that show reddish colours and may be dispersed by birds if small enough, although not clearly adapted to ornithochory (observed in scattered field notes and herbarium labels).

Spiny-echinate fruits can be found in numerous genera in all tropical areas (such as *Mallotus* Lour. or *Chaetocarpus* Thwaites). These fruits are usually dry, which could indicate epizoochory, but could also be a protection of autochorous fruits against herbivory.

The absence or presence of a caruncle on the seeds is not analysed here. It has a probable phylogenetic background, because a caruncle is consistently absent in Phyllanthoideae but variable and often present in other subfamilies, without an obvious correlated distinction in ecology etc. between the subfamilies. It is also variable within numerous genera of the family (such as *Croton* L., *Euphorbia* L.), and it is therefore difficult to compare at the genus level.

Methods

Data on the generic diversity of Euphorbiaceae were extracted from published accounts for Malesia and three other tropical areas for which recent and reliable revisions are available. Cultivated, exotic taxa were omitted.

The family is currently under revision for Flora Malesiana, and data on diversity in Malesia (Table 1) are taken from the regularly updated Malesian Euphorbiaceae Newsletter (Welzen 1997, 2000), separate revisions cited therein, and own unpublished estimations for *Breynia, Croton* and *Euphorbia*. The species numbers exclude Thai taxa not known from Malesia.

Data for extra-Malesian regions were taken, unchanged, for Tropical East Africa (Table 2, after Carter & Radcliffe-Smith 1988, Radcliffe-Smith 1987), Costa Rica (Table 3, after Burger & Huft 1996), and the Venezuelan Guayana (Table 4, after Webster et al. 1999). These areas are much smaller than Malesia, and the focus is therefore not on absolute numbers of taxa.

Diaspores were distinguished into presumably autochorous and zoochorous. These data were extracted from the cited references and usually verified in the herbarium. For Malesia, however, a considerable part of the family has not been revised yet (more than 60 genera are listed as such by Welzen 2000), and here the data are based on own observations on herbarium specimens only.

Because of the mentioned uncertainties (ongoing studies of Malesian Euphorbiaceae, sometimes problematic classification of dispersal syndromes in certain genera) no further statistics will be applied, and the data should be understood as preliminary at this stage.

Results and Discussion

Although this study was mainly based on a compilation from available publications, it leads to some conclusions that have not been discussed much before. The comparison of Tables 1 to 4 shows a number of interesting patterns:

Although there is a considerable range of fruit types within Euphorbiaceae as a whole, only very few genera are variable in their fruit type: *Alchornea*, *Mallotus*, *Omphalea*, *Phyllanthus*, and *Shirakiopsis*. The largest ones of these (*Mallotus* and *Phyllanthus*) are probably unnatural in their present circumscription (Slik & Welzen 2001, K. Wurdack pers. comm.). *Alchornea* is mentioned here with some doubt because only in the Neotropics do the fruits tend to show a slightly fleshy pericarp, tardily dehiscent, but are not clearly zoochorous. Variation in dispersal syndrome as distinguished here is usually found above the genus level only.

In Malesia the proportion of genera and species with fleshy, presumably zoochorous diaspores is higher than in Africa or the Neotropics (Table 5). This difference is even more obvious in species numbers than in numbers of genera. Whereas in all regions compared more than 50% of all genera have dry and dehiscent fruits, it is only in Malesia that the majority of species of Euphorbiaceae has zoochorous diaspores.

A large proportion of the genera endemic to, or most diversified in, Malesia shows zoochory, in particular most of the largest Malesian genera (such as *Antidesma*, *Macaranga*). This is very different in the African and American regions compared, where the most species-rich genera have 'typical' dry schizocarps.

Most pantropical genera of Euphorbiaceae have dry, dehiscent fruits (such as *Acalypha*, *Croton*, *Euphorbia*, *Microstachys*) or are variable, with a large proportion of autochory (such as *Phyllanthus*). All of these are comparatively poorly diversified in Malesia, with the centre of diversity in other continents. The only pantropical zoochorous genera are *Drypetes* (which probably has to be excluded from the family, as discussed by, e.g., Wurdack & Chase 1996) and *Margaritaria* (which is the smallest of the pantropical genera with 14 species).

Webster (1994: 18, table 3) included a brief comparison between geography and dispersal type in genera of Euphorbiaceae, and concluded that ornithochory is prevalent in tropical Asia and in Africa / Madagascar in contrast to the other continents. His data could not be confirmed in the present contribution. At the genus level, autochory is prevalent on all continents, although there seems to be a difference between Old World and New World. The diversification of zoochorous Euphorbiaceae is however certainly more obvious in Malesia than in Africa when numbers of species are considered, as done here.

Schizocarps and autochory were most probably the plesiomorphic conditions in Euphorbiaceae (Webster 1994). It can therefore be postulated that zoochorous dispersal (in most cases probably ornithochory) played a significant and underestimated role in the evolution and diversification of Malesian Euphorbiaceae, much more than it did on other tropical continents.

This contribution is only a first and preliminary step in the comparative study of Euphorbiaceae fruits, focussing on one particular aspect. It is nevertheless apparent that additional studies are desirable. For instance, a more detailed distinction between forest and savanna ecosystems and their respective dispersal syndromes within the regions compared here might be interesting. A more detailed comparison of 'typical' dry schizocarps within the family will be undertaken in a forthcoming publication.

Table 1. Malesian genera of Euphorbiaceae and the presence of zoochorous diaspores. Nomenclature follows Radcliffe-Smith (2001). Genera are sorted according to their species number. a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type	Overall number of species	Distribution
175	***Macaranga***	**z**	280	Africa to Pacific Islands
150	***Glochidion***	**z**	300	Madagascar to Pacific Islands
108	*Phyllanthus*	v	800	pantropical
70	***Antidesma***	**z**	170	Africa to Pacific Islands
63	***Drypetes***	**z**	200	pantropical
61	*Mallotus*	v	150	Indopacific
60	***Claoxylon***	**z**	80	Madagascar to Indopacific
60	*Cleistanthus*	a/d	140	Africa to Pacific Islands
55	*Croton*	a/d	800	pantropical
52	***Aporosa***	**z**	80	India to Malesia
42	*Trigonostemon*	a/d	50–60	India to Australia
39	***Baccaurea***	**z**	43	India to Pacific Islands
30	*Euphorbia* (incl. *Chamaesyce*)	a/d	2000	worldwide
28	*Acalypha*	a/d	450	pantropical
21	***Breynia***	**z**	35	India to New Caledonia
15	*Actephila*	a/d	20	Australasia
15	***Bridelia***	**z**	60	Africa to Asia
14	*Codiaeum*	a/d	16	Malesia to Pacific Islands
12	***Homalanthus***	**z**	20	Malesia to Pacific Islands
12	***Ptychopyxis***	**z**	12	Thailand and Malesia
12	***Sauropus***	**z**	80	India to China and Australia
11	***Endospermum***	**z**	12	India to China and Australia
10	*Alchornea*	a/d	60	pantropical
10	*Dimorphocalyx*	a/d	20	India to Malesia
9	*Koilodepas*	a/d	10–12	India to China
8	*Cleidion*	a/d	25	pantropical
7	*Blumeodendron*	a/d	6	Burma to Malesia
6	***Galearia***	**z**	6	Burma to Malesia
6	*Neoscortechinia*	a/d	6	Burma to Malesia
6	***Suregada***	**z**	31	Africa to Asia
5	*Agrostistachys*	a/d	10	India to Malesia
5	*Cephalomappa*	a/d	6	China to Malesia
5	*Excoecaria*	a/d	35	Africa to Polynesia
5	*Jatropha*	a/d	175	pantropical
4	*Cnesmone*	a/d	12	Southeast Asia
4	*Omphalea*	v	20	pantropical
4	***Pimelodendron***	**z**	6–8	Malesia to Australia
3	***Distichirhops***	**z**	3	endemic
3	*Epiprinus*	a/d	6	India to Malesia
3	***Micrococca***	**z**	12	Africa to Asia
3	*Shirakiopsis*	v	6	Africa to Asia
3	*Trigonopleura*	a/d	3	endemic
2	***Aleurites***	**z**	2	India to Pacific Islands
2	***Ashtonia***	**z**	2	endemic
2	***Balakata***	**z**	2	India to Malesia
2	*Chondrostylis*	a/d	2	Thailand to Malesia
2	*Dalechampia*	a/d	110	pantropical

Number of species	Genus	Diaspore type	Overall number of species	Distribution
2	*Erismanthus*	a/d	2	Malesia to China
2	***Flueggea***	**z**	15	Paleotropics, temperate Eurasia
2	***Fontainea***	**z**	6	New Guinea to Australia
2	*Gymnanthes*	a/d	45	pantropical
2	*Lasiococca*	a/d	5	India to China
2	*Leptopus*	a/d	10	Asia, Australia, America
2	***Margaritaria***	**z**	14	pantropical
2	*Spathiostemon*	a/d	4	Thailand to Malesia
2	*Syndyophyllum*	a/d	2	endemic
2	*Wetria*	a/d	2	Burma to Malesia
1	*Alphandia*	a/d	3	Malesia to New Caledonia
1	*Annesijoa*	a/d	1	endemic
1	*Austrobuxus*	a/d	20	Malesia to Fiji and Australia
1	*Baliospermum*	a/d	12	India to China
1	***Bischofia***	**z**	1	Malesia to Pacific Islands
1	*Blachia*	a/d	15	India to Southeast Asia
1	*Borneodendron*	a/d	1	endemic
1	*Botryphora*	a/d	1	Burma to Malesia
1	*Chaetocarpus*	a/d	13	America, Madagascar, Asia
1	*Cheilosa*	a/d	1	endemic
1	*Choriceras*	a/d	2	New Guinea to Australia
1	***Chrozophora***	**z**	10	Mediterranean to East Asia
1	*Cladogynos*	a/d	1	Southeast Asia
1	*Clonostylis*	a/d	1	endemic
1	*Dicoelia*	a/d	1	endemic
1	***Doryxylon***	**z**	1	endemic
1	*Elateriospermum*	a/d	1	Thailand to Malesia
1	***Erythrococca***	**z**	50	mostly Africa
1	***Falconeria***	**z**	1	India to Malesia
1	***Homonoia***	**z**	2	India to Malesia
1	*Hymenocardia*	a/d	9	Africa to Asia
1	*Kairothamnus*	a/d	1	endemic
1	*Loerzingia*	a/d	1	endemic
1	***Megistostigma***	**z**	5	Burma to Malesia
1	***Melanolepis***	**z**	2	Malesia to Indochina
1	***Microdesmis***	**z**	10	Africa to Asia
1	*Microstachys*	a/d	17	pantropical
1	*Moultonianthus*	a/d	1	endemic
1	***Neotrewia***	**z**	1	endemic
1	***Octospermum***	**z**	1	endemic
1	*Ostodes*	a/d	1–3	Himalaya to Malesia
1	*Pachystylidium*	a/d	1	India to Malesia
1	*Paracroton*	a/d	3	India to Malesia
1	***Petalostigma***	**z**	6	New Guinea to Australia
1	*Plukenetia*	a/d	15	pantropical
1	*Reutalis*	a/d	1	endemic
1	*Richeriella*	a/d	2	Malesia to China
1	*Stillingia*	a/d	27	nearly pantropical
1	*Strophioblachia*	a/d	1	Malesia to China
1	***Sumbaviopsis***	**z**	1	India to Malesia
1	*Tapoides*	a/d	1	endemic
1	***Trewia***	**z**	1	India to China
1	***Triadica***	**z**	3	India to China
1	*Vernicia*	a/d	3	Burma to East Asia

Table 2. Genera of Euphorbiaceae in tropical East Africa and the presence of zoochorous diaspores. Genera are sorted according to their species number.
a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type
208	*Euphorbia*	a/d
52	*Phyllanthus*	v
30	*Acalypha*	a/d
27	*Tragia*	a/d
23	*Croton*	a/d
22	*Jatropha*	a/d
15	***Erythrococca***	**z**
10	***Drypetes***	**z**
8	***Bridelia***	**z**
8	***Macaranga***	**z**
7	*Clutia*	a/d
6	*Zimmermannia*	a/d
5	*Alchornea*	a/d
4	*Dalechampia*	a/d
4	***Micrococca***	**z**
3	***Caperonia***	**z**
3	*Meineckia*	a/d
3	*Pycnocoma*	a/d
3	***Suregada***	**z**
3	*Thecacoris*	a/d
3	*Tragiella*	a/d
2	*Argomuellera*	a/d
2	*Cephalocroton*	a/d
2	*Cleistanthus*	a/d
2	*Excoecaria*	a/d
2	***Maprounea***	**z**
2	*Neoboutonia*	a/d
2	***Oldfieldia***	**z**
2	***Ricinodendron***	**z**
2	*Spirostachys*	a/d
2	***Tetrorchidium***	**z**
1	*Andrachne*	a/d
1	*Aristogeitonia*	a/d
1	*Cavacoa*	a/d
1	***Chrozophora***	**z**
1	*Crotonogynopsis*	a/d
1	***Discoclaoxylon***	**z**
1	***Discoglypremna***	**z**
1	*Flueggea*	a/d
1	***Givotia***	**z**
1	*Heywoodia*	a/d
1	***Maesobotrya***	**z**
1	***Mallotus***	**z**
1	*Mareya*	a/d
1	***Margaritaria***	**z**
1	*Mildbraedia*	a/d
1	*Necepsia*	a/d
1	*Neoholstia*	a/d
1	*Omphalea*	a/d
1	*Paranecepsia*	a/d
1	*Pseudagrostistachys*	a/d
1	*Pseudolachnostylis*	a/d
1	*Savia*	a/d

Table 2 cont.

Number of species	Genus	Diaspore type
1	*Sclerocroton*	a/d
1	*Shirakiopsis*	a/d
1	***Sibangea***	**z**
1	*Spondianthus*	a/d
1	*Tannodia*	a/d

Table 3. Genera of Euphorbiaceae in Costa Rica and the presence of zoochorous diaspores. Genera are sorted according to their species number.
a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type
32	*Croton*	a/p
32	*Euphorbia* (incl. *Chamaesyce*)	a/p
19	*Acalypha*	a/p
13	*Phyllanthus*	v
10	*Dalechampia*	a/p
6	*Jatropha*	a/p
6	***Sapium***	**z**
5	*Alchornea*	v
4	***Tetrorchidium***	**z**
4	*Manihot*	a/p
3	***Cnidoscolus***	**z**
3	***Drypetes***	**z**
3	*Mabea*	a/p
3	*Tragia*	a/p
2	*Bernardia*	a/p
2	***Caperonia***	**z**
2	*Gymnanthes*	a/p
2	***Hieronyma***	**z**
2	*Plukenetia*	a/p
1	*Acidoton*	a/p
1	*Actinostemon*	a/p
1	*Adelia*	a/p
1	*Adenophaedra*	a/p
1	***Alchorneopsis***	**z**
1	*Amanoa*	a/p
1	*Aparisthmium*	a/p
1	*Argythamnia*	a/p
1	*Astrocasia*	a/p
1	*Caryodendron*	a/p
1	*Conceveiba*	a/p
1	*Dysopsis*	a/p
1	*Garcia*	a/p
1	***Hippomane***	**z**
1	*Hura*	a/p
1	***Margaritaria***	**z**
1	*Microstachys*	a/p
1	*Omphalea*	v
1	*Pausandra*	a/p
1	*Pedilanthus*	a/p
1	*Pera*	a/p
1	***Richeria***	**z**
1	*Sagotia*	a/p
1	*Stillingia*	v

Table 4. Genera of Euphorbiaceae in the Venezuelan Guayana and the presence of zoochorous diaspores. Genera are sorted according to their species number.
a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type
45	*Croton*	a/d
43	*Phyllanthus*	v
15	*Mabea*	a/d
14	*Dalechampia*	a/d
11	*Euphorbia* (incl. *Chamaesyce*)	a/d
9	*Acalypha*	a/d
7	*Micrandra* (incl. *Cunuria*)	a/d
6	*Amanoa*	a/d
6	*Manihot*	a/d
6	*Pera*	a/d
5	*Alchornea*	v
5	*Plukenetia* (incl. *Apodandra*)	a/d
4	*Conceveiba*	a/d
4	*Hevea*	a/d
4	***Sapium***	**z**
3	*Discocarpus*	a/d
2	*Actinostemon*	a/d
2	*Dendrothrix*	a/d
2	***Drypetes***	**z**
2	***Hieronyma***	**z**
2	*Jatropha*	a/d
2	***Maprounea***	**z**
2	*Piranhea*	a/d
2	*Sagotia*	a/d
2	*Sandwithia*	a/d
2	*Senefelderopsis*	a/d
2	*Tragia*	a/d
1	*Acidoton*	a/d
1	*Adelia*	a/d
1	*Adenophaedra*	a/d
1	***Alchorneopsis***	**z**
1	*Aparisthmium*	a/d
1	*Astrococcus*	a/d
1	*Bernardia*	a/d
1	***Caperonia***	**z**
1	*Celianella*	a/d
1	*Chaetocarpus*	a/d
1	***Cnidoscolus***	**z**
1	*Ditaxis*	v
1	*Gavarretia*	a/d
1	***Glycydendron***	**z**
1	*Gymnanthes*	a/d
1	*Haematostemon*	a/d
1	*Hura*	a/d
1	***Jablonskia***	**z**
1	***Margaritaria***	**z**
1	*Microstachys*	a/d
1	*Omphalea*	a/d
1	*Pausandra*	a/d
1	*Pedilanthus*	a/d
1	*Podocalyx*	a/d
1	*Pogonophora*	a/d
1	*Pseudosenefeldera*	a/d
1	***Richeria***	**z**
1	*Savia*	a/d
1	***Tetrorchidium***	**z**

Table 5. Numerical comparison of fleshy (incl. indehiscent) diaspores between different tropical regions, summarising Tables 1–4.

	Malesia	Tropical East Africa	Costa Rica	Venezuelan Guayana
Total number of genera	101	59	44	56
Total number of species	1288	494	177	238
Genera with dry fruits and seeds	58 (= 57.4%)	39 (= 66.1%)	32 (= 72.7%)	42 (= 75%)
Species with dry fruits and seeds	371 (= 28.8%)	375 (= 75.9%)	135 (= 76.3%)	173 (= 72.7%)
Genera with fleshy fruits/seeds	39 (= 38.6%)	19 (= 32.2%)	10 (= 22.7%)	12 (= 21.4%)
Species with fleshy fruits/seeds	741 (= 57.5%)	67 (= 13.6%)	24 (= 13.6%)	17 (= 7.1%)
Variable genera	4	1	2	2
Species of variable genera	176	52	18	48

Acknowledgments

This work was supported by a Mercer Fellowship from the Arnold Arboretum, Harvard University. It was based mainly on the herbarium collections of the Harvard University Herbaria (A, GH).

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