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Phylogenetic Distribution and Identification of Fin-winged Fruits

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Abstract Fin-winged fruits have two or more wings aligned with the longitudinal axis like the feathers of an arrow, as exemplified by *Combretum*, *Halesia*, and *Ptelea*. Such fruits vary in dispersal mode from those in which the fruit itself is the ultimate disseminule, to schizocarps dispersing two or more mericarps, to capsules releasing multiple seeds. At least 45 families and more than 140 genera are known to possess fin-winged fruits. We present an inventory of these taxa and describe their morphological characters as an aid for the identification and phylogenetic assessment of fossil and extant genera. Such fruits are most prevalent among Eudicots, but occur occasionally in Magnoliids (Hernandiaceae: *Illigera*) and Monocots (*Burmannia*, *Dioscorea*, *Herreria*). Although convergent in general form, fin-winged fruits of different genera can be distinguished by details of the wing number, texture, shape and venation, along with characters of persistent floral parts and dehiscence mode. Families having genera with fin-winged fruits and epigynous perianth include Aizoaceae, Apiaceae, Araliaceae, Asteraceae, Begoniaceae, Burmanniaceae, Combretaceae, Cucurbitaceae, Dioscoreaceae, Haloragaceae, Lecythidiaceae, Lophopyxidaceae, Loranthaceae, and Styracaceae. Families with genera having fin-winged fruits and hypogynous perianth include Achariaceae, Brassicaceae, Burseraceae, Celastraceae, Cunoniaceae, Cyrillaceae, Fabaceae, Malvaceae, Melianthaceae, Nyctaginaceae, Pedaliaceae, Polygalaceae, Phyllanthaceae, Polygonaceae, Rhamnaceae, Salicaceae sl, Sapindaceae, Simaroubaceae, Trigoniaceae, and Zygophyllaceae. This survey has facilitated the identification of fossil winged fruits such as Combretaceae and Araliaceae in the late Cretaceous of western North America and provides additional evidence toward the identification of various Cenozoic fossils including Brassicaceae, Fabaceae, Polygonaceae, Rutaceae, and Sapindaceae.

Keywords Fin-winged fruits · Angiosperm · Phylogeny · Fossil · Cretaceous · Tertiary

Introduction

Winged fruits occur in numerous genera scattered through at least 93 families of flowering plants (Dallwitz et al., 2000 onwards). The wings of wind-dispersed fruits take various configurations and may be formed from different structures including

outgrowths of the ovary, hypanthium, perianth parts, and/or bracts. Various morphological categories of winged fruits can be distinguished, such as those with an apical or basal whorl of two or more propeller-like wings (e.g., *Dipterocarpus*, *Astronium*), those with a single encircling wing (e.g., *Asteranthos*, *Cyclocarya*, *Dioncophyllum*, *Paliurus*), and those with a single extended wing (e.g., *Fraxinus*, *Triplochiton*, *Ventilago*). The configuration of wings influences aerodynamic efficiency and mode of falling (Augsburger, 1988). There is no single source for comparative data on genera with winged fruits and not even a comprehensive worldwide list. A survey and identification guide for asymmetrically winged fruits, e.g., *Acer* and *Heteropterys*, was published by Mirle and Burnham (1999). It was accompanied by line diagrams to aid in keying out unknown specimens, but did not include photographic images, and was limited in scope to the Americas.

Here we survey fruits that have two or more lateral wings aligned with the longitudinal axis like the feathers of an arrow. Such fruits were referred to as "tumblers" by Augsburger (1988) in relation to flight pattern, as "finned" by Matlack (1987) and as "cyclically winged" by Wurdak et al. (2004). The wings are usually symmetrical with one another about the central axis. We prefer the term "fin-winged" because "tumblers" refers to flight behavior rather than morphology and "cyclically winged" could also refer to the propeller type of fruit with wings radiating in a cycle transverse to the long axis. Fin-winged fruits vary in their mode of dispersal. In some cases the entire fruit is the unit of dispersal and in others the fruits are dehiscent as capsules that shed multiple seeds, or schizocarpic, falling into separate winged mericarps at maturity. Some of the capsular fruits open completely to shed the seeds, sometimes with individual seeds adhering to the valves as they shed; others remain attached to the twig and dehisce their seeds as the fruit is shaken by the wind. The fins (or wings) may be derived from ovary outgrowth, perianth, hypanthium, or bract elaboration. We have excluded from this treatment schizocarpic fruits with laterally extended mericarp wings, e.g. *Acer*, because they also fall into the separately treated category asymmetrically winged fruits (Mirle & Burnham, 1999).

Fossil winged fruits are commonly preserved together with fossil leaves and other debris in Cenozoic lake and pond deposits (e.g., Burnham, 1995; Wilde & Frankenhäuser, 1998; Manchester, 2001). As angiosperm reproductive structures, fruits possess diagnostic features that make them especially useful in taxonomy (Tiffney, 1990). Winged fruits have many characters potentially useful for identification including size, number of wings, patterns of wing venation, wing shape and position, persistence of style(s) and pedicel, placentation type, seed number and orientation, position of micropyle and raphe, and epidermal anatomy. Nevertheless, many fossil winged fruits have eluded identification, partly due to inadequate comparative data on extant fruits. If a fossil does not match a known extant genus, it may be extinct, or it may correspond to an extant genus with which the investigator is unfamiliar. This lack of familiarity is more likely when the fossil occurrences are outside the present-day geographic range of the taxon. For example, winged fruits of *Craigia*, a genus now confined to eastern Asia, occur in the Tertiary of North America and Europe, but the fossils were formerly considered to represent an extinct genus, *Pteleaecarpum* Weyland (Bůžek et al., 1989), until identity with living *Craigia* was discovered (Kvaček et al., 1991). Many kinds of winged fruits from the Tertiary still have not been identified. Difficulty in assessing the familial

and generic affinities of fossil fruits is largely due to the inaccessibility of comparative data on extant genera (Tiffney, 1990). A thorough understanding of the morphology of extant genera is fundamental for the identification of both extant and extinct kinds of winged fruits in the fossil record.

To aid in taxonomic identifications and in systematic and phylogenetic investigations, we present here descriptions and photographic images of genera with the fin-winged morphology representing all families in which such fruits are known to us. These descriptions allow comparisons to be made to understand the phylogenetic distribution of different morphological types, and will help with the identification of unknown specimens, whether extant specimens in the field or herbarium or fossil specimens. We conclude by presenting some fossil examples whose familial and generic assignments are critiqued with attention to the comparative data summarized for extant fruits.

Materials and Methods

A list was compiled of genera known to include fin-winged fruits from floristic and taxonomic literature and internet sources. The fruit morphology of genera in this list was verified when possible by examination and imaging of specimens in herbaria. Taxonomy was updated to the APG system (APG III, 2009; Soltis et al., 2005). We did not include genera in which the planes of the wing are oblique to the central axis, for example *Pterocarya* and many Malpighiaceae, nor those considered to represent asymmetrical winged samaras (Mirle & Burnham, 1999). Although we have included some fruits with paired wings, symmetrical about the axis, within our concept of "fin-winged", those with asymmetrical development, e.g., *Ulmus* and *Eucommia* (with the vascular strand running along one side of the locular area), did not fall within our scope.

Fruits were examined and photographed with a Nikon Coolpix digital camera with reflected lighting to reveal external morphology and/or transmitted light from a light table to reveal venation patterns. Specimens were studied at the Gray (GH) and Arnold Arboretum (A) Herbaria at Harvard University, Cambridge, MA, the US National Museum at the Smithsonian Institution (US), Washington DC, the Missouri Botanical Garden (MO), St. Louis, MO, the University of Florida herbarium (FLAS), the United States National Seed Herbarium (BARC; formerly at the Beltsville Agricultural Research Center, now housed at the National Arboretum), Washington, DC, and from living collections of the Morton Arboretum, Lisle, Illinois. When specimens in the BARC collection had been obtained from other herbaria, the source herbarium with the voucher sheet is also cited (e.g., L = Leiden; K = Kew; W = Naturhistorisches Museum, Vienna). Additional images from African herbaria were studied using the collaborative internet resource, ALUKA. Fossil specimens cited are from the paleobotanical collections of the Florida Museum of Natural History (UF), Gainesville, FL, University of California Museum of Paleontology (UCMP), Berkeley, CA, University of Michigan Museum of Paleontology (UM), Ann Arbor, MI, the US National Museum of Natural History (USNM), Washington, DC, Field Museum of Natural History (FMNH), Chicago, Peabody Museum, Yale University (YPM), New Haven, CT, Florissant Fossil Beds National Monument

(FLFO), Colorado, the College of Idaho (CI), Caldwell, ID, the University of Colorado (UC), Boulder, CO, Hungarian Natural History Museum, Budapest (BP), National d'Histoire Naturelle de Paris (MNHNP), and the Natural History Museum, London (BM).

The observed specimens and detailed images were used to assess important morphological characters for these genera (O'Leary, 2007). Taxonomic literature (e.g., Goldberg, 1986; Hutchinson, 1964; Judd et al., 2007) was consulted to help with interpretation of observed characters. Fruits were categorized by the number of wings, number of carpels, mode of dispersal and/or dehiscence, ovary position, overall shape, wing texture, venation patterns, and accessory parts (such as disk scar, and persistent styles). Geographic distribution information and numbers of species in the genera are based on the compilation of Mabberley (2002) unless otherwise indicated.

Although some of the fruits discussed here qualify as samaras, being single-seeded and indehiscent, with the wing developed from the ovary, many do not fit the strict definition because of the presence of multiple seeds. We use the term "samaroid" in application to fruits that are similar to samaras in being indehiscent and having the wing developed from ovary (rather than perianth or bracts), but which may possess more than one seed. We apply the term "capsule" to fruits that open to shed seeds. If the seeds are forcibly ejected when ripe, as in *Begonia*, the term "ballistic" may be applied. If the fruit falls into separate units, each containing one or more seeds, it is termed "schizocarpic," with the separated units termed "mericarps." Fruit sizes are variable within and among species of each genus, but are useful, in combination with other characters, in the identification process. The length and width specified in Table 1 are based on measurements of selected fruits from herbarium collections.

Venation patterns on the wings are described with some of the terms commonly applied in leaf architecture from Hickey (1973) and Ellis et al. (2009). The term craspedodromous is applied to veins that extend across the wing and terminate directly at the wing margin. Veins are considered brochidodromous when adjacent veins join to form loops near the margin, or festooned brochidodromous if a series of successively smaller loops occurs as veins approach the wing margin. The smallest areas outlined by veins, referred to as areoles, may be described in terms of shape, size, orientation and presence or absence of freely ending veinlets. We recognize three predominant patterns of venation common in fruit wings: 1) "simple subparallel," dominated by veins of a single order, occasionally dichotomizing and anatomizing with or without cross veins, usually delimiting elongate areoles, sometimes with an extremely fine intervening reticulum of isodiametric areoles; 2) "fusiform-reticulate, subparallel" with a single order of very fine veins that regularly dichotomize and anatamose to form a uniform network of fusiform areoles, and 3) "complex reticulate," with veins forming reticulum of multiple vein orders, with the main veins giving rise to successively finer veins, commonly with arches and with more or less isodiametric quadrangular to polygonal areoles, occasionally with freely ending veinlets. The wings of some taxa lack veins altogether, but may still show striation patterns due to the arrangement of fibers within the wing. Vein density was measured at right angles to the trend of venation in a section midway between the center of the fruit and its lateral margin, computed based on the number of veins intercepted by a 5 mm transect. The presence or absence of a fimbrial (= marginal)

Table 1 Genera with Fin-winged Fruits Organized Phylogenetically Families and Orders of the APG System, Comparing Selected Morphological Characters

Superordinal ranks	Order	Family	Genus	Wings	Fruit type	Ovary position	Length/Width cm[a]
Magnoliidae	Laurales	Hernandiaceae	*Illigera*	2(4)	samaroid	inf.	3.6/6.9
Monocotyledonae	Asparagales	Ruscaceae	*Beaucarnea*	3	samaroid	sup.	0.9/0.9
"	"	"	*Dasylirion*	3	samaroid	sup.	0.7/0.6
"	"	Herreriaceae	*Herreria*	3	capsule	sup.	1.2/1.0
"	Dioscoreales	Burmanniaceae	*Burmannia*	3	capsule	inf.	0.6/0.4
"	"	Dioscoreaceae	*Avetra*	3	samaroid	inf.	4.0/1.7
"	"	"	*Dioscorea*	3	capsule	inf.	1.5/1.5
"	"	"	*Trichopus*	3	samaroid	inf.	
Eudicot	Caryophyllales	Aizoaceae	*Tetragonia*	3–4	samaroid	inf.	1.7/1.7
"	"	Chenopodiaceae	*Atriplex*	4	pseudosamara	sup.	1.0/1.2
"	"	Nyctaginaceae	*Abronia*	2–5	pseudosamara	sup.	0.6/0.63
"	"	"	*Ammocodon*	4–5	pseudosamara	sup	0.43/0.43
"	"	"	*Phaeoptilum*	4	pseudosamara	sup.	1.5–2.5/1.2–2.0
"	"	"	*Selinocarpus*	5	pseudosamara	sup.	0.7/7.0
"	"	"	*Tripterocalyx*	2–4	pseudosamara	sup.	2.0/1.4
"	"	Polygonaceae	*Calligonum*	4	pseudosamara	sup.	1.2/1.0
"	"	"	*Fallopia*	3	pseudosamara	sup.	1.0/0.5
"	"	"	*Neomillspaughia*	3	pseudosamara	sup.	0.62/0.5
"	"	"	*Oxyria*	2	pseudosamara	sup.	0.2/0.2
"	"	"	*Parapteropyron*	3	pseudosamara	sup.	0.7/0.67
"	"	"	*Podopterus*	3	pseudosamara	sup.	1.5/0.8
"	"	"	*Polygonella*	3	pseudosamara	sup.	0.2/0.13
"	"	"	*Pteropyrum*	3	pseudosamara	sup.	0.7/0.5

Table 1 (continued)

Superordinal ranks	Order	Family	Genus	Wings	Fruit type	Ovary position	Length/Width cm[a]
"	"	"	*Pteroxygonum*	3	pseudosamara	sup.	0.8/0.6
"	"	"	*Rheum*	3	pseudosamara	sup.	1.8/1.6
"	"	"	*Rumex*	3	pseudosamara	sup.	0.8–2.3/0.5–3.0
"	Santalales	Loranthaceae	*Nuytsia*	3	samaroid	inf.	1.0/0.8
"	Saxifragales	Haloragaceae	*Haloragis*	4	samaroid	inf.	0.5/0.36
"	"	"	*Glischrocaryon*	2–4	samaroid	inf.	0.5/0.3–0.6/0.4
Eudicot/Rosids	Myrtales	Combretaceae	*Anogeissus*	2	samaroid	inf.	0.5/0.6
"	"	"	*Combretum*	2–5	samaroid	inf.	2.3/3.0, 2.3/2.1
"	"	"	*Dansiea*	4	pseudosamara	inf.	/2.01.6
"	"	"	*Macropteranthus*	4	pseudosamara	inf.	2.2/1.6
"	"	"	*Pteleopsis*	2	pseudosamara	inf.	2.0/1.5
"	"	"	*Terminalia*	2,4,5	pseudosamara	inf.	2.8/5.6
"	"	Onagraceae	*Oenothera*	4	capsule salt-shaker	inf.	3.5–5.0/1.8–4.0
Eudicot/Fabids	Celastrales	Celastraceae	*Platypterocarpus*	4–5	samaroid	sup.	2.7/3.4
"	"	"	*Stackhousia*	3–5	schizocarp	sup.	1.5/1.0
"	"	"	*Tripterococcus*	2–4	samaroid	sup.	0.7/0.6
"	"	"	*Tripterygium*	3	samaroid	sup.	1.2/1.0, 1.6/1.4
"	"	"	*Wimmeria*	2–3–(4)	samaroid	sup.	1.2/1.8, 4.0/3.2
"	Fagales	Nothofagaceae	*Nothofagus*	2–3	winged nut	inf.	0.45/0.40
"	Malpighiales	Achariaceae	*Carpotroche*	6–20	capsule	sup.	7.8/7.1
"	"	"	*Grandidiera*	4–8	samaroid	sup.	1.3/2.5
"	"	Phyllanthaceae	*Hymenocardia*	2	schizocarpic	sup.	2.3/1.9
"	"	Podostemaceae	*Winklerella*	2	capsule	sup	0.3/0.2

"	"	Salicaceae	*Neopringlea*	3	samaroid	sup.	0.7/0.5
"	"	Trigoniaceae	*Humbertiodendron*	3	samaroid	sup.	2.5/2.3
"	"	"	*Trigoniastrum*	3	schizocarp	sup.	4.2/3
"	"	Lophopixidaceae	*Lophopyxis*	5	samaroid	sup.	3.0/1.5
"	"	Violaceae	*Anchietea*	3	capsule	sup.	4.0/3.0
"	Oxalidales	Cunoniaceae	*Gillbeea*	3	samaroid	sup.	1.6/1.0
"	Zygophyllales	Zygophyllaceae	*Bulnesia*	5	capsule	sup.	1.6–4.0/1.3–4.0
"	"	"	*Guaiacum*	2–5	capsule	sup.	1.7–1.2
"	"	"	*Morkillia*	4	capsule	sup.	3.5–3.7/2.0–2.5
"	"	"	*Zygophyllum*	5	capsule	sup.	2.0–3.0/2.5–3.0
"	Cucurbitales	Begoniaceae	*Begonia*	3	lcapsule	inf.	2.0/1.9
"	"	Cucurbitaceae	*Pseudosicydium*	2	samaroid	inf	4.0′5.0
"	"	"	*Pteropepon*	2	samaroid	inf.	1.3/1.2
"	"	"	*Sechiopsis*	2–4	samaroid	inf.	1.8/1.3
"	Fabales	Fabaceae	*Fissicalyx*	2	samaroid	sup.	5.5/4.5–6.0/5.3
"	"	"	*Piscidia*	4	samaroid	sup.	5.5/4.0, 2.5/4.0
"	"	"	*Tetrapterocarpon*	4	samaroid	sup.	3.2/2.3
"	"	Polygalaceae	*Monnina*	2	samaroid	sup.	0.8/0.8
"	"	"	*Phlebotaenia*	2	samaroid	sup.	3.9/2.4
"	"	"	*Polygala*	2	samaroid	sup.	1.0/0.65
"	"	Rhamnaceae	*Crumenaria*	3	schizocarp	sup.	0.63/0.7
"	"	"	*Gouania*	3	schizocarp	sup.	0.9–1.4/1.0–1.1
"	"	"	*Reissekia*	3	schizocarp	sup.	0.8/1.3
Eudicot/Malvids	Geraniales	Melianthaceae	*Melianthus*	4	capsule	sup.	2.4/1.6
"	Brassicales	Brassicaceae	*Brossardia*	2	samaroid	sup.	2.9/2.5
"	"	"	*Fortuynia*	2	samaroid	sup.	2.1/1.3
"	"	"	*Isatis*	2	schizocarpic	sup.	1.5/0.5

Table 1 (continued)

Superordinal ranks	Order	Family	Genus	Wings	Fruit type	Ovary position	Length/Width cm[a]
"	"	"	*Psychine*	2	samaroid	sup.	0.7/1.4
"	"	"	*Sameraria*	2	samaroid	sup.	1.6/1.4
"	"	"	*Schouwia*	2	schizocarp	sup.	1.2/1.3
"	"	"	*Thlaspi*	2	capsule	sup.	1.4/1.4
"	"	Tropaeolaceae	*Tropaeolum*	3	schizocarp	sup.	1.4/1.3
"	"	"	*Magallana*	3	samaroid	sup.	1.6/1.3
"	Malvales	Malvaceae sl	*Abroma*	5	capsule	sup.	4.0–5.0/6.0
"	"	"	*Berrya*	5	capsule	sup.	2/4
"	"	"	*Burretiodendron*	5	capsule	sup.	4.0/2.5
"	"	"	*Cavanillesia*	5	samaroid	sup.	12/14
"	"	"	*Colona*	2–5	pseudosamara or schizocarpic"	sup.	1.7/1.9
"	"	"	*Craigia*	5	capsule	sup.	3.1/2.3
"	"	"	*Kleinhovia*	5	capsule	sup.	1.4/2.3
"	"	"	*Maxwellia*	3–4(–5)	samaroid	sup.	3.0/2.3
"	"	"	*Pentace*	3,5,10	samaroid	sup.	1.7/1.0
"	Sapindales	Sapindaceae	*Bridgesia*	3	capsule	sup	1.6/2.2
"	"	"	*Dodonaea*	3-2	capsule	sup.	1.5/1.7
"	"	"	*Koelreuteria*	3	capsule	sup.	4.8/4.5
"	"	"	*Paulinia*	3	capsule	sup	1.6/1.6
"	"	"	*Boniodendron*	3	capsule	sup.	1.7/1.9
"	"	"	*Stocksia*	?	capsule	sup.	2.9/3.0
"	"	"	*Toulicia*	3	capsule	sup.	
"	"	"	*Urvillea*	2	capsule	sup.	3.6/1.7

"	"	Simaroubaceae	*Soulamea*	2	samaroid	sup.	1.7/2.3
"	"	Rutaceae	*Balfourodendron*	4	samaroid	sup.	4.3/6.2
"	"	"	*Bottegoa*	2	samaroid	sup.	3.5/3.5
"	"	"	*Ptelea*	2–3	samaroid	sup.	2.1/2.4
"	"	"	*Spathelia*	2–3	samaroid	sup.	2.1/1.4,1.7/3.8
Eudicot/Asterid	Ericales	Cyrillaceae	*Cliftonia*	1–2	samaroid	sup.	0.5/0.5
"	"	Lecythidiaceae	*Petersianthus*	3–4	samaroid	inf.	4.8/4.2, 5.1/6.1
"	"	Styracaceae	*Halesia*	2 or 4	samaroid	inf.	3.7/1.7
Eudicot/Campanulids	Apiales	Apiaceae	*Annesorhiza*	7	schizocarp	inf.	0.5/0.35
"	"	"	*Asteriscium*	4	schizocarp	inf.	0.4/0.2
"	"	"	*Dasispermum*	10	schizocarp	inf.	11/8
"	"	"	*Elaeoselinum*	4	schizocarp	inf.	1.2/1.1
"	"	"	*Heracleum*	4	schizocarp	inf.	1.0/0.72
"	"	"	*Hermas*	4	schizocarp	inf.	0.4/0.4
"	"	"	*Heteromorpha*	5	schizocarp	inf.	0.5/0.15
"	"	"	*Laretia*	4	schizocarp	inf.	1.4/1.2
"	"	"	*Lomatium*	4	schizocarp	inf.	2.3/1.3
"	"	"	*Molopospermum*	5	schizocarp	inf.	0.8/0.2
"	"	"	*Pachypleurum*	10	schizocarp	inf.	0.5/0.36
"	"	"	*Peucedanum*	4	schizocarp	inf.	1.0–0.9
"	"	"	*Polemanniopsis*	5	schizocarp	inf.	
"	"	"	*Prangos*	5	schizocarp	inf.	2.2/1.35
"	"	"	*Steganotaenia*	2	schizocarp	inf.	1.0/0.72
"	"	"	*Thapsia*	8	schizocarp	inf.	1.1/0.7
"	"	Araliaceae	*Astrotricha*	4	schizocarp	inf	1.5/1.2
"	"	Myodocarpaceae	*Myodocarpus*	4	schizocarp	inf.	1.1/0.0
"	Aquifoliales	Cardiodipteraceae	*Cardiodipteris*	2	samaroid	sup.	2.8/2.4, 3.5/2.8

Table 1 (continued)

Superordinal ranks	Order	Family	Genus	Wings	Fruit type	Ovary position	Length/Width cm[a]
Eudicot/Lamiids	Gentianales	Apocynaceae	*Cameraria*	2	samaroid	sup.	2.8/1.2
"	"	"	*Cerberiopsis*	2	samaroid	sup.	
"	Lamiales	Pedaliaceae	*Holubia*	4	samaroid	sup.	5.4/5.3
"	"	"	*Pterodiscus*	4	samaroid	sup.	3.1 to 3.3/3.1–3.4
"	"	Oleaceae	*Abeliophyllum*	2	samaroid	sup.	3/2
"	"	"	*Fontanesia*	2	samaroid	sup.	0.8/0.6
"	"	Verbenaceae	*Hymenopyramis*	4	capsule	sup.	1.0/0.7
Eudicot/Euasterid	Asterales	Asteraceae	*Anacyclus*	2	samaroid	inf.	3.2/2.0
"	"	"	*Boltonia*	2	samaroid	inf.	9.5/7.2
"	"	"	*Brachyscome*	2	samaroid	inf.	0.23/0.20
"	"	"	*Coreopsis*	2	samaroid	inf.	0.29/0.37, 0.35/0.2
"	"	"	*Dichaetophora*		samaroid	inf.	0.015/0.014
"	"	"	*Dipterocypsela*	2	samaroid	inf.	
"	"	"	*Hyoseris*		samaroid	inf.	0.9/0.3
"	"	"	*Inuloides*	3	samaroid	inf.	2.1/1.6

"	"	"	*Ixeris*	10	samaroid	inf.	
"	"	"	*Monoculus*	3	samaroid	inf.	1.8/1.5
"	"	"	*Norlindhia*	3	samaroid	inf.	
"	"	"	*Olivaea*	2	samaroid	inf.	0.30/0.27
"	"	"	*Silphium*	2	samaroid	inf.	1.0/0.6
"	"	"	*Tripteris*	3	samaroid	inf.	2/1.6
"	"	"	*Verbesina*	2	samaroid	inf.	0.53/0.4
"	"	"	*Wedelia*	2	samaroid	inf.	0.5/0.25

[a] The length and width are maximum measurements including the wings but excluding stipe, pedicel and style. These are example measurements estimated to be representative, but they are not intended to indicate the full range in size for the genus

vein, is noted based on observations by transmitted light. In some instances what we have described as a fimbrial vein might instead be an unvascularized marginal thickening. Anatomical preparations to verify vascularization were not done for this survey. Margins of the wings are entire (smooth), unless otherwise stated.

Results

We examined more than 140 genera with fin-winged fruits (Table 1). Examples are described in the following section, in alphabetical sequence of the families to which they belong, and summarized in phylogenetic sequence in Table 1. Fruit dimensions are excluded from the descriptive text but are indicated in Table 1. This fruit type is found on every continent except Antarctica, and ranges from desert (*Macropteranthus*) to rainforest (*Cavanellesia*) to alpine (*Oxyria*) habitat. They are borne on trees (e.g., *Cavanellesia*, *Craigia*, *Balfourodendron*), shrubs (e.g., *Maxwellia*, *Phaeoptilum*, *Wimmeria*) vines (e.g., Cucurbitaceae, Dioscoreaceae, *Kleinhovia*, *Triptergium*, *Urvillea*) and herbs (e.g., *Abronia*, *Polygonum*, *Stackhousia*). The genera fall into at least 25 orders and 45 families. Arranging these taxa according to more inclusive phylogenetic clades (Table 1; Fig. 1), it becomes clear that the fin-winged condition is most prevalent among Eudicots, but occurs occasionally in Magnoliids (Hernandiaceae: *Illigera*), and monocots (e.g., *Burmannia*, *Dioscorea*, *Herreria*). Although convergent in general form, the fruits of different genera generally can be distinguished by details of the wing number, texture, shape and venation, along with characters of persistent floral parts and dehiscence mode.

The relative position of perianth and ovary, reflecting whether the fruits developed from inferior or superior ovary, is a helpful trait, because the perianth, or at least the scar(s) of the perianth, are generally discernable on the mature fruit. Perianth position, whether hypogynous at the junction with pedicel, or epigynous at the fruit apex, or expanded to form wings, helps with familial and ordinal identification (Table 1). Epigynous perianth characterizes the fin-winged fruits of Aizoaceae, Apiaceae, Begoniaceae, Burmanniaceae, Combretaceae, Cucurbitaceae, Dioscoreaceae, Lecythidiaceae, Haloragaceae, Hernandiaceae, Onagraceae, and Styracaceae. Hypogynous perianth characterizes fruits of the Brassicaceae, Cardiopteridaceae, Celastraceae, Cunoniaceae, Cyrillaceae, Fabaceae, Herreriaceae, Lophopixidaceae, Malvaceae, Melianthaceae, Nyctaginaceae, Pedaliaceae, Polygalaceae, Polygonaceae, Phyllanthaceae, Rhamnaceae, Rutaceae, Sapindaceae, Simaroubaceae, Trigoniaceae, Tropaeolaceae, and Zygophyllaceae. Those with superior ovaries are sometimes stipitate, but this feature is more variable. Some families will usually have a nectariferous disk that preserves above the perianth scar in mature fruits, e.g. Sapindaceae and Rutaceae.

There are phylogenetic patterns in the number of fruit wings (Table 1), which often reflect the number of carpels. Three-winged fruits are characteristic not only of monocots (Burmanniaceae, Dioscoreaceae, Herreriaceae, Ruscaceae), but also are the standard condition in the analyzed genera of Burseraceae, Celastraceae, Cucurbitaceae, Polygonaceae, Rhamnaceae, Sapindaceae, and occur in some genera of Asteraceae. Four-winged fruits are characteristic of Pedaliaceae, *Melianthus*,

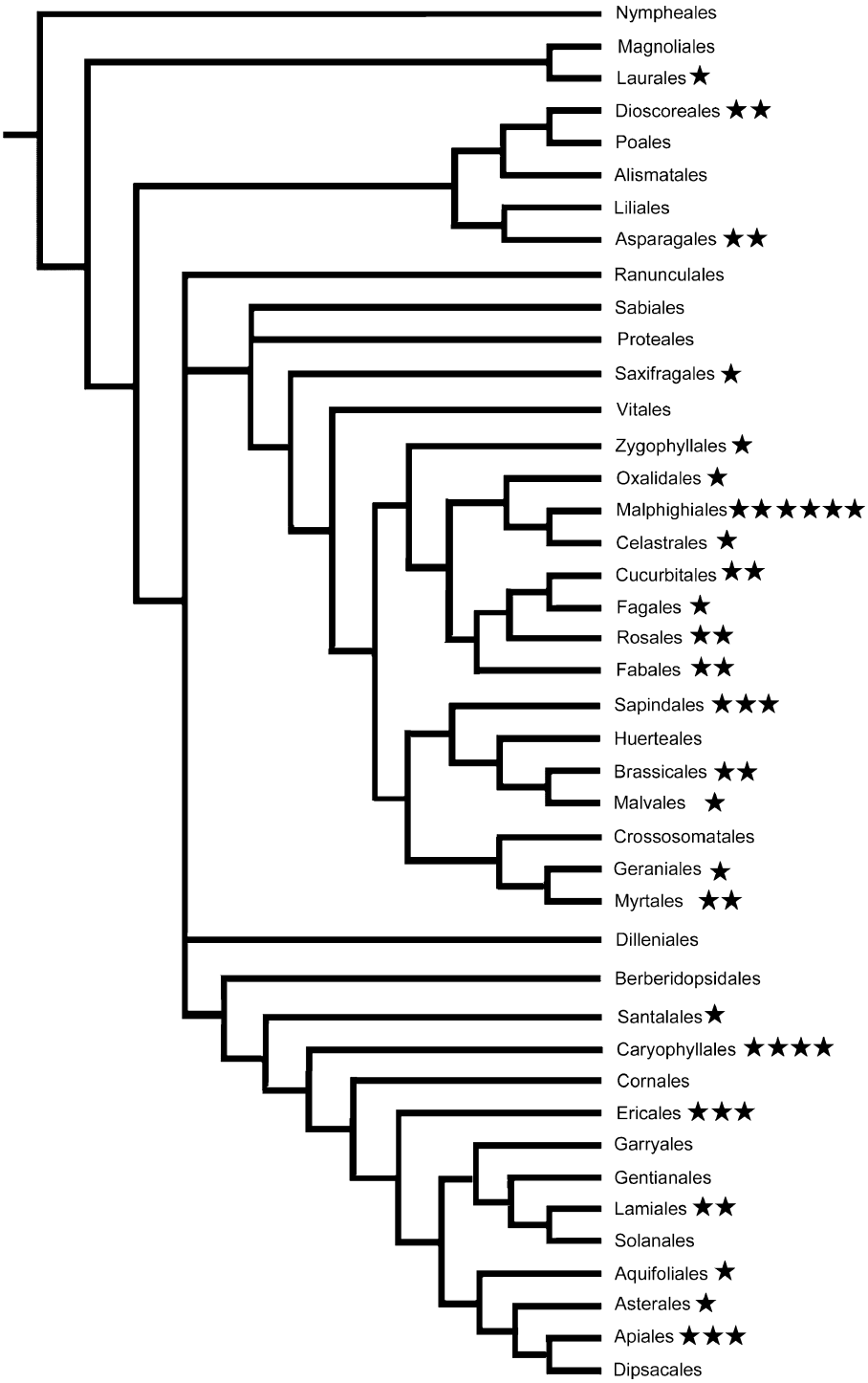


Fig. 1 Phylogenetic distribution of fin-winged fruits. Each *star* represents a family that contains at least one species with fin-winged fruits, as documented in Table 1. Topology abridged from APG III (2009)

Oenothera, *Petersianthus*, *Hymenopyramis*, several apiaceous genera, and some Combretaceae. Five-winged fruits are more common to Malvaceae, Zygophyllaceae and *Lophopixus*, while 2-winged fruits characterize the fin-winged fruits of most Asteraceae, Brassicaceae, Leguminosae, Oleaceae, and Polygalaceae. More than six wings is an unusual condition, noted only in Achariaceae.

The dispersal mechanism itself also appears to be canalized within phylogenetic groups. Indehiscent fruits, in which the entire fruit comprises the dispersal unit, characterize many orders and families, e.g., Caryophyllales (Aizoaceae, Nyctaginaceae, Polygonaceae), Ericales (Cyrillaceae, Styracaceae) and Rutaceae, and Combretaceae. Capsular fruits may open partially from the apex to release seeds, as in *Oenothera*, *Dioscorea*, or the valves may fall completely away, as in many Malvaceae and Sapindaceae and some Brassicaceae. Schizocarpic fruits, in which the fruit falls completely apart into separate mericarps, characterize Apicaceae, and Rhamnaceae.

Venation pattern of the wings is another important feature. With the exception of a marginal vein in some of the winged-fruited species, Apiaceae fruit wings typically do not possess any venation. Veins are lacking from the fruit wings of *Nothofagus*. The presence or absence of a well-defined intramarginal vein is useful for identification, being characteristic of Styracaceae (*Halesia*), some Polygonaceae (*Pteropyrum*, *Rheum*) some Rhamnaceae, some Apiaceae and some species of *Polygala*. The presence of a marginal, or fimbrial vein, is more widespread, and tends to be shared among related taxa. Marginal veins occur in all fin-winged Sapindaceae and Malvaceae, but do not occur in the fruits of Combretaceae. The lack of a marginal vein in *Combretum* often results in fraying of the wing margins upon drying. The common pattern of wing venation found in most families is subparallel, sometimes dichotomizing and anastomosing with veins radiating outward into the wings from the fruit body. Vein density is highest in Cardiopteridaceae, some Combretaceae (*Combretum*, *Pteleopsis*, *Terminalia*), Dioscoreaceae, some Nyctaginaceae (*Phaeoptilum*, *Selinocarpus*), many Polygonaceae, and in Ruscaceae.

Venation differs according to the derivation of the tissue forming the wings. Wings developed from the ovary and/or fruit wall tends to have a simpler vein pattern than wings elaborated from perianth or bracts. It is useful to note whether the wing has a single pattern of venation spreading in one plane, or if there are two overlapping sets of veins indicative of coalescent or adnate laminae. Thickness and translucency of the wing is another character useful for identification. Delicate, hyaline wings characterize fruits of some Nyctaginaceae, Polygonaceae, and Asteraceae (e.g., *Tripteris*), while thick, nearly opaque wings are found in *Cliftonia*, *Gouania*, *Guaiacum*, *Nothofagus*, and *Oenothera*.

Fin-winged Fruit Survey, Extant Taxa

Through this survey, we became aware of at least 124 genera in which radially finned fruits occur. Each of these is described below, arranged alphabetically by family. A phylogenetic listing is provided in Table 1. These data serve as the basis for the comparative analyses of fossil fin-winged fruits presented at the conclusion of this article.

Achariaceae Achariaceae usually have capsular or berry-like fruits but *Carpotroche* and *Grandidiera* Jaub. have fin-winged fruits. These genera were formerly placed in the Flacourtiaceae but that family was determined to be polyphyletic and many genera have been transferred to Achariaceae (APG II, 2003; Chase et al., 2002).

Carpotroche Endl. (Fig. 2a, b) includes three species of trees distributed in tropical America. The indehiscent fruit is formed from a superior ovary of multiple carpels, apparently with each carpel developing a marginal wing, such that a single fruit may have 6–20 wings. The fruits are globose to elliptical in outline, and relatively large, e.g. 7.8 cm long×7.1 cm wide, with a disk persisting at the base. The locule contains numerous seeds. Wings are coriaceous with entire to undulate margins and are supplied with closely spaced radiating striae, without a fimbrial vein.

Grandidiera Jaub. (Fig. 2c, d) with three species of trees or shrubs in tropical Africa, has 4- to 6-winged indehiscent fruits bearing small ovoid seeds (Sleumer, 1975). The fruits are wide-elliptical to wide-obovate. The pedicel is relatively thick and is shed with the fruit; a hypogynous perianth scar is seen at the junction of pedicel with base of the fruit. The wings are chartaceous, distally attenuate and crenate, pubescent, with simple subparallel venation oriented transverse to the fruit body and radiating toward the distal margins of the wings. A fimbrial vein was not detected. Vein density is ca 2–4 per mm.

Aizoaceae The fruits of this family are typically loculicidal capsules, but those of *Tetragonia* L. are indehiscent and winged. *Tetragonia* (Fig. 2e, f), with about 85 species of shrubs, occurs in tropical and temperate regions of the Southern Hemisphere with a center of distribution in southern Africa. The wide-elliptical indehiscent 3- to 4-winged fruits develop from an inferior ovary. The wings are coriaceous with main veins fanning into the wings from the endocarp with a festooned brochidodromous pattern. The density of main veins is 1.2 per mm. A fabric of finer veins between the main veins forms an irregular reticulum of polygonal areoles. Although some authors have included *Tribulocarpus* in *Tetragonia* (Adamson, 1955; Thulin, 1993), the fruit of the former is compound and fused to spiny bracts, whereas the latter is simple and free from bracts (Bittrich & Hartmann, 1988; Hartmann, 2001; Klak et al., 2003).

Apiaceae Winged fruits occur in at least 75 genera of Apiaceae (Liu et al., 2006). The winged fruits in this family are formed mainly by compression of the carpels (dorsally or laterally) but in some cases by elaboration of ribs into membranous extensions. The family is readily recognized because the two carpels remain partially separated from each other through development, with the fruit being a schizocarpic, separating into a pair of mericarps, each with remnants of the epigynous perianth and stylopodium. In the case of a 4-winged fruit, typically each dispersed mericarp will possess two wings.

Examples of winged apiaceous fruits were studied anatomically and morphologically in the context of phylogeny by Liu et al. (2006) including the genera *Annesorhiza*, *Asteriscium*, *Choritaenia*, *Dasispermum*, *Elaeoselinum*, *Heptaptera*, *Hermas*, *Heteromorpha*, *Laretia*, *Molopospermum*, *Myodocarpus*, *Pachypleurum*, *Peucedanum*, *Polemanniopsis*, *Polylophium*, *Rouya*, and *Tordylium*. Other examples of genera with winged fruits not included in that study include *Anethum*, *Angelica*, *Cymopterus*, *Ferula*, *Heracleum*, *Laserpitium*, *Ligusticum*, *Lomatium*, *Pastinaca*,

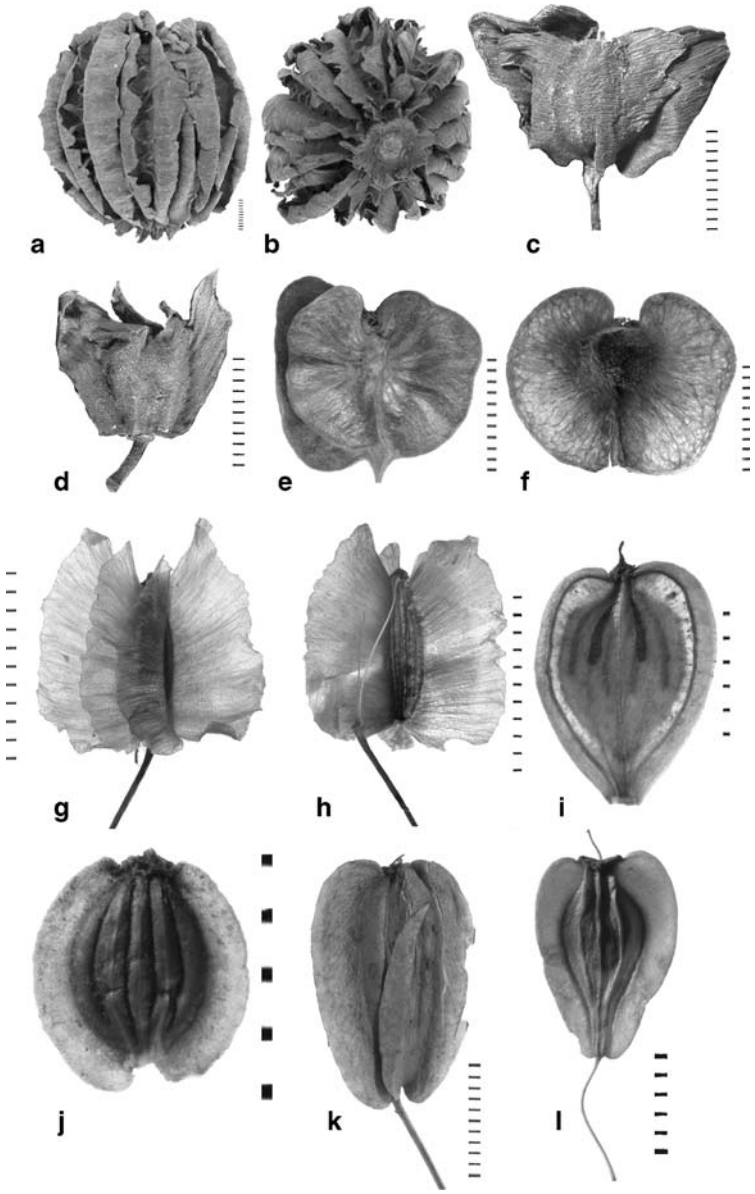


Fig. 2 Achariaceae (**a–d**), Aizoaceae (**e–f**), Apiaceae (**g–l**). **a**, **b** *Carpotroche amazonica.* **a** Lateral view showing several transversely striate longitudinally oriented wings (BARC: B.A. Krukoff 9001), Sao Paulo, Brazil. **b** Basal view showing remnant perianth and about 20 wings. **c** *Grandidiera boivinii* Jaub. UC1218907: Tanner 3378, Tanganyika, Africa. **d** *G. boivinii* Jaub. (UC1233310: R.E.S. Tanner 3320), Tanganyika. **e** *Tetragonia macroptera* Pax. BOL128311 (ALUKA): R. Marloth 1427, Namibia. **f** *T. fruticosa* L. showing two of three wings (MO 566863: Slageren & Newton 628), South Africa. **g**, **h** *Elaeoselinum fontanesii* Bois. (GH: P. Jamin 35), Algeria. **i** Mericarp of *Heracleum lanatum* Michx. showing intramarginal vein and persistent epigynous perianth (NEBC: A. S. Pease 958), Coos Co., New Hampshire. **j** Mericarp of *Peucedanum palustre* (L.) Moench. showing ribbed endocarp and veinless wings (NEBC: L.E. Richardson sn), Middlesex Co., Massachussets. **k** *Prangos ferulacea* Lindl. (GH: J. Gay sn), Paris. **l** Fruit of *Steganotaenia araliacea* Hochst. with intact pedicel and style (A: R. Seydel 4460A), Karabib. Scales calibrated in mm

and *Thapsia*. Liu et al. (2006) found that fruit characters in the studied genera, including developmental origin of the wings, shape of the carpel, presence of elongated oil canals (vittae), and other anatomical features, correspond with molecular cladograms giving added confidence to the taxonomic value of fruit characters in this group. The number of wings varies among different genera (Table 1). The wings are often hyaline, without venation, or with only a fimbrial vein, but in a few cases they are markedly striate (e.g., *Elaeoselinum* and *Thapsia*, Figs. 2g, h, 3a). Examples of genera with fin-winged fruits are described below; others not observed in this study are treated by Liu et al. (2006).

The fossil fruit, *Umbelliferospermum latahense* from the Middle Miocene of Washington, represented by dispersed mericarps with paired veinless wings and an apically positioned persistent perianth, displays characters diagnostic for the family (Berry, 1929). Probably the Late Cretaceous fossil, *Carpites ulmiformis* Dorf also belongs to Apiaceae, as we discuss in chapter 5.

Annesorhiza Cham. & Schltdl., endemic to Africa, has about 15 species of perennial herbs. *A. macrocarpa* (Fig. 2B in Liu et al., 2006) is 7-winged, and asymmetrically schizocarpic, with three wings (a median and two marginal wings) on one mericarp, and four wings (two lateral and two marginal) on the other. The wings are without obvious veins.

Dasispermum Neck. ex Raf., a monotypic genus endemic to South Africa, has exceptionally polymorphic fruits (major morphological differences can be found among fruits collected from different plants; Tilney & Van Wyk, 1995). *D. suffruticosum* may have either asymmetrically or symmetrically schizocarpic mericarps. A specimen of this species illustrated by Liu et al. (2006, their Fig. 3D) displays ten wings.

Elaeoselinum Koch. ex DC. (Fig. 2g, h) is a genus of four species distributed in the Mediterranean region. *E. fontanesii* Bois. has 4-winged fruits. The fusiform endocarp is longitudinal ribbed. The wings develop from furrows between ribs, with a pair of marginal wings on each mericarp (Liu et al., 2006). The wings are markedly striate with striae fanning outward from the endocarp. No marginal vein is developed.

Heracleum L. (Fig. 2i) has about 65 species of biennial herbs distributed in north temperate areas and tropical mountains. The fruits have a persistent stylopodium and four wings in two parallel planes, schizocarpic between the planes. Each mericarp is obovate in outline with cuneate-rounded base and rounded to subcordate apex and shows an intramarginal vein. The wings are finely striate between the locular area and intramarginal veins. Two to four longitudinal vittae are situated over the locular region, symmetrically about the central fruit axis (Fig. 2i).

Heteromorpha Cham. & Schldl. has eight species of perennial herbs in tropical and South Africa. *H. transvaalensis* is 5-winged and asymmetrically schizocarpic, with three wings (one median and two marginal) on one mericarp and two marginal wings on the other (Fig. 2C in Liu et al., 2006). The wings each have a fimbrial vein.

Laretia Gillies & Hook. has two species of cushions in the Andes of Chile. *L. acaulis* has 4-winged fruits, with a pair of marginal wings on each mericarp. Fimbrial veins are present, but no veins occur over main part of wing.

Molopospermum Koch. is a monotypic genus of shrub in the western Mediterranean region. *M. peloponessiacum* has asymmetrically schizocarpic 5-winged fruits, with

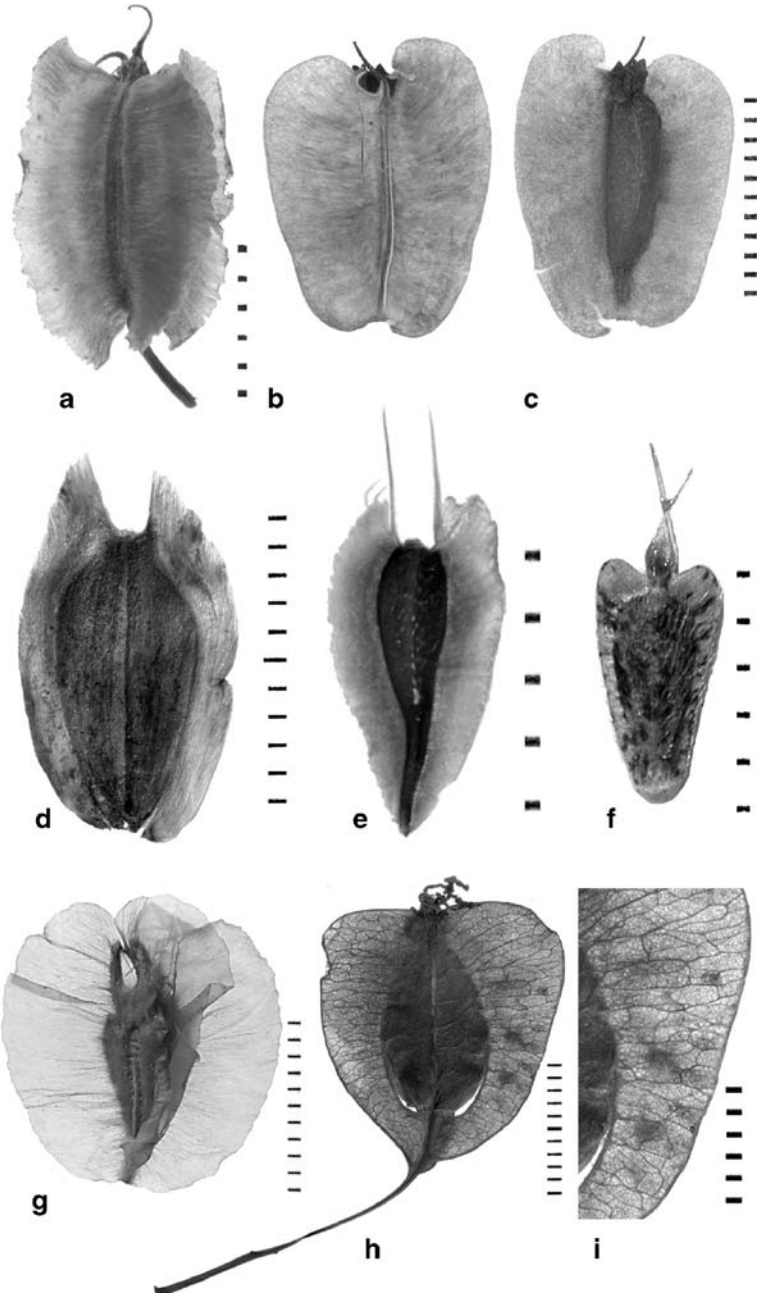


Fig. 3 Apiaceae (**a**), Araliaceae (**b**, **c**), Asteraceae (**d**–**g**), Begoniaceae (**h**, **i**). **a** *Thapsia polygama* Desf. (GH: E. Cosson sn, 28 June 1861), Algeria. **b**, **c** *Astrotricha cordata* A. Bean (MO: R.O Makinson 1432), New South Wales, Australia, ventral and dorsal surfaces of the same mericarp. **d** *Silphium speciosum* Nutt., UC 1278934: F.C. Gates 20939, Geary Co., Kansas. **e** *Verbesina guatemalensis* Robinson & Greenman, UC 1492641: T.B. Croat 47529, Chiapas, Mexico. **f** *Wedelia acapulcensis* Kunth in H.B.K. UC917778: F.W. Gould 5732, Sutton Co., Texas. **g** *Tripteris sinuata* DC (A: R.D.A. Bayliss 4931), S. Africa. **h** *Begonia malabarica* Lam. (GH: Wight 1028), eastern India. **i** Same, detail of venation. Scales calibrated in mm

three wings on one mericarp (one median and two lateral) and two lateral wings on the other (Liu et al., 2006).

Pachypleurum Ledeb. is a genus with two species of perennial herbs distributed in Europe and Asia. *P. lhasanum* has 10-winged fruits with five wings per mericarp, each developed from a main rib (Fig. 3G in Liu et al., 2006).

Peucedanum L. (Fig. 2j) has about 50 species of herbaceous perennials in Eurasia; ca 50 additional species from Africa formerly placed in this genus have been shown to be distinct, and are now placed in six additional genera (Winter et al., 2008; Magee et al., 2009). *Peucedanum* and the African segregates typically have mericarps with paired lateral wings that are veinless (well documented in the images of Fig. 7 in Magee et al., 2009). The fruit of *P. palustre* (L) Moench is circular in outline but with a basal cleft, with a longitudinally ribbed, elliptical endocarp capped by remains of the stylopodium. Each mericarp has two lateral wings, without venation.

Polemanniopsis B.L. Burtt is a monotypic genus of large woody shrubs endemic to the west Cape of Africa. *P. marlothii* fruits are 5-winged, and asymmetrically schizocarpic with three wings (one median and two marginal) on one mericarp and two lateral wings on the other (Fig. 2A in Liu et al., 2006).

Prangos Lindley (Fig. 2k) is a genus of 38 species of tall, perennial herbs distributed in Eurasia and the Mediterranean. The fruits are 5-winged and elliptical. The pedicel is shed with the fruit, but styles and perianth do not persist. The wings, derived from ovary ribs, are coriaceous and appear to lack venation.

Steganotaenia Hochst. (Fig. 2l) is a genus of three species of small trees distributed from Ethiopia to South Africa. The fruits vary among species from only slightly to prominently winged (Hyde & Wursten, 2009). The 2-winged elliptical fruit develops from a 5-carpellate ovary and has a relatively thin and long persistent pedicel (see also Fig. 2–8I in Liu et al., 2006). In *S. araliacea* Hochst. the endocarp is obovate with three prominent longitudinal ribs on the external face and capped by the persistent stylopodium. The wings are coriaceous and lacking venation and nonstriate.

Thapsia L. (Fig. 3a) has six species of herbaceous perennials in the Mediterranean area (including the segregate, *Rouya* with one species in northern Africa, Corsica and Sardinia). *T. polygama* (Fig. 3C, E in Liu et al., 2006) fruits have eight wings, four on each mericarp. The endocarp is fusiform, longitudinally ribbed and capped by persistent remains of the calyx and styles. The wings develop from furrows such that there are two inter-rib marginal wings on each mericarp, as well as two inter-rib lateral wings (Liu et al., 2006). The wings are translucent with densely spaced radiating striae but lack fimbrial veins.

Araliaceae Fruits of this family are commonly drupaceous, and only rarely winged. *Astrotricha* DC. (Fig. 3b, c) is a genus of shrubs with 16 species in Australia with fin-winged fruits. The fruits are schizocarpic with a carpophore bearing two biwinged mericarps (a rare feature for Araliaceae, arguing for repositioning in the related family, Apiaceae), that are laterally compressed into wings. The fruit is obovate in face view, cordate basally and apically, with a smooth, fusiform endocarp, capped by remains of the perianth and style. The wings are finely striate transverse to the long axis of the fruit.

Asteraceae This family is best known for achenes with dispersal by an apical tuft of hairs (pappus), but lateral wings occur on the achenes of numerous genera (Anderberg et al., 2007). Examples in *Coreopsis*, *Silphium*, *Verbesina* are described and illustrated in Bojnansky and Fargasova (2007). The number of wings ranges from two (e.g., *Garuleum*, *Pterocypsela*; Zhu et al., 2006), to three (e.g., *Norlindhia*, *Inuloides*, *Monoculus*, *Tripteris*; see Fig. 58 in Anderberg et al., 2007). Fin-winged achenes occur in various tribes. The phylogeny of tribe Heliantheae as reconstructed from nuclear and chloroplast DNA, indicates that winged fruits have evolved two or three times in *Coreopsis* (Crawford and Mort, 2005). The wings are thin and lack venation. Examples are considered below and in Table 1.

Silphium (Fig. 3d) includes about 20 species of herbaceous perennials in eastern North America. *S. speciosum* Nutt. fruits are approximately elliptical in outline, with a prominent apical notch, and are lenticular in cross section. The achene is smooth and obovate with a prominent midrib, and a pair of lateral wings. The wings extend apically along a pair of awn-like apical extensions of the endocarp. The wings are chartaceous, without venation, but strongly striate longitudinally.

Tripteris Less. includes about 70 species of herbs and shrubs distributed in Africa (Fig. 3g). *Tripteris sinuata* D.C. fruits are trigonally symmetrical with three hyaline wings lacking venation. The achene is elliptical to oblanceolate, triangular in cross section, and has three nearly flat lateral faces, each with a median longitudinal groove containing a single prominent vein. The apical margins of each of the three flat faces are developed into protruding incurved awns; three of these awns occur on each fruit. The translucent wings spread from the edges of the endocarp and awns, and are very finely striate, with striae radiating outward from the endocarp.

Verbesina L. (Fig. 3e) is a New World genus with more than 200 species of perennial herbs. The achenes are 2-winged with narrower or wider wings depending on the species, and with a "pappus" of two asymmetrically developed apically extending awns (Olsen, 1986). The endocarp of *V. guatemalensis* Robinson & Greenman is elongate-oblanceolate, with a median ridge, and lenticular in cross section. The wings, are membranous without venation, but with radiating striations. In contrast to *Silphium speciosum*, the awns protrude independently of the wings. Similar morphology occurs in *Boltonia* L'Hér.

Wedelia (Fig. 3f) has about 70 species of herbs and subshrubs distributed in tropical and warm regions. Fruits of *W. acapulcensis* Kunth in H.B.K. are obovate in outline, rounded basally and apically cordate, with an obovate achene, lenticular in cross section, and a pair of lateral wings. A pair of apically extending awns arises from the upper part of the wings. The wings are membranous or chartaceous with striae oriented at about 30° to the long axis of the fruit.

Begoniaceae Both genera of Begoniaceae, *Begonia* L. and its sister genus *Hillebrandia* Oliver (Clement et al., 2004), have species with prominently winged fruits.

Begonia (Fig. 3h, i) is widely distributed in the tropics, with about 1,400 species of herbs and shrubs. The fruits have a persistent epigynous disk where the perianth and numerous stamens were attached. *Begonia* fruits are capsules developed from an inferior ovary of 3–5 carpels, typically with a corresponding number of wings. Different fruit morphologies are associated with different dispersal syndromes. Wind

dispersed *Begonia* fruits tend to have two locules and three nearly equal sized wings, while rain dispersed species have fruits with one large wing and two smaller wings (Tebbitt et al., 2006). The fruits are often asymmetrical with one locule and wing larger than the others. Outline varies from longer than wide to wider than long. Dehiscence occurs by splitting along sutures to release seeds explosively. As illustrated by *B. malabarica* (Fig. 3h, i), the pedicel and stigmatic disk often persist on the dispersed fruit. The locular area is ovate, with a median suture, and a thickened separation rim along its basal margin. The wings have complex reticulate venation. The main veins are straight to sinuous, radiating from the locular areas and extending to the fimbrial vein with occasional cross oblique cross veins. A fabric of thinner veins fills the regions between main veins.

Brassicaceae The mustards are a large family of about 340 genera. Although characterized mainly by 2-valved, wingless capsules, the family also includes genera with indehiscent fruits, and multiple genera with 2-winged fruits (Appel and Al-Shehbaz, 2003). The fruits develop from a bicarpellate, 2-loculed superior ovary that may be flattened and/or winged at right angles to the plane of the septum (angustiseptate), or parallel to the septum (latiseptate). The listing of fin-winged fruits below is exemplary rather than complete.

Brossardia Boiss. (Fig. 4a) is a monotypic genus of perennial herbs distributed in Iraq and Iran (Appel and Al-Shehbaz, 2003). The opinion of Khosravi et al. (2008), based on ITS analyses, that this genus be subsumed within *Noccaea* Moench., a genus with dehiscent, nonwinged fruits and smooth rather than ridged seeds is not accepted here. The fruits are 2-winged, obovate symmetrical, indehiscent silicles. The style is persistent and remnants of the hypogynous perianth often persist above a very short stipe. The pedicel is shed with the fruit. The locular area is inflated, fusiform in outline, extending about 80 percent of the fruit length toward the apex, bearing two seeds. Venation forms a coarse reticulum over the locular area with polygonal areoles, with main veins fanning outward into the wings, straight or sinuous, craspedodromous and joining a well-defined fimbrial vein. The main veins are widely spaced, ca 1.5–2 mm apart, but finer veins form a tighter fabric between the main veins, with areoles mostly elongate perpendicular to the wing margin.

Fortuynia (Fig. 4c) Shuttlew. ex Boiss. includes two species of perennial subshrubs distributed in Iran, Pakistan, and Afghanistan (Appel and Al-Shehbaz, 2003). The 2-winged fruits are stipitate, dehiscent silicles. The fruit of *F. garcini* is symmetrical, obovate in outline with a truncate to emarginate apex, sometimes with a persistent style. The locular area is obovate, situated centrally between base and apex of fruit, occupying about 1/3 of the fruit length. The pedicel is shed with fruit and swollen at junction with stipe where the perianth abscised. Wings are chartaceous. Venation consists of a strong median longitudinal vein plus a system of fine, closely spaced subparallel veins curved upward. Vein density is 2–3 per mm, veins 0.2–0.5 mm apart.

Isatis L. (Fig. 4b) has approximately 50 species of annual, biennial and perennial herbs in the Middle East, Central Asia to Europe, eastern Asia and North Africa. Fruits indehiscent, single-seeded, including siliques and silicles ranging from orbicular to oblong, obovate, ovate, or obpyriform, with septum lacking. Fruits of different species vary from laterally keeled to slightly or conspicuously winged

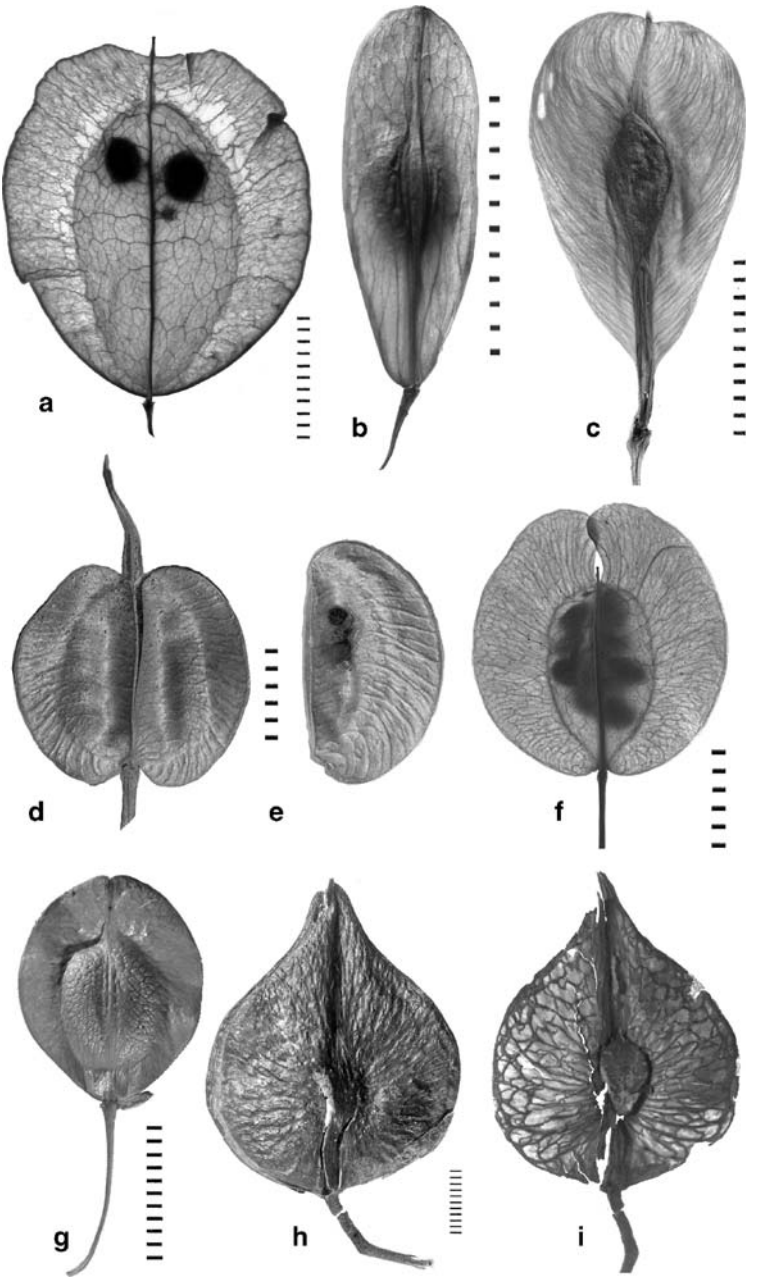


Fig. 4 Brassicaceae (**a**–**g**), Burseraceae (**h**, **i**). **a** *Brossardia papyravea* Borss. (BARC; W: C. Haussknecht sn 1867), Near East. **b** *Isatis maritima* Rupr. (GH: Baenitz 4181), Olskav, southern Sweden. **c** *Fortuynia garcini* Shuttl. ex Boiss. (BARC; W: A. Gabriel sn), Iran. **d** Fruit of *Schouwia purpurea* (Forsk.) Schweinf. with prominent apical projection (ALUKA; MPU: R. Volkonsky sn; 4-1941), central Sahara, Algeria. **e** Mericarp from the same collection as d. **f** *Thlaspi arvense* L. fruit by transmitted light showing several seeds within the locule (FLAS127139: Brumbach 4858), Pennsylvania. **g** *Sameraria armena* (L.) Desv. (US: W. Koelz 15678a), Iran. **h**, **i** *Triomma malaccensis* Hook. f. Leiden Endert 27 E, P615. Det. Kalkman 1953, Sumatra. Scales calibrated in mm

(Appel and Al-Shehbaz, 2003). *Isatis maritima* fruits are obovate with an elliptical central locule. The locular area is elliptical, situated centrally between base and apex of fruit occupying about 1/4 to 1/3 of the fruit length. Venation comprises a system of moderately spaced fine, longitudinally oriented veins that form elongate areoles in the lower half but in the apical half interconnect into a reticulum with more or less isodiametric polygonal areoles. Vein density is 1.2–2.5 per mm.

Psychine Desf. is a monotypic genus of annual herbs distributed in Morocco, Algeria, and Tunisia. The fruits are cordate silicles flattened at a right angle to septum (angustiseptate); valves prominently reticulately veined, and keeled or winged (Appel and Al-Shehbaz, 2003). *Psychine stylosa* fruits are wider than high, with the pair of outstretched chartaceous wings forming a semicircular margin to the lower half of the fruit, but obtusely cleft apically, with a persistent elongate stylar extension equal to the length of the fruit and a stout pedicel, shortly stipitate. The locular area is ellipsoidal with biseriate seeds. Main veins radiate from the locular area into both wings. They are subparallel, straight to sinuous and craspedodromous, with occasional oblique cross veins with a finer set of intervening veins forming a reticulum. The vein density is 1.6–3.3 per mm.

Sameraria Desv. (Fig. 4g) has nine species of annual herbs distributed in the Middle East and central Asia (Appel and Al-Shehbaz, 2003). The fruits are 2-winged, symmetrical, and indehiscent. In *S. armenia*, the fruit is obovate to circular to cordate, with a small apical notch. The endocarp is elliptical and bloated, extending from the base about 2/3 of the fruit length to the apex. The fruit is dispersed with the pedicel, showing a perianth scar, and/or remnant perianth parts at the junction between them. Wings are chartaceous with a fimbrial vein. Venation over the endocarp and in the wings forms a fine reticulum with polygonal, approximately isodiametric, areoles.

Schouwia DC (Fig. 4d, e) is a monotypic genus of herbs in North Africa, Saudi Arabia, and Yemen. The dehiscent 2-winged fruit has a subcircular outline with a cordate base and apex and an elongated protruding apical extension. The locular area is broadly elliptical and extends nearly the full length of the fruit from base to apex. The wings are chartaceous, with main veins downward arching and craspedodromous, abutting a prominent fimbrial vein. Vein density is 1–1.25 per mm.

Thlaspi L. (Fig. 4f) is a genus of about 60 species of herbs in the Northern Hemisphere. The dehiscent 2-winged fruit is nearly elliptical, with retuse apical margin. The elliptical locular area, covered with reticulate venation, contains several elliptical seeds. The chartaceous wings extend laterally and apically from the locular area. Main veins fan outward from the locule and are craspedodromous to the fimbrial vein, with sinuous cross veins forming irregular polygonal areoles. Overlapping venation patterns indicate that the wings are bilamellate. We accept Becker's assignment of fossil fruits from the Oligocene of Montana to this genus (Becker, 1961; see "Evaluation of Fossil Fruits", Fig. 21h–k).

Apocynaceae Fin-winged fruits are known in two genera of Apocynaceae. *Cameraria* L. of Guatemala, Belize, and the West Indies, is a genus of shrubs or small trees with a 2-winged fruit. The fruit of *C. latifolia* L. is ovate, symmetrical with a proximal elliptical seed and chartaceous wings extending laterally distally, with venation diverging from the midline of the fruit with each wing having venation similar to that of an *Acer* samara. A good photograph of the fruit may be found in Lenz and Dickau

(2005, p. 196). *Cerberiopsis* Vieill. ex Pancher & Sebert, with three species of trees in New Caledonia, has 2-winged schizocarpic samaroid fruits, illustrated diagrammatically for *C. candelabra* and *C. neriifolia* (Boiteau, 1981, Pl. 40, 41).

Burmanniaceae Burmannia L. (Fig. 5a) has about 60 herbaceous species of widespread distribution. The fruit is a 3-winged capsule, formed from a partly inferior uni- or trilocular ovary. The disseminule is elliptical to elongate-elliptical, with semielliptical wings persisting from the strongly winged floral tube of the flower (Gentry, 1993). As seen in *B. bicolor* Mart., the pyriform fruit body is perched near the apex and the wings are membranous, without obvious striation or venation, except for a median set of 3–5 longitudinal veins extending from the pedicel to the base of the fruit body, each paralleled by a thinner vein to the inside.

Burseraceae This family has mostly berry-like fruits, but the monotypic genus *Triomma* Hook. f., with large trees native to western Malaysia, Sumatra, Borneo, is an exception, having 3-winged fruits that dehisce into three valves as well illustrated by Leenhouts (1956). The fruits of *Triomma malaccensis* (Fig. 4h, i) are borne on a thick peduncle. They develop from a superior ovary, and are ovate-pyriform in shape, with three wings diverging from a small hard central obovate endocarp. Each wing is formed by a pair of loosely adherent laminae, which separate at maturity along the lines of carpel suture into three valves. This arrangement is analogous with that of *Gouanea* in Rhamnaceae. The separated wing laminae are chartaceous, but prior to separation the doubled wings may be almost opaque. Each of the laminae is supplied with complex reticulate radiating veins with the dominant veins fanning out from the endocarp and craspedodromous to a fimbrial vein. Finer irregular cross veins form a reticulum of irregular polygonal areoles with rare freely ending veinlets.

Cardiopteridaceae This family includes the genus *Cardiopteris* Wallich ex Royle (Fig. 5b, c) with two species of twining herbs native to Malesia and SE Asia. It was formerly misplaced in the Icacinaceae but is more closely related to Aquifoliaceae (Kårehed, 2001). The fruit is indehiscent, formed from a superior bicarpellate, unilocular ovary. It is elliptical to obovate, apically rounded to cordate, basally cuneate to round. There are two symmetrical wings surrounding a narrowly fusiform, smooth endocarp. The style persists as a prominent protuberance, about 1/3 to 1/2 the length of the fruit. The fruit is stipitate with a basal calyx scar. The coriaceous wings develop from the ovary wall and have a prominent fimbrial vein, and very fine closely spaced striae radiating outward from the longitudinal axis.

Celastraceae have several genera with fin-winged fruits, including *Macgregoria* and *Stackhousia* (both formerly placed in Stackhousiaceae), *Platypterocarpus*, *Tripterococcus*, *Tripterygium*, and *Wimmeria*. The wings develop from the pericarp of superior ovaries.

Macgregoria F. Muell. is a monotypic genus of annual herbs from central Australia. Its fruits are schizocarpic, composed of 5-winged mericarps (Simmons, 2004).

Platypterocarpus Dunkley et Brenan wings (Fig. 5e) is a monotypic genus of trees in Tanzania. *P. tanganyikensis* Dunkley & Brenan has samaras of 4–5 lateral

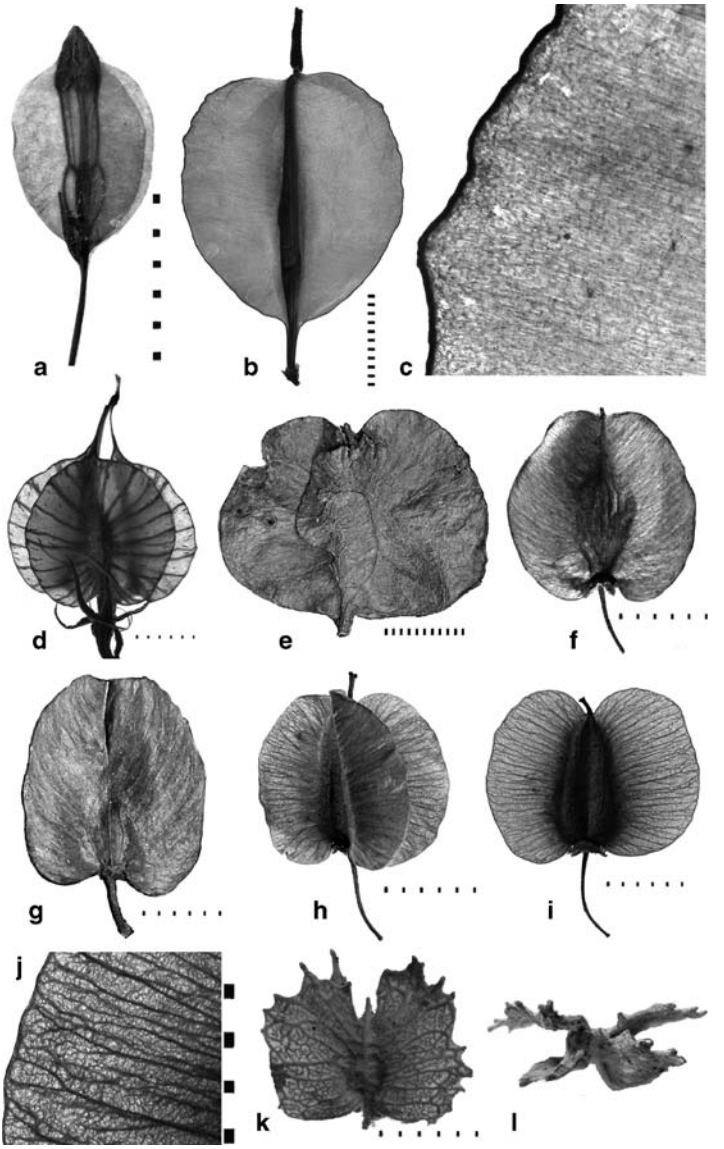


Fig. 5 Burmanniaceae (**a**), Cardiopteridaceae (**b**, **c**), Celastraceae (**d–j**), Chenopodiaceae (**k**, **l**). **a** *Burmannia bicolor* Mart. (GH: G.A. Romero, F. Guanchez, E. Melgueiro 2036), Venezuela. **b** *Cardiopteris quinqueloba* (Hassk.) Hassk. (A: C.W. Wang 80602), Yunnan, China. **c** Same, detail of wing showing fimbrial vein (*left*) and finely striate wing lacking prominent veins. **d** *Tripterococcus brunonis* Endl. showing three loosely adherent wings with styles adnate at *top*, and persistent sepals at *base* (A: A. Travers 19), Perth, Australia. **e** *Platypterocarpus tanganyikensis* Dunkley & Brenan (ALUKA; EA: Fletcher H66/36), Tanzania. **f** *Tripterygium wilfordii* Hook. f. showing narrow pedicel, basal perianth remnants and apical style (A: Togashi 531), Negano, Honshu, Japan. **g** *Tripterygium forestii* Loesn. (PE 1254867), SW China. **h** *Wimmeria mexicana* (DC.) Lundell (1938) showing three wings (GH: E. Palmer 261), Chihuahua, Mexico. **i** *W. mexicana* showing thin pedicel, basal perianth, apical style and a pair of wings (GH: E.H. Goldman 227), Chihuahua Mexico. **j** *W. mexicana*, detail of wing venation from **h**. **k** *Atriplex canescens* (Pursch) Nutt. (A: W.H. Henning 163), Nevada. **l** Apical view of same fruit, showing four wings. Scales calibrated in mm

wings and one flattened seed. The wings are chartaceous to subcoriaceous (Simmons, 2004). Main veins fan outward from the central axis, somewhat sinuous in course, occasionally dichotomizing and anastomosing, craspedodromous, abutting to join fimbrial vein. The main veins are widely spaced, (ca 1.5–2 mm apart), with interconnections creating a reticulum of equidimensional polygonal areoles, ca 1.2-1 mm in diameter.

Stackhousia Sm. includes 12 species of herbs found in Australia and New Zealand. It has schizocarpic fin-winged fruits. The genus was long placed in its own family, but recent molecular work supports the current hypothesis that it is nested within the Celastraceae (Simmons, 2004). Fruits of *S. megaloptera* F. Muel., illustrated by Sweedman (2006, p. 160), are elliptical with rounded to cordate base and apex, and have membranous wings with subparallel complex reticulate venation; main veins are somewhat sinuous, craspedodromous to the fimbrial vein.

Tripterococcus Endl. (Fig. 5d) includes two species of perennial herbs in southwestern Australia, placed along with *Stackhousia* either in the Stackhousiaceae or Celastraceae. This genus is sometimes treated as a synonym of *Stackhousia*, but the fruits are readily distinguished in wing morphology and vein density. The fruit develops from an ovary of (1–)3–5 carpels, with a corresponding number of wings. Fruits of *Tripterococcus brunonis* Endl. (also illustrated by Sweedman, 2006, p. 167) are elliptical to obovate or ovate, with an acuminate apex and cordate base. The hypogynous calyx consists of five elongate persistent sepals at the base of a short stipe. Each valve of the fruit is subcircular in outline, but cordate basally, and abruptly narrowed apically into a stylar extension 1/4 to 1/2 as long as the fruit itself; these stylar extensions adhere only by their apices. Adjacent half valves are loosely adherent, forming membranous, hyaline wings. Venation is simple, subparallel and widely spaced, with about 6–10 unbranched or rarely branched veins radiating from the fusiform central body into each semicircular wing, arching slightly upward; these veins craspedodomous, abutting the well developed fimbrial vein, without cross-veins, or anatomosing; only rarely dichotomizing. Vein density is 0.8–1.6 per mm.

Tripterygium Hook.f. (Fig. 5f, g) includes two species of lianas or scandent shrubs distributed in eastern China and Japan. The fruit is indehiscent, 3-locular and 3-winged, elliptical in outline, rounded to cordate apically and cordate basally. A single style, with an apical stigmatic bulge persists, and floral remnants, including calyx and stamens, persist at the base. The pedicel, which is narrow (0.3 mm) and about 1/3 the length of the fruit, is usually shed with the fruit. The locular area is long-ovoid, with fine longitudinal veins on surface. The chartaceous wings are derived from the ovary. Main veins over the locular area form a coarse reticulum with polygonal areoles ranging from equidimensional to axially elongate. Main veins of the wing are simple subparallel, fanning outward from the locular area, seldom dichotomizing and anastomosing, straight to curved, craspedodromous, abutting a weak fimbrial vein. These veins are closely spaced, 1.6–5 per mm. An intervening reticulum of finer veins forms a very fine meshwork. Each wing by transmitted light shows two overlapping venation systems, reflecting the connation of two laminar surfaces.

Wimmeria Schltdl. (Fig. 5h–j) includes 16 species of trees and shrubs distributed in central America (e.g. Lundell, 1938). The fruit with 2–4 (usually three) symmetrical wings, is an indehiscent samara with a corresponding number of

locules, with 4–6 ovules per locule (Simmons, 2004). Fruits are elliptical (*W. concolor*, *W. bartlettii*) to widely elliptical (*W. mexicana*, *W. persicifolia*), cordate basally and apically. The locular area is ovate, with fine, irregular widely spaced longitudinal striations. A single style, about 1 mm long, persists at apex with three apical stigmatic bulges; a disk and subtending calyx 1–2 mm diameter persist at base. The slender pedicel, ca 1/3 to half the length of fruit, is shed with the fruit at dispersal. The chartaceous wings are derived from ovary. Main veins fan outward from the locular area, straight to sinuous, occasionally dichotomizing and anastomosing; adjacent veins form loops, or series of loops as they approach the margin, or are craspedodromous and extending directly to the margin, abutting to the fimbrial vein. Main veins are closely spaced, density 0.5–0.7 per mm. A very fine fabric reticulum is developed between the major veins. Each wing by transmitted light shows two overlapped venation systems, indicating a doubled lamina.

Chenopodiaceae This family has fruits that are generally wingless nuts. Fin-winged fruits occur in some species of the shrubby genus *Atriplex* L. (Fig. 5k, l). In particular, *Atriplex canescens* (Pursh) Nutt. has four well-developed chartaceous wings originating from bracts (Hitchcock and Cronquist, 1973). The wings are serrate-margined, concave sinuses between the spiny teeth. The achene is elliptical with a longitudinal median rib. Main veins fanning outward from the achene, spaced about 1–2 mm apart, are craspedodromous to the margin. A meshwork of successively finer veins occupies the space between main veins.

Combretaceae are a pantropical family of about 20 genera of trees, shrubs, and lianas with fruits variously adapted for animal-, water- and wind dispersal. Fin-winged fruits occur in five genera. Some fossil examples of this family from the mid-Cretaceous Dakota Formation of Kansas and Nebraska are described here under the new name *Dilcherocarpon* (see "Evaluation of Fossil Fruits").

Anogeissus Wall. (Fig. 6a) includes seven species of trees in western tropical Africa to Southeast Asia (Scott, 1979; Stace, 2007). Most species have 2-winged fruits although one has 4-ribbed, wingless fruits. The indehiscent fruits are orbicular to broader than long, with a prominent apical beak. Wings are chartaceous, translucent at edges, without any obvious veins.

Combretum Loefl. (Fig. 6b, c, e) (including *Meiostemon* and *Thiloa* per Stace, 2007) is a genus of about 260 species of shrubs, lianas, and rarely trees distributed pantropically except for the Pacific Islands and most of Australia (Stace, 2007). The fruits are indehiscent with four or five wings, and range in outline from widely elliptical, to ovate, to narrowly elliptical. The endocarp is fusiform and centrally positioned. Sometimes a stylar protrusion persists at apex, and the base often narrows to a short, thick, stipe-like projection culminating at the detachment scar. Wings are chartaceous, with entire to undulate margin, often tattered in dispersed fruits. Venation consists of closely spaced, straight to slightly curved subparallel fine bundles mostly transverse to the longitudinal axis of the fruit that extend to the margins without looping (Fig. 6e). Vein density is high, about five or more per mm, giving a striate appearance to the wing surface. *Combretum* fruit wings lack a fimbrial vein or thickening; hence the margins tend to fray upon drying.

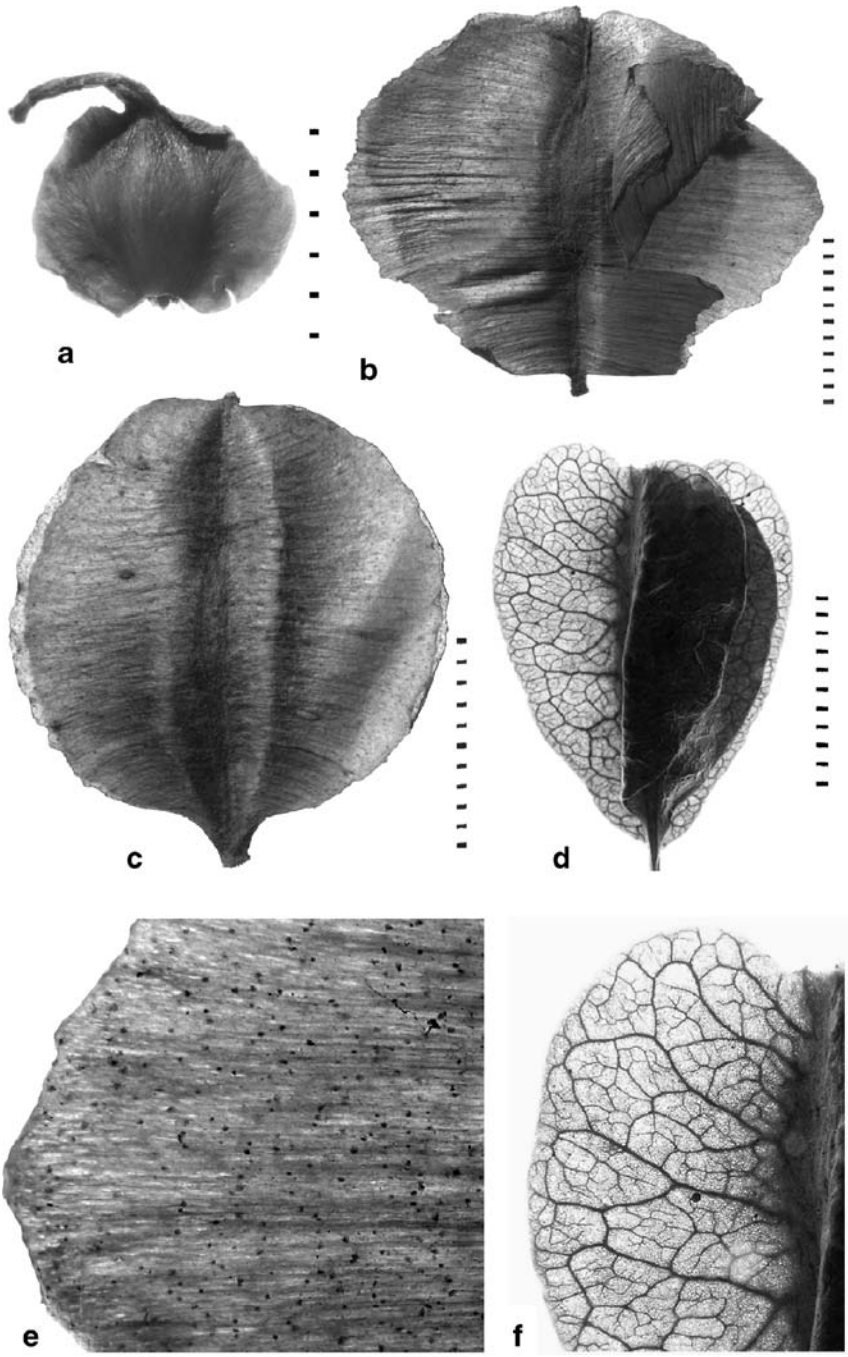


Fig. 6 Combretaceae. **a** *Anogeissus latifolia* (Roxb.) Bedd.; (GH: Wight 1003), eastern India. **b** *Combretum alfredii* Hance (A: E.D. Merrill 14972), Kwangtung, China. **c** *Combretum squamosum* Roxb. (A: G.E. Edaño 17939), Luzon, Philippines. **d** *Macropteranthes fitzalanii* F. Muell. (BARC; US: W.D. Francis sn), Australia. **e** Detail of wing venation from **b**. **f** Detail of wing venation from **d**. Scales calibrated in mm

Dansiea Byrnes, with two species of large trees in Australia, has elliptical 4-winged fruits. The wings, developed from two folded accrescent prophylls, are membranous, with main veins radiating from the lower 1/3 of the central axis, 1–2 mm apart, forming reticulate festooned brochidodromous pattern, looping, with an intervening reticulum of looping finer veins. The wings lack a fimbrial vein.

Macropteranthes F. von Mueller (Fig. 6d, f) is a genus of five species of trees or shrubs in Australia (Stace, 2007). The winged fruits of this genus are wide elliptical to elongate obovate in outline. Calyx lobes may persist at fruit apex. The fruits are pedicellate, and the pedicel may disperse with the fruit. There are four wings, composed of two folded accrescent prophylls. They are chartaceous, with a leaf-like, festooned brochidodromous pattern of reticulate venation consisting of looped secondary and tertiary lateral veins (Fig. 6f). The secondary veins do not reach the margin of the wing, but instead arch to form one or two loops about 1 mm inside of the margin; an outer set of smaller loops formed by the tertiary veins, reaches to the wing margin but there is no fimbrial vein. Areoles outlined by the junction of primary, secondary, and/or tertiary veins are irregularly polygonal to rounded and frequently give rise to one or more freely ending veinlets that are unbranched to twice branched. This pattern of complex venation is somewhat similar to that of *Dansiea*, but distinct from that of *Combretum* and *Terminalia*. This reflects the developmental origin of the wings from prophylls in *Macropteranthes* and *Dansiea*, but from ovary wall in other genera.

Pteleopsis Engl. (Fig. 7a–d) is a genus of shrubs with about ten species of trees distributed in tropical Africa (Stace, 2007). The 2-winged indehiscent fruits are elliptical in outline, sometimes with a v-shaped notch at the apex, and a cuneate base. The narrow pedicel is dispersed with fruit. The wings are chartaceous with fine, closely spaced subparallel venation mostly transverse to the long axis of the fruit. The veins are craspedodromous (not looped at margin); a weak fimbrial vein may be present. Vein density is high, as in *Combretum*.

Terminalia L. (Fig. 7e–i), is a genus of about 190 species of trees and large shrubs distributed pantropically. Whereas all species of *Combretum* have winged fruits, *Terminalia* includes species with large drupe-like fruits as well as those with winged fruits. The latter have 2-, 4-, or 5-winged fruits that range from longitudinally elliptical to widely elliptical, sometimes with a short stylar protrusion. The relatively thick pedicel is sometimes shed with fruit. The wings are chartaceous to coriaceous with radiating subparallel venation, straight to sinuous occasionally dichotomizing and anatomizing, craspedodromous to the margin, without a fimbrial vein. Veins are densely spaced, 2–3 per mm. The margins in some species are easily tattered on drying, but in others the edge of the wing is reinforced by increased vein density through additional dichotomizations near the margin. Fossil fin-winged fruits from the Neogene of Potosi Mountain, Bolivia named *Terminalia antiqua* Britton (1893) YPM, were reexamined for this study at YPM and appear likely to be identified correctly. Some younger reports of this family from the Tertiary of western North America (*Terminalia oregona* (Sanborn) Meyer and Manchester 1997), are no longer considered convincing, because they show numerous longitudinal veins over the locular area that are not seen in any of the extant genera of Combretaceae.

Cucurbitaceae This family includes ca 120 genera, mostly with fruits that are berries, sometimes capsules developed from inferior ovaries. A few genera have

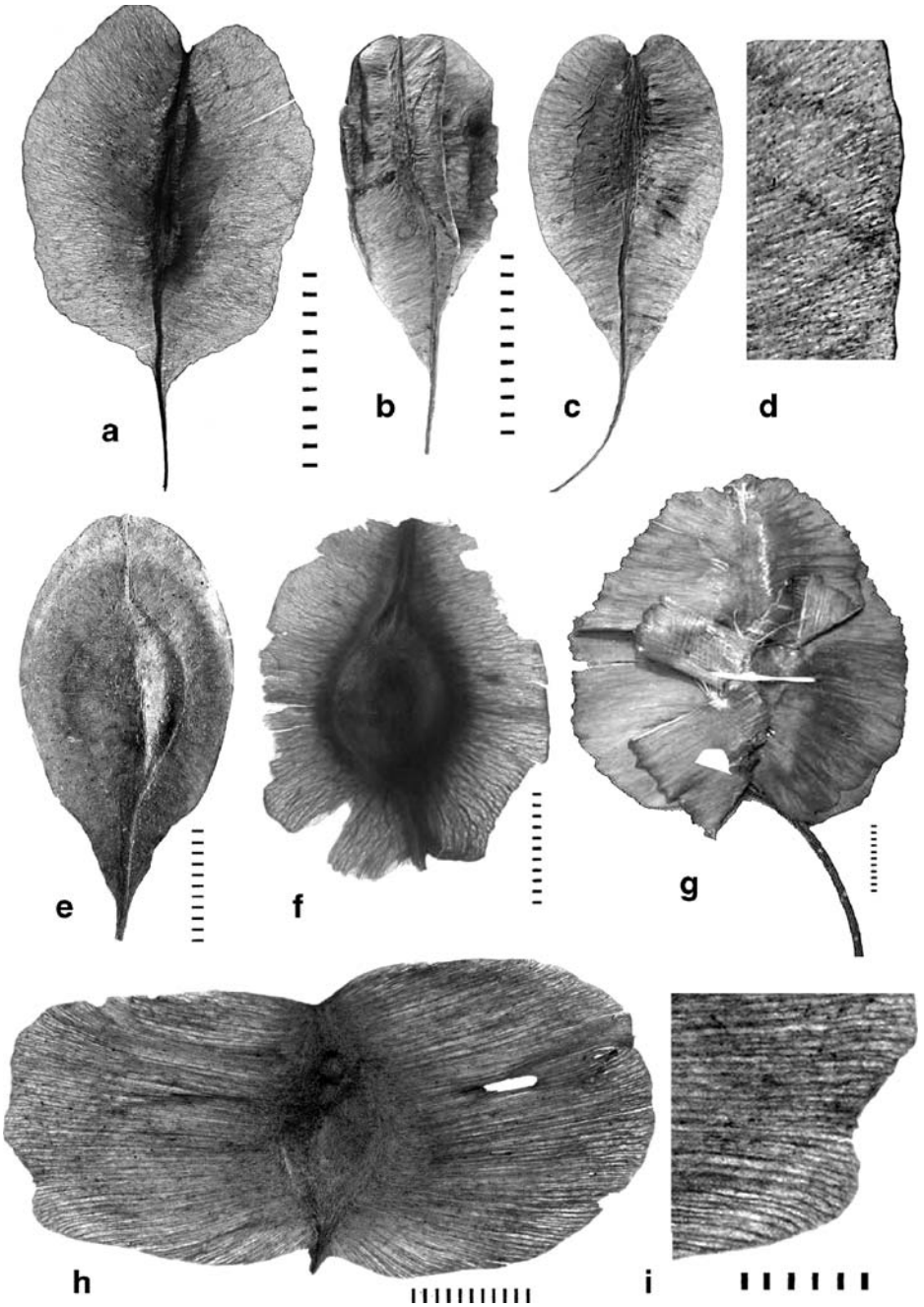


Fig. 7 Combretaceae continued. **a** *Pteleopsis hylodendron* Mildbr. (A: Le Tertu 9492), Gabon. **b**, **c** *Pteleopsis anisoptera* Engl. & Diels. (A: J. Boyle 240). L. Marques, Pretoria. **d** Enlargement of venation from **a**. **e** *Terminalia silozensis* Gibbs (US1991477: Rodin 4496). N. Rhodesia. **f** *Terminalia brownii* Fresen (Harvard Herbaria), Uganda. **g** *Terminalia tomentosa* (A: A.J.S. Butterwick 2), Burma. **h** *Terminalia argentea* Mart. & Zucc. (GH: E.S. Irwin, H. Maxwell, D.C. Wasshausen 19027), Serra dos Pirineus, Brazil. **i** Same, magnified to show details of venation. Scales calibrated in mm

winged fruits (Kearns, 1992), including *Cyclantheropsis*, *Pseudosicydium*, *Pteropepon*, *Sechiopsis*, and some species of *Sicyos*.

Pseudosicydium Harms. (Fig. 8a, b) is a monotypic genus of vines distributed in Peru, Bolivia and Panama. *P. acariaeanthum* produces widely elliptical samaroid fruits with a pair of symmetrical wings fused along a thick median axis connecting from the pedicel to the style. The elliptical endocarp is positioned in the upper half of the fruit, and occupies only about 1/3 of the full length of the wing. Prominent, widely spaced veins (1–2 mm apart) radiate outward from endocarp; most are unbranched to the margin, but a few of the veins dichotomize or anastomose once or twice. The veins extend directly to the margin, joining a fimbrial vein. Between the major veins is a very fine fabric of thin veins (Fig. 8b).

Pteropepon Cogn. (Fig. 8c) includes three species of herbaceous vines in Argentina, Brazil and Peru. Its fruits are indehiscent with 2 (−3?) wings. The fruit is suborbicular in outline with cordate base and apex. A thin pedicel is shed with the fruit, and perianth remnants may persist at the apex. The elliptical locular area has a median rib and a reticulum of isodiametric polygonal areoles. Main veins of the wings, radiating from the locular area, are straight to sinuous, and craspedodromous, joining into a prominent fimbrial vein. These veins are widely spaced, 1–1.3 mm apart.

Sechiopsis Naudin (Fig. 8d) includes five species of annual clambering vines in western Mexico and Guatemala (Kearns, 1992). The single-seeded indehiscent fruit is 2-, 3- or 4-winged depending on the species, cordate at the base, rounded or acuminate at the apex. The fruit of *S. triquetra* is ovate to elliptical, inflated in the locular area, but the distal part of each carpel drawn into a membranous or chartaceous wing with radiating irregular reticulate venation and a thin fimbrial vein. Areoles are polygonal, decreasing in size toward the periphery. The narrow pedicel is dispersed with fruit.

Cunoniaceae With ca 25 genera, this family is diverse in fruit morphology (Dickison, 1984).

Gillbeea F. Muell. (Fig. 8e, f) includes three species of trees and shrubs and is distributed in New Guinea and Queensland. The indehiscent 3-winged fruit develops from a superior, 3-carpellate ovary. It is longitudinally elliptical in outline, with rounded base and rounded to cordate apex. The fruit body is ellipsoidal, mostly confined to the lower half of fruit, producing a strong medial vein to the apex that divides at the apical notch. Three styles persist, one on the apical margin of each wing, and within the apical cleft of the fruit (Fig. 8e). A thick disk persists at base of the fruit, where stamens and the perianth were attached. The fruits are borne on a narrow pedicel that is often retained on twig when the fruit is shed. Wings are derived from the ovary wall. They are chartaceous, with an entire to irregularly undulate margin. Venation consists of a straight axial bundle composed of three strong veins that extend from the locular area directly into each of the three styles, and a system of major lateral veins radiating from the midline of the fruit, these veins irregularly sinuous, running directly to the margin and contributing to the fimbrial vein, or dichotomizing once or twice, sometimes forming a loop near the margin. Areoles elongated with a trend acute to the longitudinal axis of the fruit in the upper half of the fruit, but less elongate, nearly isodiametric in the lower half of the fruit,

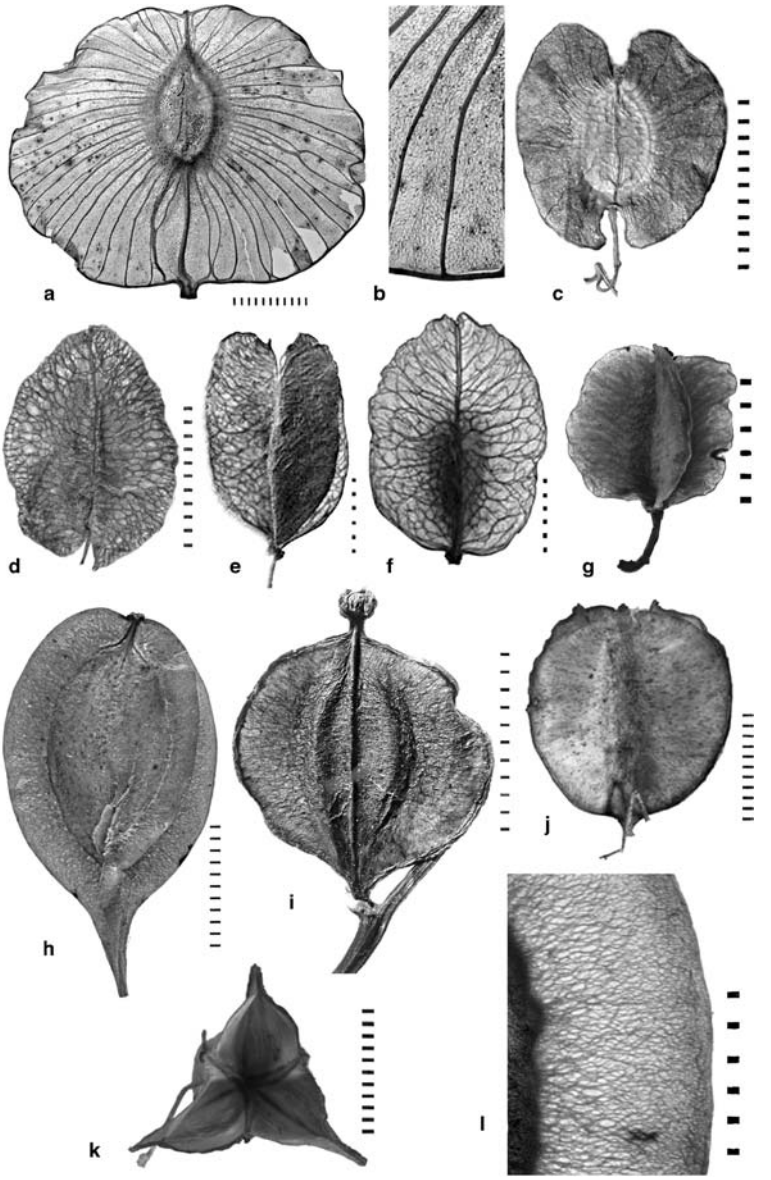


Fig. 8 Cucurbitaceae (**a–d**), Cunoniaceae (**e**, **f**), Cyrillaceae (**g**), Dioscoreaceae (**h–l**). **a** *Pseudosicydium acariaeanthum* Harms. S. Manchester s.n. 2009, Barro Colorado Island, Panama. **b** Detail of wing venation from a. **c** *Pteropepon parodii* Mart. Crov. (NY: M. Nee et al. 52082), Santa Cruz, Bolivia. **d** *Sechiopsis triquetra* (Ser.) Naud. (NY: T.C. Andres & J.J. Wyland 38), Michoacan, Mexico. **e** *Gillbeea papuana* Schltr. fruit showing thick scar of perianth and disk, reticulate venation of wings; one of the three persistent styles is visible at arrow (A: L.J. Brass 31815), Purosa, New Guinea. **f** *G. papuana* (A: W. Takeuchi 6084), Papua, New Guinea. **g** *Cliftonia monophylla* (Lam.) Britt. ex Sarg. (A: Jun Wen 1066), Candler Co., Georgia. **h** *Avetra sempervirens* H. Perrier (BARC; L: Lam and Meeuse 5755), Madagascar. **i** *Dioscorea alata* L. showing persistent epigynous calyx (FLAS: J. Weimer sn), Alachua Co., Florida. **j** *D. quaternata* J.F.Gmel. L. (V. Call 172), Brown Co., Indiana, USA. **k** Same, apical view showing opened capsule from which winged seeds are shed. **l** *Avetra sempervirens* H. Perrier (MO6038777: R. Razakamalala et al. 1642) Madagascar. Detail of wing venation. Scales calibrated in mm

with freely ending veinlets. There are two overlapping patterns of venation on each wing, indicating that two systems developed, and the wing is likely a folded structure.

Cyrillaceae Although *Cyrilla* Garden ex L. has nonwinged capsular fruits, the only other genus placed in the Cyrillaceae family, *Cliftonia* Banks ex Gaertm.f., has small indehiscent fin-winged fruits.

Cliftonia (Fig. 8g) is a monotypic shrub distributed in southeastern US. The fruits have two, three, or four wings and are developed from superior ovary with a corresponding number of carpels. They are longitudinally elliptical to more or less circular. The apex is emarginate, frequently with a thickened stigmatic area and the base is rounded. The pedicel is dispersed with fruit, revealing a prominent hypogynous thickened disk and persistent calyx lobes. The wings are coriaceous. Venation is fine or absent, and the wing tissue striate, with radiating subparallel striae.

Dioscoreaceae In the most recent revision, four genera were recognized in this monocotyledonous family (Caddick et al., 2002). Caddick et al. (2002), proposed a cladistically based recircumscription of *Dioscorea*, sinking the morphologically distinct but cladistically internested genus *Rajania*, which has a distinctive, asymmetrical, single-winged samara. He also favored a merger of the Madagascan fin-winged fruit genus *Avetra* with *Trichopus* of Sri Lanka, India and Malesia. Because of their distinctive fruits, we maintain the traditional classification. The fruits develop from a tricarpellate inferior ovary and the epigynous perianth often persists. Fossil fruits of this family include those described as *Dioscoreocarpum* from the Early Oligocene of Eger–Kiseged, Hungary (Andreánsky, 1959).

Avetra Perrier (Fig. 8h, l) has one species of herbaceous climber in eastern Madagascar. The fruit is 3-winged, indehiscent, obovate–elliptical, rounded apically, with persistent remains of epigynous perianth. The base is acutely narrowed without articulation into the thin pedicel. The fusiform endocarp is centrally positioned. A median vein connects between the endocarp and pedicel and to the fruit apex. The wings spread from the fusiform central body and are enervated with fine, subparallel, fusiform-reticulate venation with areoles becoming smaller and denser toward the margin. Areoles trend perpendicular to the wing margin (Fig. 8l). Vein density is high, 4–6 per mm.

Dioscorea L. (Fig. 8i–k) includes about 350–400 species of lianas widely distributed in tropical and subtropical regions, particularly in seasonally wet climates, with a few species extending into temperate regions. The fruit of *Dioscorea* is a 3-winged, apically opening capsule developed from a 3-carpellate ovary. The fruit dehisces apically to release several winged seeds. In *D. alata*, the fruit is narrowly to widely elliptical in outline, varying from longer than wide to round to wider than long. The endocarp is fusiform, centrally positioned, with a strong median vein extending fully from base to apex of fruit. The fruit is crowned by remains of perianth including six similar tepals, often basally connate into a tube (Fig. 8i). Wings derived from the ovary, with thick marginal suture. Venation is very fine, forming a tight reticulum with striations mostly transverse to the long axis of the fruit.

Fabaceae Several genera in the Fabaceae that have winged fruits and some have samara-like fruits, somewhat convergent with those of *Acer*. Much has been published about the fruits of this family (Gunn, 1984; Kirkbride et al., 2003; Stirton and Zarucchi, 1989) including the morphology and aerodynamics of wind dispersed legumes. The term wing, as applied in the literature on legumes, is frequently used in reference to a narrow marginal flange incomparable to the wings of most fruits considered in the present treatment. However, at least three genera have well-developed fin-winged fruits. Consistent with other members of the family, the fruits develop from unilocular superior ovaries.

Fissicalyx Benth. (Fig. 9a, b) is a member of the dalbergioid legumes, a group which has at least 16 genera with winged fruits (Lavin et al., 2001). *Fissicalyx* has one species of trees in Venezuela and Guyana. It has 2-winged indehiscent pods (Dwyer and Hermann, 1965) which are elliptical in outline with an acuminate apex and emarginate apex, and slight stylar protrusion. The fruits are shortly stipitate, and often are dispersed with the pedicel. Wings, derived from the ovary wall, are chartaceous. A straight, thick longitudinal rib runs along the axis of bisymmetry on both faces of the fruit. The fusiform locular area has reticulate venation with more or less equidimensional areoles, but this reticulum connects with the wing venation pattern which is simple, subparallel, composed of fine veins radiating from the central area out to the margins with occasional dichotomies and anatomoses, and craspedodromous to a fimbrial vein (Fig. 9b). Major vein density is 1–3 per mm. We consider the fossil fruit genus *Dodonaeites* Saporta from the Oligocene of France ("Evaluation of Fossil Fruits," Fig. 21a–g) to be closely similar to *Fissicalyx*.

Piscidia L. (Fig. 9c–e) includes seven species of trees distributed in Central America, the Caribbean and Florida. The fruits are pedicellate, 4-winged indehiscent pods variable in shape from elongate or oblong–elliptical to obovate, to widely elongate, depending in part on how many seeds develop within the pod (see also illustrations in Dwyer and Hermann 1965). The apex is rounded to emarginate, usually with a prominent beak. The fruits are stipitate, commonly with the campanulate calyx persisting at the junction of stipe and pedicel. The locular area is fusiform with a smooth (not longitudinally ribbed) surface. The wings are chartaceous with simple subparallel venation oriented perpendicular to the long axis of the fruit, or (in the apical part), forming an angle of about 70° to the long axis. The main veins are straight to sinuous, occasionally dichotomizing and anatomosing, and are craspedodromous to the margin (Fig. 9e). Vein density is 1.6–2 per mm.

Tetrapterocarpon Humbert (Fig. 9f–h) is a monotypic genus of trees native to Madagascar. The fruits have four wings, but two of them dominate, forming the elliptical outline of the fruit, while the other two are small (1/3 as large as the other two) forming a smaller ellipse centered over the locular area. The apex is emarginate with a narrow persistent style. The base is acute to acuminate and stipitate with a persistent disk at the position of perianth. A median rib or suture runs the full length of the fruit on both faces. The fruits are bilaterally symmetrical with a vertical rib or suture in the center of symmetry, and a fusiform locular area. The wings are chartaceous with complex reticular venation consisting of two to three orders, fanning out from the center line with a subparallel pattern; main veins sinuous, branching irregularly, festooned brochidodromous at margin. Areoles are irregular in shape, bounded by straight and curved veins, mostly elongate (Fig. 9h). Vein density is 1.6–2.2 per mm.

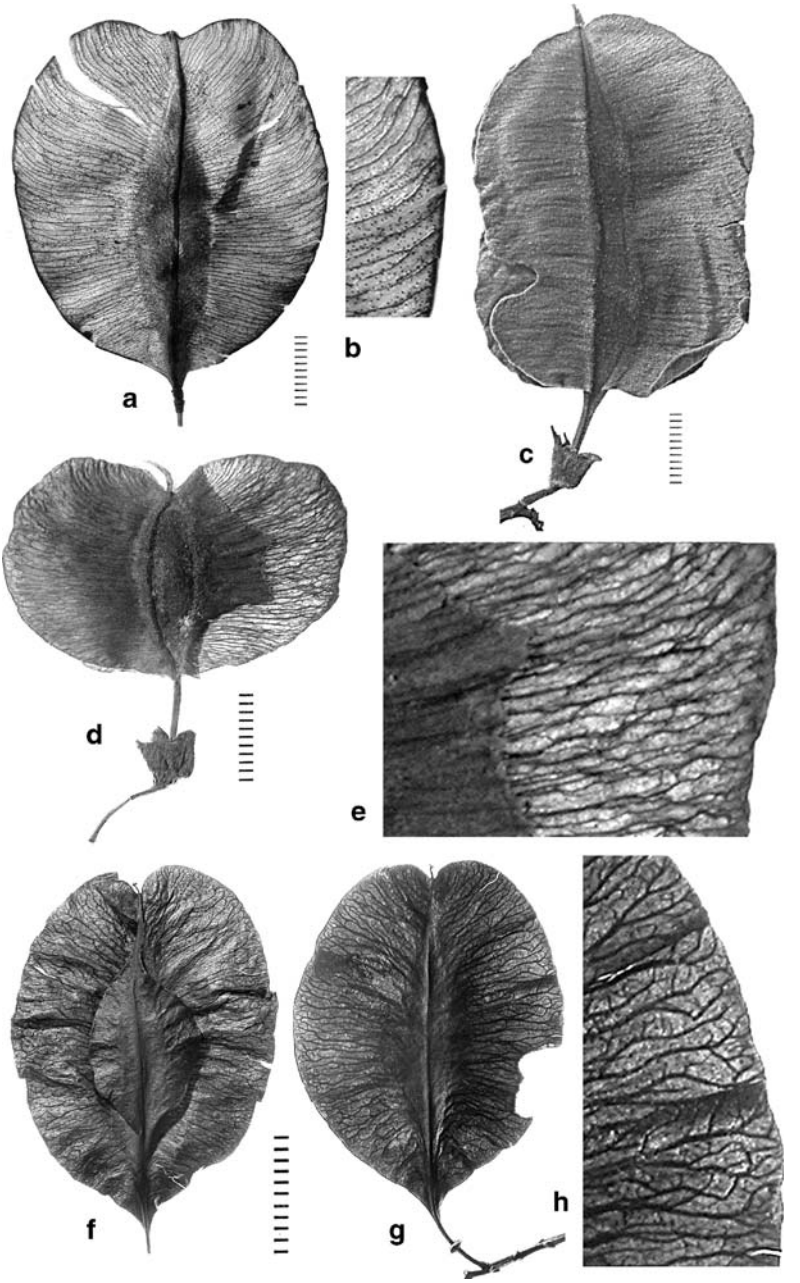


Fig. 9 Fabaceae. **a** *Fissicalyx fendleri* Benth. (MO: R. Liesner & M. Guariglia 11842), Venezuela. **b** Enlargement from **a**, showing craspedodroumous veins. **c** *Piscidia grandiflora* var. *gentryi* Rudd, four-winged fruit showing persistent calyx and stipe at *base* and stylar protrusion at *apex* (MO: M. Sousa, C. Ramos, O. Tellez 6127), Oaxaca, Mexico. **d** *Piscidia carthagenensis* Jacq. with one of the four wings partially broken away, revealing venation of the underlying wing by transmitted light (MO: N. Zamora 2255), Guanacaste, Costa Rica. **e** Enlargement from **d**, showing subparallel fine venation, weak or absent fimbrial vein. **f–h** *Tetrapterocarpon geayi* Humb. opposite sides of same fruit (MO: M.H. Humbert 12827), Madagascar. **h** Enlargement from **g**, showing detail of venation. Scales calibrated in mm

Haloragaceae is a cosmopolitan family of saxifragalean affinities with eight genera and about 120 species ranging from xeric to submerged aquatic plants (Moody and Les, 2007).

Glischrocaryon Endl. (Fig. 10a–c) (syn. *Loudonia* Lindley, see Orchard, 1970); has four species of tufted perennial, herbs in southern and southwestern Australia. The fruits are 2- or 4-winged (or in some cases just ribbed) indehiscent, single-seeded, developed from a 4-carpellate inferior ovary (Kubitzki, 2007). Those of *G. flavescens* are obovate in outline, with acute to attenuate base and rounded to truncate apex, sometimes with persistent calyx at apex of fruit. Fruits are shed without the pedicel but may retain perianth and stylar remains at the apex. Venation is reticulate over the central, fusiform locular areas, but fans outward into the wings in a simple subparallel pattern, with straight to sinuous veins extending to the margin or near to the margin, either forming a loop within the margin, or abutting to the fimbrial vein, with rare freely ending veinlets. Vein density is 4–5 per mm.

Haloragis Forst. & G. Forst. is a genus of about 28 species of annual, perennial herbs and shrubs mostly confined to Australia and New Zealand with fruits that may be smooth, ribbed or winged (Kubitzki, 2007). Those with wings (e.g. *H. gossei*, and *H. odontocarpa*, illustrated by Sweedman, 2006, p. 124), have a fin-winged organization and are tuberculate over the locular area. The fruits are 4-winged developed from an inferior ovary, and have a 4-locular woody endocarp with 1–4 seeds. Prominent calyx lobes persist at the apex. Venation is simple subparallel, brochidodromous, fanning outward from the locular area, forming two to three sets of successively smaller loops toward the margin.

Hernandiaceae This Lauralean family is the only member of the Magnoliids sensu APG (2003) that has winged fruits. Winged fruits occur in three of the five genera (Kubitzki, 1993) but only *Illigera* has fin-winged fruits.

Illigera Blume (Fig. 10f, g) includes about 20 species of scandent shrubs and lianas distributed from Western Africa to Madagascar, and from southern China through Malesia to western New Guinea. The fruit is developed from a unicarpellate inferior ovary, indehiscent, and prominently winged, although coded as a drupe by Renner (1999). It is usually 2-, but sometimes 3- or 4-winged (Kubitzki, 1993) but the 3rd and 4th wings, when present, are reduced in size. Fruit shape is widely elliptical (Fig. 10f), with a cordate to cuneate base and cordate apex, sometimes with style base persisting. Wings, developed from the ovary, are chartaceous, with an entire to slightly undulate margin. Main veins radiate from the endocarp outward into the wings, in subparallel pattern, straight to very sinuous, occasionally dichotomizing and anastomosing, craspedodromous to the fimbrial vein. These veins are spaced 1.4–1.6 per mm, with an intervening dense reticulum of finer veins with more or less isodiametric areoles (Fig. 10g). We now recognize fossil fruits from the Middle Eocene of western North America ("Evaluation of Fossil Fruits," Fig. 22a–e).

Herreriaceae Herreria (Fig. 10d, e) includes seven species of acaulescent to climbing perennial herbs in South America. *Herreria montevidensis* Klotzsch fruits are elliptical 3-winged, longitudinally splitting capsules, rounded basally and apically cordate, borne on relatively thick pedicel. A scar and/or remains of

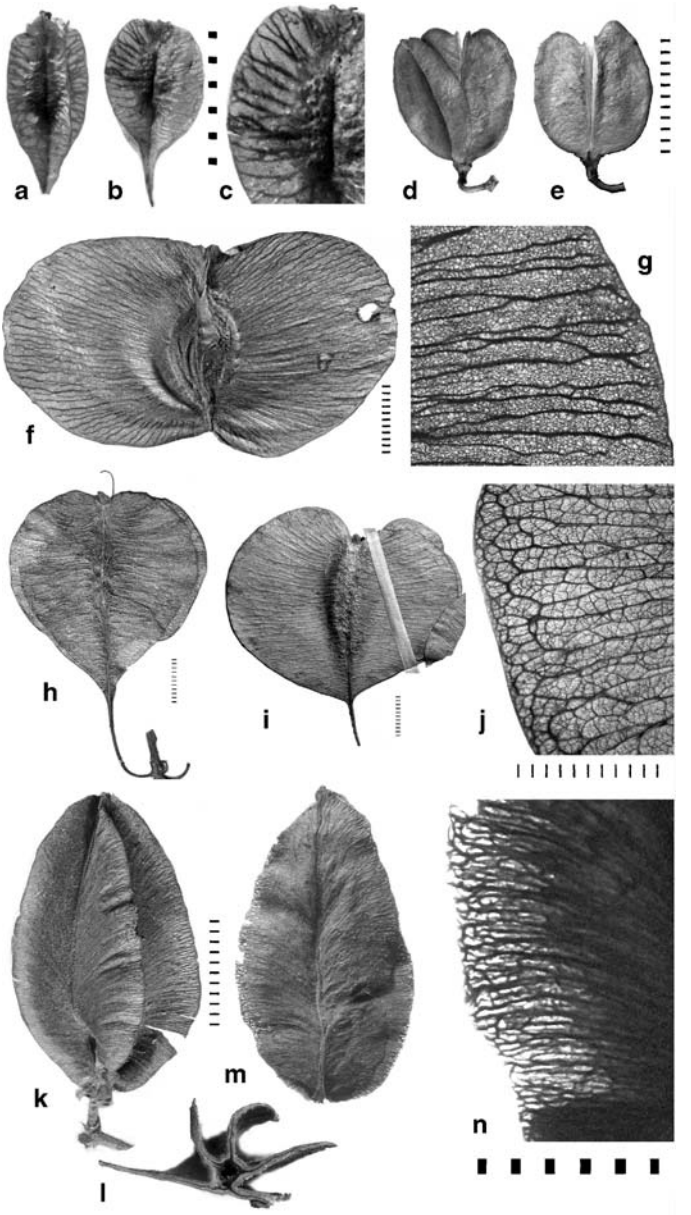


Fig. 10 Haloragaceae (**a**–**c**), Herreriaceae (**d**, **e**), Hernandiaceae (**f**, **g**), Lecythidaceae (**h**–**j**) Lophopixidaceae (**k**–**n**). **a**–**c** *Glischrocaryon flavescens* (Drumm.) Orchard (Dieter Mai seed coll., Humboldt Museum, Berlin: Kings Park, SW Australia, 1987). **d**, **e** *Herreria montevidensis* Klotzsch (MO5900846: M. Nee 51241), Santa Cruz, Bolivia. **f** *Illigera grandiflora* W.W. Sm & J.F. Jeffrey (GH: Li Heng 10346), Gaoligong Shan, Yunnan, China. **g** Enlargement from f showing detail of venation. **h** *Petersianthus macrocarpus* (P.Beauv.) Liben. (K: Erlach 4591), Angola. **i**, **j** *P. macrocarpus* (P: R. Schnell 2799) Macenta, Guinea, W. Africa. **k** *Lophopyxis pentaptera* Engl. (A: D. Sayers NGF 24150), New Britain, New Guinea. **l** *L. maingayi* Hook.f. fruit in transverse section showing single locule and five wings (A: R. Schodde 4063), Bougainville. **m** same in longitudinal view. **n** Increased magnification from **m** with transmitted light showing venation to wing margin. Scales calibrated in mm

hypogynous perianth is situated at the junction of pedicel and fruit. The wings are coriaceous, lacking obvious venation.

Lecythidiaceae Although his family is best known for its woody "monkey pot" fruits with circumscissile capsular dehiscence, it also includes *Petersianthus* Merr., a genus of two species with fin-winged fruits in tropical western Africa and the Philippines.

Petersianthus fruits (Fig. 10h–j) develop from an inferior ovary and are convergent in general form with those of *Combretum,* but with more widely spaced veins. The fruits are indehiscent, 4-locular, 4-winged, elliptical to obovate in outline, emarginate apically and rounded to cuneate basally (Prance and Mori 2004). The locular area is fusiform, situated in the apical 3/4 of the fruit. The wings are chartaceous, with a complex reticulate venation pattern of three or four orders. The main veins fanning from the central axis of the fruit are straight to sinuous, spaced 0.8–1 per mm, and form arches near the margin, with additional small arches at the margin (festooned brochidodromous). Between the main veins is a reticulum of successively smaller veins, forming an irregular mesh of intermediate order and a regular mesh of very fine veins (Fig. 10j).

Lophopyxidaceae Lophopyxis Hook.f. (Fig. 10k–n), a monotypic genus distributed in Malesia and the western Pacific, is the only genus in the Lophopyxidaceae—a family which is now placed in the Malphigiales (Soltis et al., 2005). The indehiscent 5-winged fruit develops from a superior 5-carpellate ovary of five locules with two ovules per locule (Sleumer, 1971), and is obovate, ellipsoidal, or elongate-ovate in outline. The mature fruit is unilocular, and one-seeded (Sleumer, 1971), usually with a persistent short stylar protrusion at the apex, and is subtended by a disk and whorl of five sepals which usually remain on the twig but occasionally are shed in attachment with the fruits. The wings, developed from the ovary, are chartaceous and densely pubescent, with unbranched hairs. Venation radiates from the central axis of the fruit, consisting of fine, closely spaced (four veins per mm) subparallel veins, with frequent diagonal cross veins at irregular angles (Fig. 10n).

Loranthaceae Loranthaceae is known for being parasitic on tree branches. Although most genera have berries, *Nuytsia* R. Br. ex G. Don f. has fin-winged fruits. This is a monotypic genus of trees or shrubs distributed in western Australia. Lamont (1985) studied the dispersal of these fruits and found a maximum dispersal capability of 50 m. The indehiscent 3-winged fruit forms from an inferior ovary and is widely elliptical in outline. The style does not persist but the pedicel is dispersed with fruit. The wings, derived from ovary, are coriaceous with fine, closely spaced striae radiating from the locular area (illustrated by Sweedman, 2006, p. 143).

Malpighiaceae This tropical family includes some genera with drupes, but many with winged fruits, usually schizocarpic. The fin-winged pattern is seen in a few genera.

Aspidopterys A. Juss., (Fig. 11a, b), with about 20 species of lianas in Indomalesia, has schizocarps consisting of three biwinged elliptical to orbicular mericarps. The fruit body is fusiform, confined mainly to the middle, or to the upper half of the fruit. A median vein runs along the lower portion of the fruit, connecting

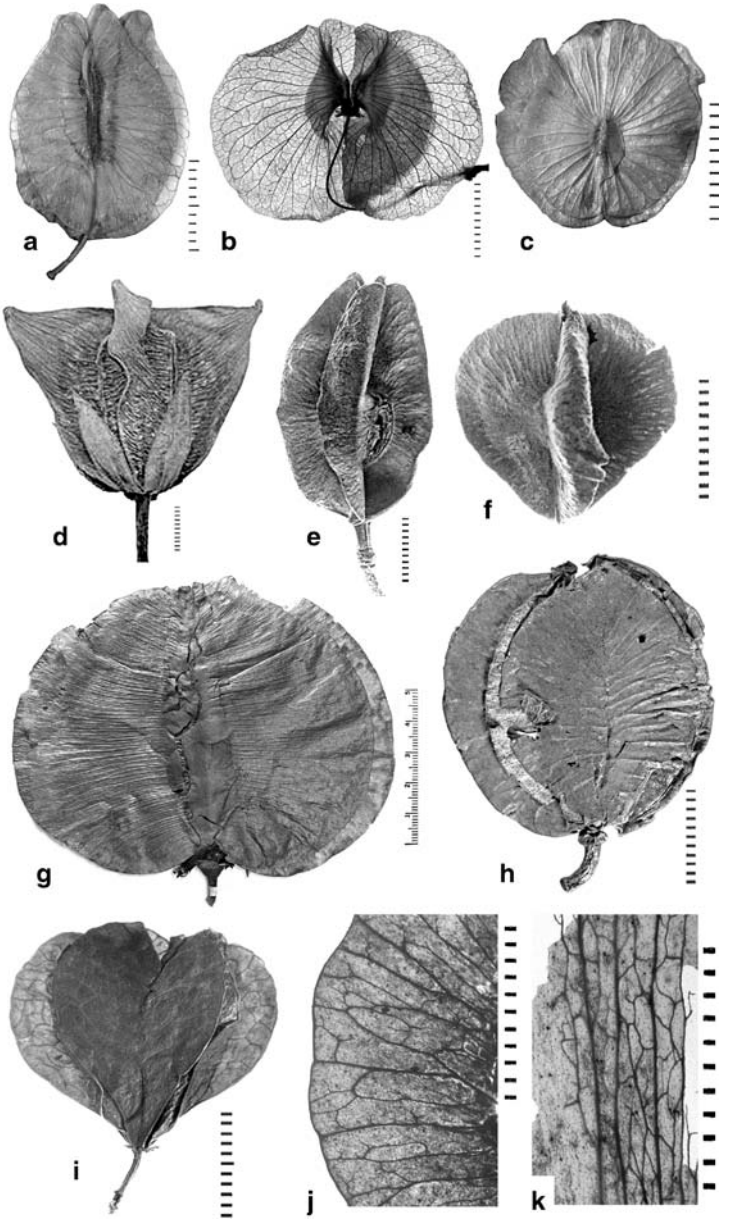


Fig 11 Malpighiaceae (**a**–**c**), Malvaceae (**d**–**k**). **a** *Aspidopterys oligoneura* Merr. UC 1008245: A. Pételot 2100, Vietnam **b** *Aspidopterys elliptica* (Bl.) Juss. A: Ambriansyah & Arifin AA201. East Kalimantan, Indonesia. **c** *Mascagnia divaricata* (J.B.K) Nied., UC 1619431: A. Krapovickas & C.L. Cristóbal 40992, Parana, Brazil. **d** *Abroma angusta* L.f. (A: C. Wang 41264), Kwangsi, China, **e** *Burretiodendron esquirolii* (H. Lév.) Rehder (A: Malelen et al. 1160). **f** *Colona aequilateralis* (C.T. White & W.D. Francis) Merr. & L.M.Perry (A: A.N. Gillison NGF 22206), Papua New Guinea. **g** *Cavanillesia platanifolia* Ruiz & Pav. (GH: P.H. Allen 296), Darien Prov., Panama. **h** *Craigia yunnanensis* Smith et Evans (SYS 163771: Zhuge Ren 10272), Fa-Dao, southeastern Yunnan, China. **i** *Kleinhovia hospita* L. (A: A. Henry 12), Taiwan. **j** Detail of venation, *Craigia yunnanensis* (UF modern fruit ref. coll. 1123), Fa-Dao Yunnan, China). **k** Detail of wing venation, *Cavanillesia platanifolia* (GH: Foster 2247), BCI, Panama. Scales calibrated in mm

between the pedicel and endocarp. The wings are membranous, with venation fanning outward from the endocarp, spaced about 1–1.5 mm apart and extending to the fimbrial vein with occasional cross veins and loops between adjacent veins linking to form an irregular network between adjacent main veins, with occasional freely ending veinlets.

Mascagnia Bert. ex Colla (Fig. 11c) includes about 50 species distributed from Mexico through Argentina. The fruits are orbicular schizocarps composed of three orbicular-winged mericarps. The wings of adjacent mericarps are loosely appressed with one another to give a fin-winged appearance. An additional smaller vertical wing may arise over the locular region of each mericarp. The endocarp is relatively small and confined to the central 1/4 of fruit length. The wings are membranous, with veins radiating in all directions from the endocarp into each of the three valves. The main veins occasionally dichotomize and anatomose and either loop near the margin or join the fimbrial vein. Main vein density 1–1.6 per mm. The main veins are interconnected by cross veins forming polygonal areoles of irregular size and shape, with occasional freely ending veinlets.

Malvaceae Included in the broad concept of this family are Tiliaceae, Sterculiaceae and Bombacaceae as well as traditional Malvaceae. The fruits, which in some cases are fin-winged, develop from superior ovaries.

Abroma Jacq. (Fig. 11d) is a genus of two species of small trees distributed from tropical Asia to Australia. The 5-winged fruit, formed from a pentalocular ovary, is a loculicidal capsule, obovate in outline with a truncate apex and rounded base. The calyx persists at base of fruit but the pedicel does not typically disperse with the fruit. The wings are chartaceous, with thick veins ascending to tips, dichotomizing and anastomosing, occasionally forming transversely elongate areoles. The margins are thickly sutured and the surfaces are covered by tribranched hairs.

Burretiodendron Rehder (Fig. 11e) includes six species of trees distributed in southwestern China, northern Vietnam, Myanmar, and Thailand. The fruits are elliptical, developed from a sessile or stipitate ovary, with five wings. The fruit breaks septicidally into 1-seeded mericarps (Zhuge, 1990). The main veins fan outward into the wings from the elliptical central body, and are straight to somewhat sinuous in course, occasionally dichotomizing and anastomosing. Vein density 0.2–0.4 per mm.

Cavanillesia Ruiz & Pav. (Fig. 11g, k), with three species of tall trees in tropical America has the largest fin-winged fruits of any angiosperm. The huge 5-winged fruit, commonly 12 cm high and 14 cm wide, is an indehiscent capsule formed from a 5-carpellate ovary; it is widely elliptical with a cordate base and apex. There is an apical protuberance, but pedicel does not disperse with the fruit. The broad, membranous to chartaceous wings are derived from the ovary. Wings are supplied with a strong set of subparallel veins, with an intervening reticulum of higher order veins forming areoles of 1 mm or less. The veins are very fibrous and remain as a skeleton after the intervening wing tissue has deteriorated.

Colona Cav. (Fig. 11f) has about 25 species of trees and shrubs distributed from southeastern China through Malaysia, Philippines, New Guinea and the eastern Pacific Islands. The fruits are 5- (to 2-) winged and may be indehiscent, or dehiscent into mericarps (Bayer and Kubitzki, 2003). Wings are chartaceous, with main veins

fanning outward into the wings from the globose central body, sinuous, occasionally dichotomizing and anastomosing craspedodromous to the margin, 2.2–2.8 veins per mm, with an intervening network of finer veins.

Craigia W. W. Sm. & W. E. Evans (Fig. 11h, j) has two species today, found in eastern Tibet and China; but fossils fruits of this genus are common in the Tertiary of North America, Europe and Asia (Kvaček et al., 1991). The fruit is a 5-winged capsule bearing several seeds. The capsules are elliptical with membranous wing-like valves derived from the ovary wall. The main veins radiate from the midline of each valve, and spread toward the margin, straight to sinuous, occasionally dichotomizing and anastomosing, and are craspedodromous to the fimbrial vein. Areoles are elongate with occasionally branched freely ending veinlets. Veins density is 0.5–1 per mm.

Kleinhovia L. (Fig. 11i) is a monotypic genus of trees of Asia and Australia. The fruit is a 5-winged inflated loculicidally dehiscent capsule, obcordate in outline, formed from a 5-carpellate ovary. Remnants of perianth persist at the base of fruit. The fruit is stipitate and the thick pedicel is usually dispersed with fruit. The wings are chartaceous with strong fimbrial veins. Main veins are reticulate, radiating from the central axis. Areoles are irregular, polygonal, more or less isodiametric to transversely elongated, with occasional freely ending veinlets.

Maxwellia Baill. (Fig. 12a) is a small tree endemic to New Caledonia with the unusual condition of having many small seeds in an indehiscent fruit with 3–4 (–5) wings (Wilkins and Chappill, 2002). It is formed from an ovary of 3–4 (–5) carpels and is elliptical in outline, cordate apically and basally. Perianth remnants persist at the base, and the thick pedicel may be dispersed with the fruit. Wings are coriaceous, with subparallel venation radiating from the central body and joining into a margin vein.

Pentace Hassk. (Fig. 12b) has 25 species of trees distributed from Burma to west Malesia. The fruits are 5-winged indehiscent samaras formed from a 2–10-carpellate ovary. Fruits of *P. laxiflora* are elliptical in outline, with perianth persisting at base, and two or more styles persisting at the apex. The relatively thin pedicel is dispersed with fruit. The wings are chartaceous, with subparallel veins radiating from the central axis of the fruit, sinuous with some dichotomizing and anastomosing near the margin, craspedodromous to the fimbrial vein.

Melianthaceae Melianthus L. is a genus of six species of trees and shrubs in South Africa. The fruit is a 4-winged capsule opening apically, often winged or inflated, membranous or leathery, containing multiple globose or pear-shaped seeds (Linder, 2007). The capsule is elliptical to obovate, rounded apically and basally, with a narrow style sometimes persisting that is about 1/3 the length of the fruit. The hypogynous calyx persists with long narrow lobes. The pedicel is ca 1/3 length of the fruit and often disperses with the fruit. The venation comprises two to three orders forming a well-organized reticulum of polygonal areas with occasional free-ending veinlets, with a weak or absent fimbrial vein.

Myodocarpaceae This family was formerly included in the Araliaceae (APG III, 2009). *Myodocarpus* Brong. & Gris. has ten species of shrubs in New Caledonia. The fruit is cordate-shaped with two laterally compressed schizocarpic mericarps. A

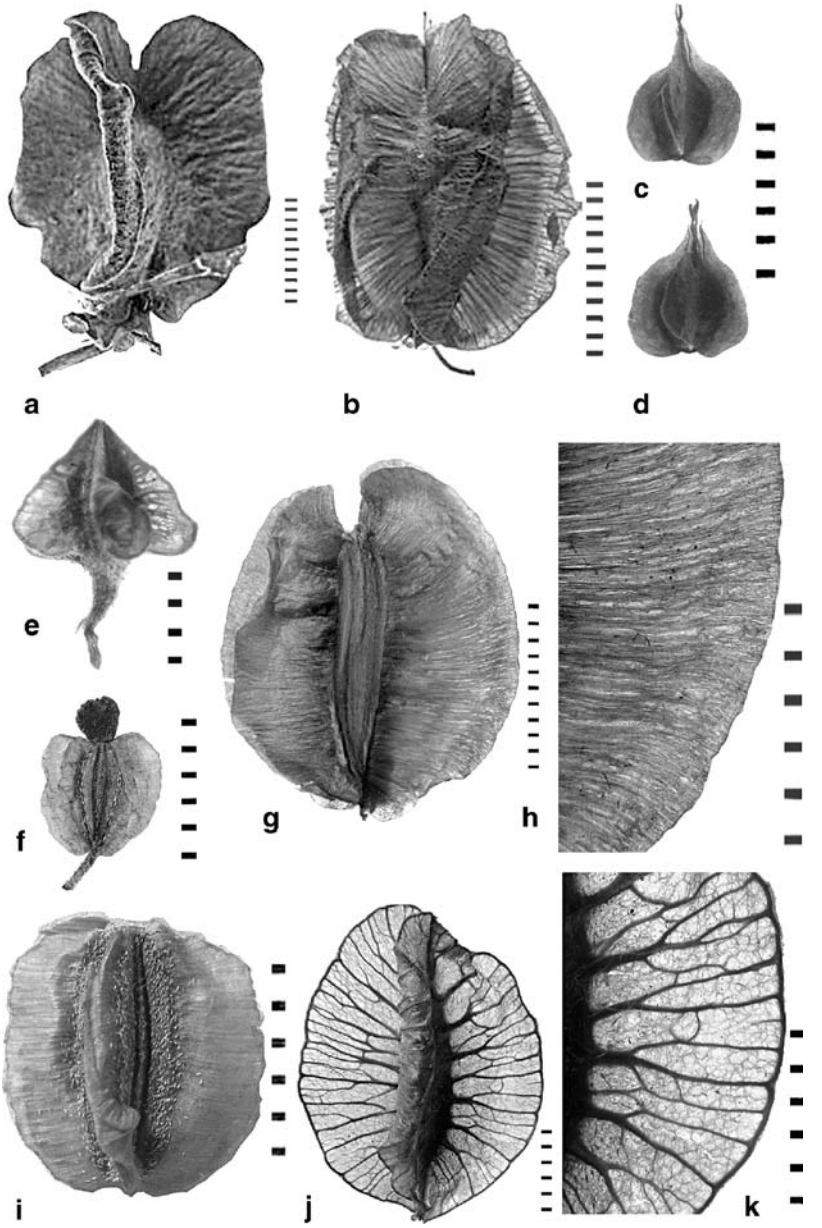


Fig. 12 Malvaceae (**a**, **b**), Nothofagaceae (**c**, **d**), Nyctaginaceae (**e–k**). **a** *Maxwellia lepidota* Bail. (A: Guillaumin et Baumann 13129), New Caledonia. **b** *Pentace laxiflora*Merr. (A: Leopold 78602), Sandakan, Sabah. **c**, **d** *Nothofagus antartica* (Forst) Oerst. (MO 1971548: M. Gusinde 9), Isla Navarino, Argentina. **e** *Abronia fragrans* Nutt. ex Hook. (GH: Forwood 42), SE Idaho. **f** *Ammocodon chenopodioides* (Gray) Standl. (MO 5827773: Siegler, Hilu & May 8497), New Mexico. **g** *Phaeoptilum spinosum* Radlk. (BARC; A: Seydol 3199), Southwest Africa. **h** Detail of wing striation from **g**. **i** *Selinocarpus diffusus* A. Gray (MO 1744905: Reverchon 4283), Texas. **j** *Tripterocalyx micranthus* (Torr.) Hook. [*Tripterocalyx pedunculatus* (Jones) Standl.] (GH: B.R. & C.B. Maguire 4799), Mohave Co., Arizona. **k** Enlargement of wing from **j**. showing lateral veins merging with fimbrial vein, interspersed by a reticulum of finer veins. Scales calibrated in mm

fimbrial vein is developed on each mericarp (Fig. 1B in Liu et al., 2006). The surface of the wing is strongly striate with striae arching downward.

Nothofagaceae Nothofagus Bl. (Fig. 12c, d) nuts are typically trigonal, non-winged, but in some species wings develop along the marginal angles of the nut, as *N. antarctica* (Forst) Oerst. and *N. obliqua* (Mirb.) Oerst. The wings, developed from the ovary wall, are membranous and lack veins. Elsewhere in the Fagales, similar but reduced wings may occur on the trigonal nuts of some *Fagus* species and biwinged fruits occur in *Alnus* and *Betula*.

Nyctaginaceae This family has many species and genera with fin-winged fruits formed from accrescent tepals (Spjut, 1994). Fruits of this family, referred to as anthocarps (Galloway, 1975; Bogle, 1974), are achenes or utricles, developed from a unicarpellate superior ovary often enclosed in the persistent base of the perianth tube. Levin (2000) concluded that winged fruits evolved multiple times within the family because they reoccur in unrelated clades, including *Boerhavia* L. and *Selinocarpus* (Nyctagineae: Boerhaviinae), *Colignonia* Endl. (Nyctagineae: Colignoniinae), *Phaeoptilum* (Nyctagineae: Phaeoptilinae), *Abronia* (tribe Abronieae), and *Grajalesia* Miranda (tribe Pisonieae). Two distinct kinds of wing venation are expressed in the family: 1) dense subparallel and lacking a fimbrial vein (Fig. 12h), and 2) widely spaced major veins, with intervening fine reticulum and having a prominent fimbrial vein (Fig. 12k).

Abronia Juss. (Fig. 12e) has about 20 species of annual and perennial herbs in North America. The fruits of some species are not winged; others have two to five nearly opaque wings with subparallel veins oriented transverse to the long axis of the fruit, and with a fimbrial vein. The wings usually do not extend above and below the fruit body (Galloway, 2003). Venation of the wings corresponds to Nyctaginaceae type 2 (see above). The major subparallel veins are spaced 2–3 per mm, and are craspedodromous to the prominent fimbrial vein. This genus has been thoroughly studied for fruit anatomy (Wilson, 1974, 1975) and dispersability (Wilson, 1976).

Ammocodon Standl. (Fig. 12f) has one species of perennial herb living in the southwestern US and northern Mexico. It has small elliptical indehiscent fruits with 4–5 fin wings and a prominent apical bulge. The narrow pedicel usually is not shed with the fruit. The wings are membranous with fine, closely spaced subparallel veins (Nyctaginaceae type 1, see above) radiating from the central axis.

Phaeoptilum Radlk. (Fig. 12g, h) has one species of shrub in southwestern Africa. The fruit is a 4-winged indehiscent anthocarp, elliptical in outline, square in cross section, with cordate base and apex. The wings, derived from accrescent tepals, are chartaceous and more or less semi-circular. The venation (Nyctaginaceae type 1) consists of straight to sinuous subparallel veins radiating from the central axis.

Selinocarpus A. Gray (Fig. 12i), with eight species of woody perennials in southwestern US and Mexico, is morphologically very similar to *Acleisanthes* A. Gray which has herbaceous perennials. Although molecular work fails to distinguish these genera, *Selinocarpus* species have characteristic five-winged fruits, unlike the ribbed but wingless fruits of *Acleisanthes* (Levin, 2000). Fruits of *Selinocarpus diffusus* are similar in shape and wing venation (Nyctaginaceae type 1) to those of *Phaeoptilum*, but are much smaller.

Tripterocalyx Hook. (Fig. 12j, k) includes four North American species of perennial herbs. Some authors treat this genus within *Abronia*, but Galloway (1975, 2003) maintains them as distinct genera. The fruits have 2–4 membranous, translucent wings arising from a fusiform central body. In contrast with *Abronia*, the wings extend beyond the apex and base of the fusiform fruit body. Veins (type 2) fan outward from the central body, extending straight or with a few branches toward the margin, and entering a prominent fimbrial vein; with a finer mesh between the major veins (Fig. 12k).

Oleaceae This family is represented mostly by drupes, but winged fruits occur in some genera. The familiar samaras of *Fraxinus* appear to have a single wing arising from the seed body, but a median line in the plane of symmetry indicates the suture of two carpels, hence they consist of two wings, positioned as in fin-winged fruits. *Fontanesia* Labill. of western Asia and China and *Abeliophyllum* Nakai, of Korea are also fin-winged, with a pair of wings. In these genera the wings are broader, giving the fruit a more circular outline. Although *Fraxinus* is well confirmed by fruits in the Tertiary fossil record (Call and Dilcher, 1992), other winged-fruited members of the family have still not been observed as fossils.

Abeliophyllum (Fig. 13a, b) is a monotypic genus of shrub endemic to Korea. The fruit is a symmetrical samara with two wings giving a cordate outline (cordate apically and acute basally), shortly stipitate. The fruits are shed with, or without, the narrow pedicel and persistent hypogynous perianth. The venation consists of spreading reticulate veins. The locule is also cordate in outline, somewhat inflated, bisected by the septum and a strong vein continuous with the pedicel and style, in the plane of bisymmetry. An elliptical ovule is pendulous from the apex of each locule. The style persists with a capitate bilobed stigma. The median vein gives rise to pinnate secondary veins that traverse the locules and extend to the wing margins, dichotomizing and occasionally anastomosing. A fine irregular reticulum is formed by tertiary and higher order veins. Wings are chartaceous, entire-margined and lack a fimbrial vein.

Fontanesia Labill. includes two species of shrubs in western Asia and China. The fruits are indehiscent and fin-winged, normally with two wings but rarely three. The locular area is fusiform. The style base (and/or two stylar arms), and hypogynous perianth may persist. The wings are coriaceous, without any obvious venation. These fruits are smaller than those of *Abeliophyllum* and easilly distinguished by the lack of wing venation.

Onagraceae Onagraceae is a family of 18 genera having fruits that can be berries, nut, or loculicidal capsules (Wagner et al., 2007).

Oenothera L. (incl. *Megapterium* Spach) (Fig. 13c) is a genus of ca 120 mainly temperate species native to the Americas. It includes a few species with fin-winged capsules that operate like salt-shakers. The fruit of *Oenothera macrocarpa* Nutt. (=*O. missouriensis* Sims.) is a 4-winged loculicidal capsule developed from an inferior ovary. The fruit is elliptical to nearly circular in outline, with rounded apex and base. Styles and perianth do not persist in the fruit. Wings, derived from the ovary, are chartaceous, sometimes pubescent. Venation tends to be obscure or arching upward with fine, closely spaced radiating striations.

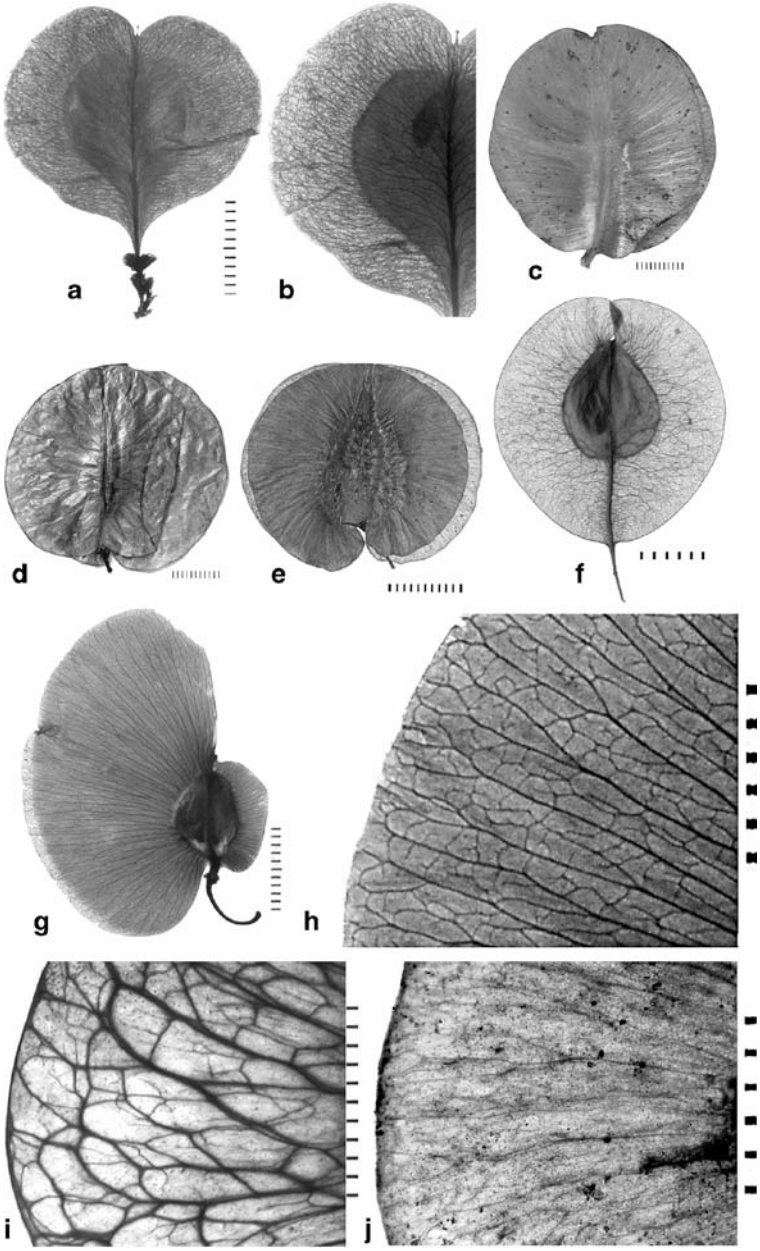


Fig. 13 Oleaceae (**a**, **b**), Onagraceae (**c**), Pedaliaceae (**d**, **e**, **i**, **j**), Phyllanthaceae (**f**), Polygalaceae (**g**, **h**). **a**, **b** *Abeliophyllum distichum* Nakai, UF mod. ref. coll.1415, Morton Arboretum (Native to Korea). **c** *Oenothera missouriensis* Sims. (GH: Merrill 806), Murray Co., Oklahoma. **d** *Holubia saccata* Oliver (BARC; K: Mogg 24419), South Africa. **e** *Pterodiscus aurantiacus* Welw. (A: Dinter 4635), SW Africa. **f** *Hymenocardia ulmoides* Oliver (BARC; US: W. Robyns 799, Belgian Congo). **g** *Phlebotaenia cowellii* Britton fruit with unequal wings. Note that each wing is composed of two coalescent laminae, one which can be seen slightly overlapping at the left margin (BARC; US: Britton 10129), Puerto Rico. **h** Same, detail of venation. **i** *Holubia saccata* Oliv. enlargement from **d**, showing reticulate venation. **j** *Pterodiscus aurantiacus* Welw., enlarged from **e**, showing fine venation. Scales calibrated in mm

Pedaliaceae This family includes two genera with indehiscent fin-winged fruits: *Holubia*, and *Pterodiscus*. In both cases the fruit develops from a superior, bicarpellate ovary.

Holubia Oliv. (Fig. 13d, i) is a monotypic genus of herbs native to southern Africa. The fruit is 4-winged, elliptical to round in outline. Styles and perianth do not persist but the pedicel is often dispersed with fruit. Wings, derived from ovary, are chartaceous, entire-margined to slightly undulate, with a fimbrial vein. Venation radiates outward; subparallel, dichotomizing and anastomosing to form transverse longitudinal to polygonal areoles, craspedodromous to the fimbrial vein.

Pterodiscus Hook. (Fig. 13e, j) has 18 species of perennial herbs of dry open woody and scrub from tropical and South Africa. The fruit is 4-winged, with a bilocular ovary having a single seed per locule. The fruit of *P. aurantiacus* is ovate to wide-ovate to wide-elliptic, with a rounded apex, sometimes with a stylar protrusion, and cordate base. The pedicel is less than 1/4 the length of the fruit, often dispersed with fruit and retaining the remnants of perianth. Wings are chartaceous, developed from the ovary; venation is very fine, forming an elongate reticulum, radiating outward with both dichotomizing and anastomosing particularly towards the fimbrial vein.

Phyllanthaceae Hymenocardia Wall. ex Lindl. (Fig. 13f) is the only wind-dispersed member of the Phyllanthaceae and has previously been placed in Euphorbiaceae, or into its own family, Hymenocardiaceae (Wurdak et al., 2004). The genus has seven species of shrubs and trees, distributed mostly in tropical to South Africa, with one species distributed from southeastern Asia to Sumatra. The fruit is a 2-winged, bilocular bisymmetrical schizocarp formed from a superior ovary. The fruits vary from round-elliptical with a slight apical notch and rounded base with the two wings joining together above and below the locular area (e.g., in *H. ulmoides* Oliv., Fig. 13f) to prominently apically cordate with the two wings free from each other (e.g. *H. acida* Tul.; see Palgrave, 2002). Fruits of the former species have a central ovate locular area positioned in the distal 2/3 of the fruit, with a pair of pendulous seeds. Styles and perianth do not persist. The fruit is stipitate and the narrow stipe and pedicel are usually dispersed with fruit. The chartaceous wings are derived from ovary. A median vein extends along the axis of bisymmetry and over the seed cavity. Main lateral veins radiate transversely and dichotomize and anastomose irregularly, weakening before entering the fimbrial vein. A very fine mesh intervenes the stronger reticulum.

Podostemaceae Winklerella Engl., with one species in west equatorial Africa, has small biwinged capsules with a pair of persistent styles, and two chartaceous wings without venation arising from an elliptical fruit body traversed by three or more longitudinal veins on each face. A v-shaped apical notch is formed by the junction of the two wings. An example of the fruit of *W. dichotoma* is illustrated by Nemirovich-Danchenko (1996, p. 128).

Polygalaceae Fruits of this family are typically capsules, nuts, or drupes, but fin-winged fruits occur in a few cases. The wings develop as a lateral crest along each of the two carpels. Each wing represents two adjacent valves of each carpel, and

actually consists of two appressed laminae, which typically begin to split apart at maturity.

Monnina Ruiz & Pav. (Fig. 14a) has ca 150 species including herbs, shrubs, small trees, and canopy climbers (Gentry, 1993) distributed from the SW United States and Mexico to Chile. Many species have drupaceous fruits but some have winged fruits, e.g., *M. angustifolia*, in which there is a pair of hemielliptical wings. Each wing is membranous and supplied with very fine veins or striae that fan outward from the fruit body, diminishing in route to the margin, sometimes craspedodromous and entering the fimbrial vein.

Phlebotaenia Griseb. (Fig. 13g, h), with two species of trees distributed in Cuba and Puerto Rico, has prominently winged asymmetrical fruits. *P. cowellii* has a pedicellate, stipitate fruit with an elliptical endocarp, and two semielliptical wings of unequal size. Each of the two lateral wings represents one carpel and is a double structure with two distinct venation patterns. Although separation of the two laminae may occur near the margins of the fruit, the wings remain coalescent and do not split sufficiently to allow dehiscence of the seed. Rather, the whole fruit serves as the dispersal unit. The main veins radiate from the fruit body into the wings, with straight to sinuous course, occasionally bifurcating and anastomosing, brochidodromous to the margin; main veins are 1.4–2.2 per mm; the main veins are interconnected by a reticulum of finer veins forming irregular polygonal areoles (Fig. 13h).

Polygala L. (Fig. 14b) is a diverse genus of perhaps 500 species of trees, shrubs and herbs, is nearly cosmopolitan except New Zealand (Banks et al., 2008; Forest et al., 2007). Most species are small herbs or shrubs of open areas and fruits are usually capsular (Gentry, 1993). Although nonwinged fruits are widespread in the genus, winged fruits have developed (Fig. 13b), especially in the *Hebecarpa* group (e.g., Banks et al., 2008, Forest et al., 2007 and references therein). In *P.* cf. *durandi*, the fruit is obpyriform with a retuse apex. An apical protrusion may persist in fruit, and a small disk persists at junction of pedicel and fruit. There is a straight central axis with a single-seeded carpel on either side, flattened and drawn laterally into a rounded wing. The wings have a prominent intramarginal vein, inset 0.5–0.8 mm from the margin. The rest of the veins form a regular polygonal reticulum extending over the entire fruit surface from locular area to the margins.

Polygonaceae The fruit type in this family is an achene, and the wings, when present, generally develop from part of the hypogynous perianth (Fedotov, 1991; Brandbyge, 1993; Ronse Decraene et al., 2000). Genera with fin-winged fruits in at least some of their species include *Calligonum*, *Fagopyrum*, *Fallopia*, *Neomillspaughia*, *Oxygonum*, *Oxyria*, *Parapteropyrum*, *Podopterus*, *Polygonella*, *Pteropyrum*, *Pteroxygonum*, *Rheum*, and *Rumex*. In most cases, the wings are supplied only with very fine, subparallel, fusiform-reticulate venation and lack a fimbrial vein, but in some genera there is a prominent intramarginal vein in each wing. *Calligonum* and *Rumex* differ from the usual pattern, have a complex reticulate, rather than fusiform-reticulate pattern, and *Colligonum* has a prominent fimbrial vein.

Fin-winged fruits of Polygonaceae are readily recognized in the fossil record. Weyland (1937, p. 87, pl. 11, Fig. 1) documented a well preserved fruit from the late Oligocene of Rott, Germany, for which he erected the binomial *Polygonocarpum*

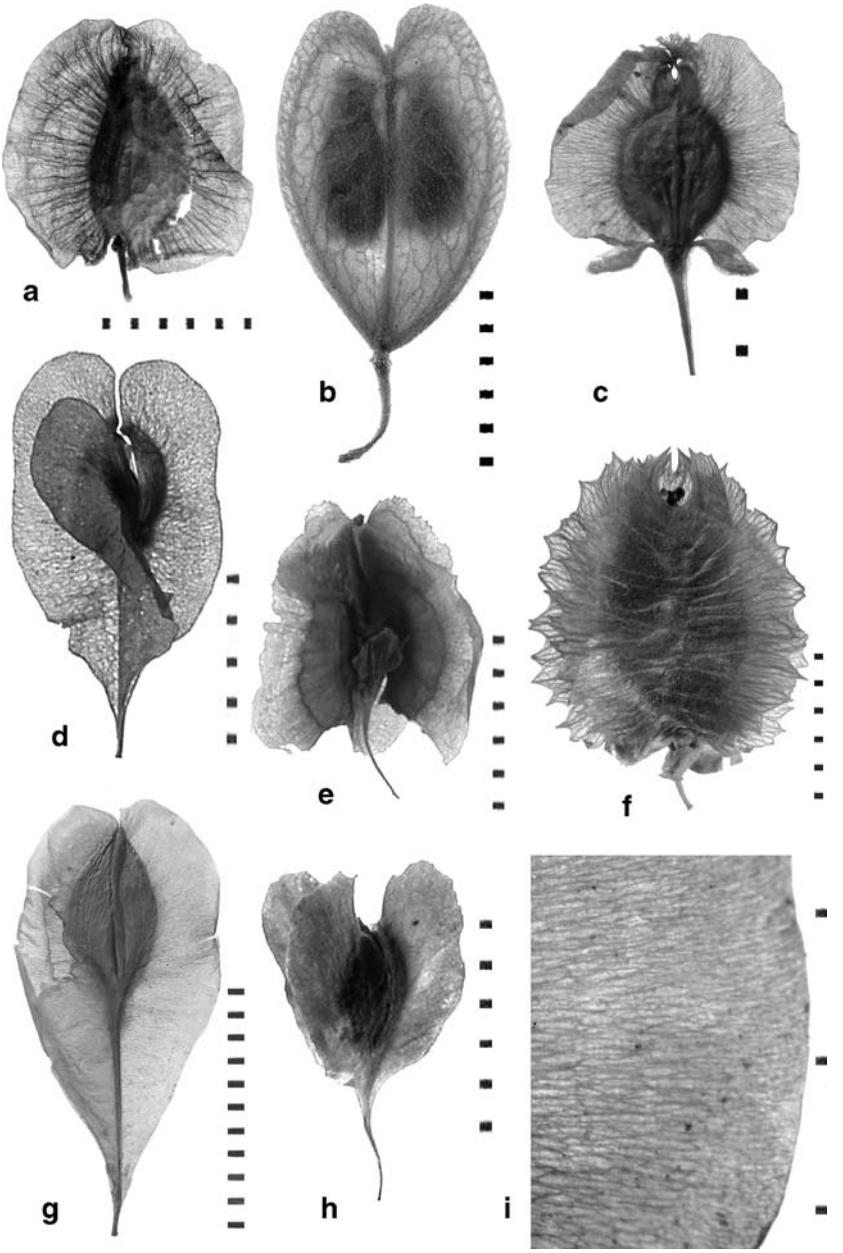


Fig. 14 Polygalaceae (**a–b**), Polygonaceae (**c–i**). **a** *Monnina angustifolia* DC. (MICH: Simon 176), Chile. **b** *Polygala* cf *durandi* Chodat (FLAS: Abbott 19688), Chiapas, Mexico. **c** *Oxyria digyna* (L.) Hill. (GH: Oldenburg 45-701), Mackenzie, N.W. Territories, Canada. **d** *Fallopia japonica* (Houtt.) Ronse Decr. fruit showing three wings, with fine reticulate venation (BARC; W: Togasi 1264), Japan. **e** *Pteropyrum oliveri* Jaub. & Sp. showing prominent veins outlining the locular area (BARC; US: Koelz 16061), Iran. **f** *Calligonum leucocladum* (Schrenk) Bunge, showing serrate margin and fine venation (A: G. N. Nejli 212), northern Tadzhikistan. **g** *Podopterus cordifolius* Rose & Standl. (FLAS184735: E. Lott 3558), Edo. De Jalisco, Mexico **h** *Neomillspaughia emarginata* (Gress) Blake (BARC; MO: Hermilo Quero Rico 2444), Mexico. **i** Detail of wing venation from **g**. Scales calibrated in mm

fimbriatum. It is small, 3.5 mm long and 3 mm wide with at least two lateral wings and a recurved basal pair of sepals (Fig. 22f), similar to the situation in extant *Oxyria*. We now recognize new examples of polygonaceous fossil fruits from the Late Cretaceous and Paleocene of North America, which we present in "Evaluation of Fossil Fruits" (Figs. 22h–j, 23a–m).

Calligonum L. (Fig. 14f) has 80 species of Mediterranean shrubs. The fruit, developed from a 4-carpellate ovary, has two pairs of prominent wings formed by persistent deflexed perianth parts (Ronse Decraene et al., 2000). Fruits of *C. leucocladum* have wings with serrate margins—a condition that is rare among fin-winged fruits. Each of the four wings is double-layered structure formed by acrescence and coalescence of the persistent perianth lobes. Major veins are subparallel, transverse over the central locular area and fan outward into the wings, straight to curved, occasionally dichotomizing, craspedodromous, joining into a thick fimbrial vein. A finer set of veins forms a fine reticulum between the major veins. Vein density is 5–6 per mm.

Fagopyrum Mill. includes eight species of perennial or annual herbs distributed in Asia and eastern Africa. The trigonal achenes are sometimes winged, but were not examined in this study.

Fallopia Adans. (Fig. 14d) includes ~25 north temperate species of herbaceous perennials. The genus has deeply tripartite styles with fimbriate stigmas. As summarized by Mandák et al. (2004), there are three different opinions on the generic classification as applied to *Fallopia*, *Reynotria* and *Polygonum*: 1) All three may be treated as distinct genera, 2) *Reynoutria* is subsumed within *Fallopia* as a section (i.e. *Fallopia* sect. *Reynoutria* (Houtt.) Ronse Decr.) (Ronse Decraene and Akeroyd, 1988); 3) Both *Fallopia* and *Reynoutria* within a broad concept of *Polygonum* (Zika & Jacobson, 2003). For present purposes we follow the second option. The fruit of *Fallopia* (additional illustrations in Bojnansky & Fargasova, 2007) is obovate with a cuneate base and retuse apex, with three longitudinal lateral wings. Venation of the wings is fusiform reticulate, forming a fine reticulum, with elongate polygonal areoles and a fimbrial vein. Vein density is high, 8–10 per mm.

Neomillspaughia S.F. Blake (Fig. 14h) includes two species of shrubs or small trees endemic to Central America. The fruit is 3-winged, obovate in outline with a cuneate base and retuse apex. The achene is trigonal in cross section and obovate in face view, borne on a very thin pedicel. The membranous wings develop from accrescent perianth (Brandbyge, 1993) and have a fine fusiform-reticulate venation similar to that of *Fallopia*.

Oxyria A. Hill (Fig. 14c) is a monotypic genus of Arctic and alpine perennial herbs of Europe, Asia, and North America. The fruit is bicarpellate, lenticular and broadly 2-winged. The achene is elliptical with two persistent appendages at base, a pair of semicircular wings, and a persistent apical stigmatic frill (Fig. 14c). The wings have fine, subparallel fusiform-reticulate venation fanning outward from the fruit body with occasional convex-rounded crossveins. There is no fimbrial vein. The fruit of *O. digyna* (L.) Hill is also diagrammed by Bojnansky and Fargasova (2007).

Parapteropyrum A. J. Li. includes one species of small shrub in Tibet. The fruits have 3-winged achenes. The achenes are obovate in face view, trigonal in transverse

view. The hypogynous perianth persists in fruit with two smaller segments basally recurved and three others enlarged and coalescent with the achenes. Wing venation is fine, subparallel fusiform-reticulate, without a fimbrial vein but with a prominent intramarginal vein (diagram in Ying et al., 1993).

Podopterus Humb. & Bonpl. (Fig. 14g, i) has three species of shrubs and small trees in Mexico and Guatemala. The fruits are 3-winged, with wings decurrent on the pedicel. The elliptical achene is situated in the upper 2/3 of the fruit, connected by a prominent vertical rib connecting to the pedicel without articulation. The wings have a fine, subparallel fusiform-reticulate venation system oriented mostly transverse to the longitudinal axis of the fruit joining to a fimbrial vein. We recognize a fossil species of this genus from the Paleocene of North Dakota (see "Evaluation of Fossil Fruits").

Polygonella Mixchx. has several species of shrubs in eastern North America. The fruits may be nonwinged, or winged, depending on the species. Fruits of *P. americana* (F. & M.) Small develop from flowers with five sepals, the three inner ones forming orbicular cordate wings and the two outer becoming recurved in fruit (Britton & Brown, 1913).

Pteropyrum Jaub. & Spach (Fig. 14e) has five species of shrubs in southwestern Asia and the middle East. The fruits are 3-winged achenes with cordate-ovoid, membranous wings. A prominent arched vein in each wing outlines the locular area, midway between the central axis of the fruit and the distal wing margins. Remaining veins form a fine radiating reticulum similar to that of *Fallopia*.

Pteroxygonum Damm. & Diels has a single species of perennial herbs in central China. It has a distinctive winged achene with three sharp horns at the base and an elongate floral tube in the fruiting stage (Sun et al., 2008). Although some authors considered this species to belong within *Fagopyrum*, Sun et al. (2008) provide molecular and morphological evidence favoring the separate generic status. The wings have subparallel fine fusiform venation, and no fimbrial vein, but have an intramarginal vein (Fig. 10 in Sun et al., 2008; Ying et al., 1993).

Rheum L. (Fig. 15a, c) has about 30 species of temperate and subtropical perennial herbs in Asia and eastern Europe. As seen in *R. turkestanicum* (Fig. 15a), the fruits are ovate with cordate base and rounded apex, and have longitudinal three hyaline wings. A coarse intramarginal vein is situated about 1.2 mm inside the margin of each of the wings. Two or three similarly strong veins extend from the central body across each wing to join the intramarginal vein. The remaining tissue of the wing, both inside and outside the intramarginal vein, is enervated with a fine reticulum (Fig. 15c) similar to that of *Fallopia*. Additional species are described and illustrated by Bojnansky and Fargasova (2007, p. 129–123).

Rumex L. (Fig. 15b) is a genus of about 200 species of herbs and shrubs widely distributed in temperate areas particularly Northern Hemisphere. The 3-winged fruits of 19 species are illustrated in Bojnansky and Fargasova (2007, p. 115–119). The fruit is indehiscent, obovate to wide–elliptical. The hypogynous calyx has six sepals; the three outer ones remain unchanged near the base of the fruit, while the three inner ones mostly develop into the fruit wings which may be entire, dentate, or fringed with spiny teeth (Britton & Brown, 1913). As seen in *Rumex venosus* the wings are chartaceous; venation forms a reticulum with main veins running laterally into each wing, straight to sinuous, interconnecting to form polygonal areoles that

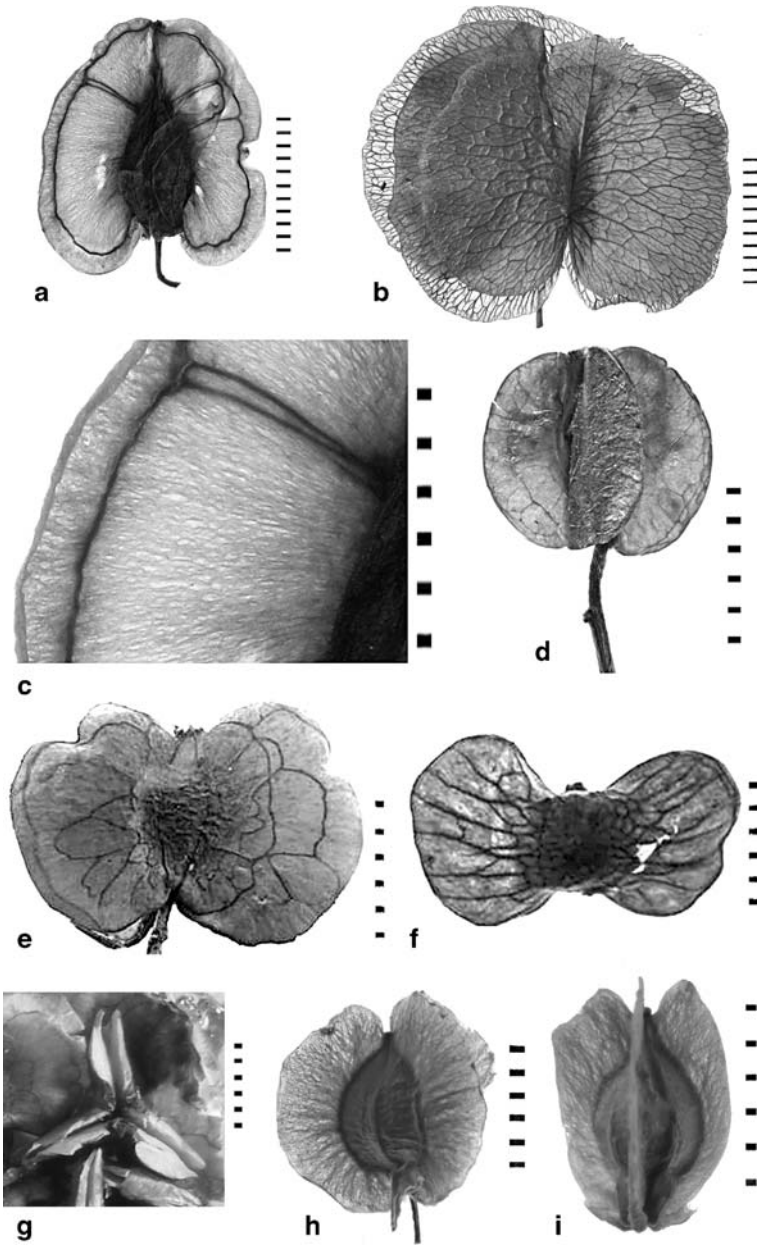


Fig. 15 Polygonaceae (**a**–**c**), Rhamnaceae (**d**–**g**), Ruscaceae (**h**, **i**). **a** *Rheum turkestanicum* Janisch (Mo 5614037: Kurbanov 1102), western Kopet Dag, Turkmenistan. **b** *Rumex venosus* Pursh (GH: Drake & Dickson, s.n., May 30, 1886), Umatilla River, Oregon. **c** Enlargement of wing venation from a. **d** *Crumenaria polygaloides* Reiss. (GH: Dusén 10866), Brazil. **e** *Gouania lupuloides* Urb. (A: L. Rodriguez 2566), Guadeloupe, French Antilles. **f** *Reisseika cordifolia* Standl. (BARC; GH: L.O. Williams & V. Assis 6834), Minas Gerais, Brazil. **g** *Gouania lupuloides* apical view showing a fruit separating along the wings into three valves (GH: Brumbach 9537), Florida Keys, USA. **h** *Beaucarnea gracilis* Lem. (MO 4914514: O'Kane, Collwell & Salinas 3410), Puebla, Mexico. **i** *Dasylirion wheeleri* S. Wats. ex Rothr. (GH: Waterfall 3916), SW Texas. Scales calibrated in mm

diminish in size toward the margin; festooned brochidodromous. Vein density is 0.7 per mm.

Rhamnaceae This family of about 50 genera includes some genera with drupaceous fruits and others with dry schizocarpic fruits. Winged fruits occur in several genera. Anatomy and dispersability of the winged fruits of one subfamily, the Gouaniaeae, has been studied in detail (Medan, 1988).

Crumenaria Mart. Nov. (Fig. 15d) has six species of annual or perennial herbs in tropical Brazil, northeastern Argentina, and Guatemala. The fruit is a 3-winged schizocarp derived from a 3-carpellate superior ovary, separating septicidally into three 2-winged cocci. The fruit is elliptical in outline, slightly emarginate apically and basally. The wings of adjacent mericarps are coalescent, until separating at maturity. The perianth and style are not persistent. Each of the six semicircular wings is chartaceous, supplied with a low-density venation that includes both a marginal vein and a sinuous arched intramarginal vein. These veins and those of the central body interconnect in a reticulate pattern forming areoles of irregular shape and size.

Gouania Jacq. (Fig. 15e, g), including *Pleuranthodes* Weberbauer according to St. John (1969), is a pantropical genus with about 50 species of climbing shrubs and lianas. The fruit is a 3-winged schizocarp derived from a 3-carpellate superior ovary, separating septicidally into three 2-winged cocci (Medan and Schirarend, 2004). The fruit is widely elliptical in outline, with a persistent apical disk, and a basal stipe. The wings are coriaceous with venation consisting of a meshwork of irregularly spaced veins forming large irregular areoles delimited by both curved and straight veins. The venation pattern of each wing is distinct from the others of same fruit, but typically includes both a marginal vein and an intramarginal vein (Fig. 15e).

Reissekia Endl. (Fig. 15f) is a shrub native to Brazil with one species (Medan and Schirarend, 2004). The fruit is an inflated 3-winged schizocarp developed from a tricarpellate, superior ovary. The two wings of each mericarp are chartaceous. As seen in *R. cordifolia* (Fig. 15f), a retiticulum is formed over the central locular area; main veins of the wing fan out from the locular area and are straight and craspedodromous, entering into strong fimbrial veins. There are occasional cross veins. Vein density is 1–1.25 per mm.

Ruscaceae The Ruscaceae is a family in the order Asparagales that includes several genera previously included in the Liliaceae in the Cronquist system. The Angiosperm Phylogeny Group (APG III, 2009) system recommends its inclusion in Asparagaceae but allows for its optional recognition as a monophyletic family (Hernandez-Sandoval, 2001).

Beaucarnea Lem. (Fig. 15h) has about eight species of xerophytic trees in Central America having slender stems with swollen bases. The fruits are 3-winged "indehiscent capsules" (Hernández and Zamudio, 2003) or samaras (Bogler, 1998) wide-elliptical in form with semicircular wings. The fruits have a persistent hypogynous calyx and a moderately thick pedicel. The endocarp is trigonal in cross section, and ovate in lateral view, with a median vertical suture on each face. Wings are chartaceous, supplied with fusiform-reticulate venation, consisting of very fine,

densely spaced veins radiating from the central body, dichotomizing and anastomosing, forming smaller areoles distally.

Dasylirion Zucc. (Fig. 15i), with about 16 species of shrubs in Mexico and the southwestern United States, has 3-winged samaras (Bogler, 1998) that are morphologically very similar to those of *Beaucarnea* (compare Fig. 15h, i).

Rutaceae Within Rutaceae, indehiscent fin-winged fruits occur within the subfamilies Pteleinae (*Ptelea* and *Balfourodendron*) and Spathelioideae (*Spathelia*), and in the group previously treated as Ptaeroxylaceae (*Bottegoa*). The thickened area at junction of the fruit with pedicel, bearing scars of the hypogynous perianth and floral disk, beneath a very short stipe (Fig. 16i) are useful in the identification of winged fruits belonging to this family.

Balfourodendron Mello ex Oliv. (Fig. 16a, e) includes two species of trees in Brazil, Paraguay and Argentina (Pirani, 1998). The 4-winged indehiscent fruit forms from a 4-carpellate ovary and typicaly has three single-seeded locules in which most of the seeds are aborted (Pirani, 1998). The fruit is wide-elliptical in outline, and stipitate, with remnants of hypogynous perianth, and sometimes the style base, persisting. The chartaceous wings have complex-reticulate venation with main veins subparallel, extending from the central area to the margins, sinuous, arching downwards, irregularly bifurcating and anastomosing, with some veins looping near the margin, others craspedodromous to the fimbrial vein. Intervening finer veins are of at least two orders, forming an irregular fine reticulum with small polygonal areoles with freely ending veinlets (Fig. 16e).

Bottegoa Chiov. (Fig. 16b) is a monotypic genus of shrubs or slender trees in Ethiopia, Kenya and Somalia. A detailed morphological and anatomical analysis of flower, fruit, seed, leaf and pollen indicates sapindalean affinity within the Ptaeroxylaceae (van der Ham et al., 1995), which is currently placed in the Rutaceae (Soltis et al., 2005). The fruit is a subcircular samara with retuse apex and base with a central rounded locular area surrounded by a pair of wings. A remnant of the style protrudes slightly form the apex. A slender pedicel and stipe are usually dispersed with the fruit. The wings are chartaceous, derived from the ovary, with subparallel venation radiating from the locular area. The main veins are craspedodromous, spaced ca 1 mm apart, joining a fimbrial vein.

Ptelea L. (Fig. 16c) includes about 11 species of small trees and shrubs in North America (Bailey, 1962). The fruit is a samara of two (to rarely three wings on the same specimen) wings formed from an ovary of 2 (−3) carpels. Fruit outline varies from round to elliptical. A remnant of the style protrudes slightly from the apex, while remnants of a hypogynous disk and perianth are found at the junction with the slender pedicel which is usually dispersed with the fruit. The wings are chartaceous, derived from ovary. In *P. crenulata* the veins dichotomize and anastomose irregularly forming elongate areoles; in *P. trifolata* the main veins are oriented transversely across the locular area, fanning outward into the two semicircular wings. Main veins of the wing are subparallel, dichotomizing and anastomosing, often craspedodromous to a fimbrial vein, but also forming loops to create a reticulum of polygonal areoles (Fig. 16c).

Fossilized *Ptelea* samaras from North America were critically examined by Call and Dilcher (1995). They found a combination of three features to be particularly important in identifying the fruits of this genus: 1) Superior ovary demonstrated by

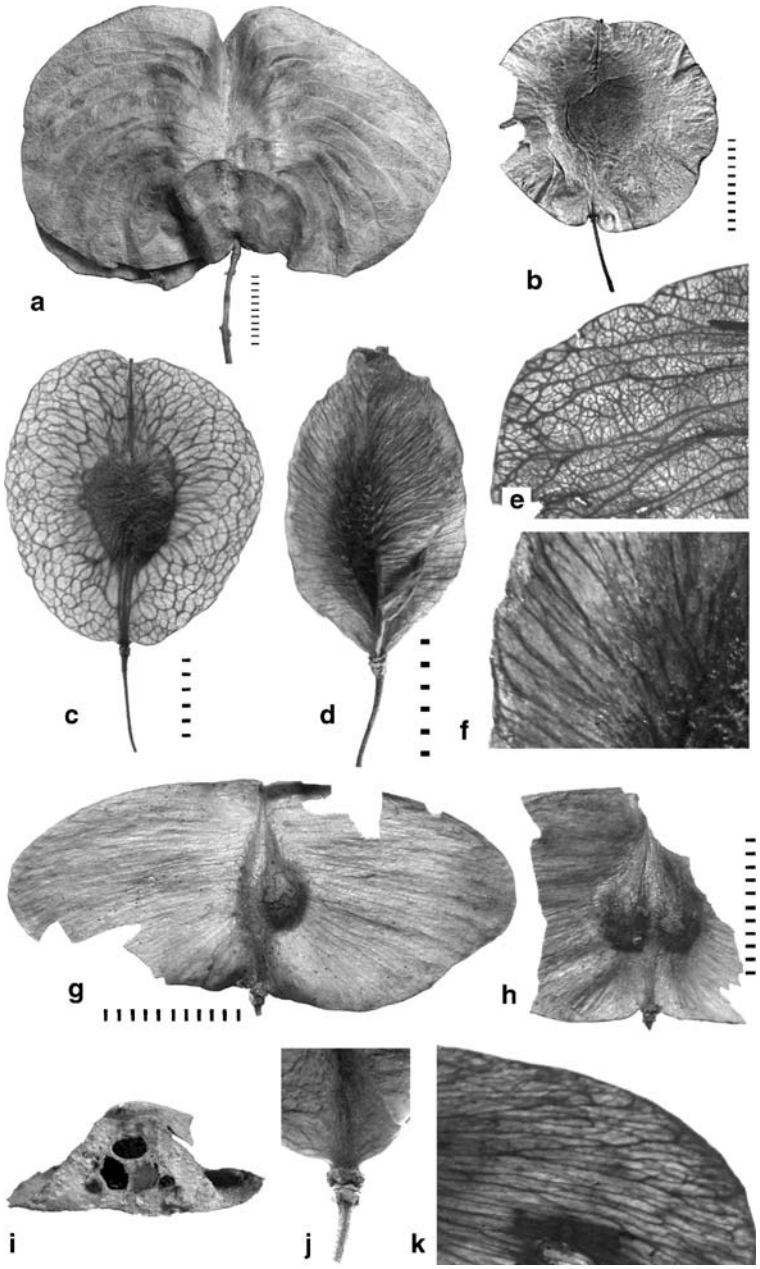


Fig. 16 Rutaceae. **a** *Balfourodendron riedelianum* Engl. (MO 5999750: R. Vanni, et al. 891), Argentina. **b** *Bottegoa insigna* Chiov. BARC sn, Ethiopia. **c** *Ptelea trifoliata* L. (FLAS: J.C. Easterday 856), Paynes Prarie, Florida. **d** *Spathelia pinetorum* M. Vict. (GH: Clemente 4424), Cuba. **e** Enlargement of fruit wing venation from *Balfourodendron riedelianum* Engl., same specimen as **a**. **f** Enlargment of the wing from **e**. **g** *Spathelia terminalioides* Gentry (MO: Gentry et al. 31751), Maynas Prov., Peru., fruit with only two wings, wider than high. Only one seed has developed. **h** Fragmentary specimen from same collection as **f**, showing the bulges of two pendulous seeds, one in each carpel. **i** Transverse section of the fruit showing three locules, *Spathelia glabrescens* Planch. (GH: G.R. Proctor 15652), Jamaica. **j** Detail from **d**, scars on pedicel typical of Rutaceae. **k** Detail of venation from **g**. Scales calibrated in mm

floral disk at the base of the fruit where it joins the pedicel, 2) wings fused above and below the locule, and 3) three slightly diverging veins extending medially through the lower half of the samara forming a coarse transversely oriented reticulum over the surface of the fruit body and a radiating looping reticulate pattern on the wings. We recognize an additional species from the Eocene of North America, *P. paliuroides* (Brown) comb n. ("Evaluation of Fossil Fruits," Fig. 24d–g).

Spathelia L. (Fig. 16d, f–j) includes 15 species of trees in the West Indies to northern South America. The fruits are samaroid, indehiscent, usually with three (or two) wings and usually longer than wide. The fruit of *S. pinetorum* (Fig. 16d) is typical with an elliptical samara formed from an ovary of 2 (−3) carpels. The fruit is dispersed with the narrow pedicel including a prominent scar of disk and perianth at junction with fruit. The wings are chartaceous with main veins subparallel, radiating from the central area into the wings, craspedodromous, joining a fimbrial vein (Fig. 16f). S. *terminalioides* fruits have just two wings and are more than twice as wide as long (Fig. 16g) such that they "look almost exactly like those of *Terminalia*" Gentry (1993, p. 753). In comparison with the highly similar fruit of *Terminalia argentea* (Fig. 7g), they may be distinguished by the typical rutaceous double thickening at the top of the pedicel (Fig. 16h) which is lacking in the fruits of Combretaceae which develop from inferior ovaries. Venation fans outward into the wings from the locular area, straight to sinuous, bifurcating and anastomosing to form elongate areoles, craspedodromous, joining to a fimbrial vein (Fig. 16k).

Salicaceae The willow family, now considered to include many former Flacourtiaceae as well as *Salix* and *Populus,* includes a variety of fruit types. Fin-winged fruits occur in *Neopringlea* S. Watson (Fig. 17a) which includes three species of shrubs widespread in Mexico and Guatemala (Lemke, 1983). The fruit is a small symmetrical 3-winged elliptical samara with a retuse apex and rounded base. Hypogynous perianth lobes persist at the junction with the pedicel and stylar remnants sometimes persist at the apex. The locule is rather inflated, and the three wings are membranous, supplied with simple subparallel venation that is craspedodromous to the fimbrial vein.

Sapindaceae The Sapindaceae includes many genera with fruits adapted for wind dispersal. Some of these fruits are fin-winged (e.g., *Dodonaea*, *Paulinia*) and others are balloon-like capsules (e.g. *Arfeuillea*, *Boniodendon*, *Cardiospermum*, *Conchopetalum*, *Koelreuteria*, *Erythrophysa*, and *Stocksia*). Depending on the extent of inflation, in some instances the balloon-like capsules intergrade with the fin-wing morphology, leading us to include *Koelreuteria* and *Boniodendron* in this treatment. All develop from superior ovaries, and generally show remnants of perianth and/or disk at the junction of pedicel with base of the fruit. All of the fin-winged fruits have a fimbrial vein. Detailed comparisons of the fruits of the Paullineae have been made by Weckerle and Rutishauser (2005). Genera with fin-winged fruits include *Bridgesia*, *Dodonaea*, *Majidea*, *Stocksia*, and *Urvillea*.

Boniodendron Gagnep. (=*Sinoradlkofera* F.G. Mey.) (Fig. 17h, i) is a monotypic genus of trees in southern China and Vietnam. The fruits are three-winged, trilocular loculicidal capsules. A prominent scar from hypogynous perianth and floral disk occurs at the top of the pedicel as in other Sapindaceae (Fig. 17h). Main veins are

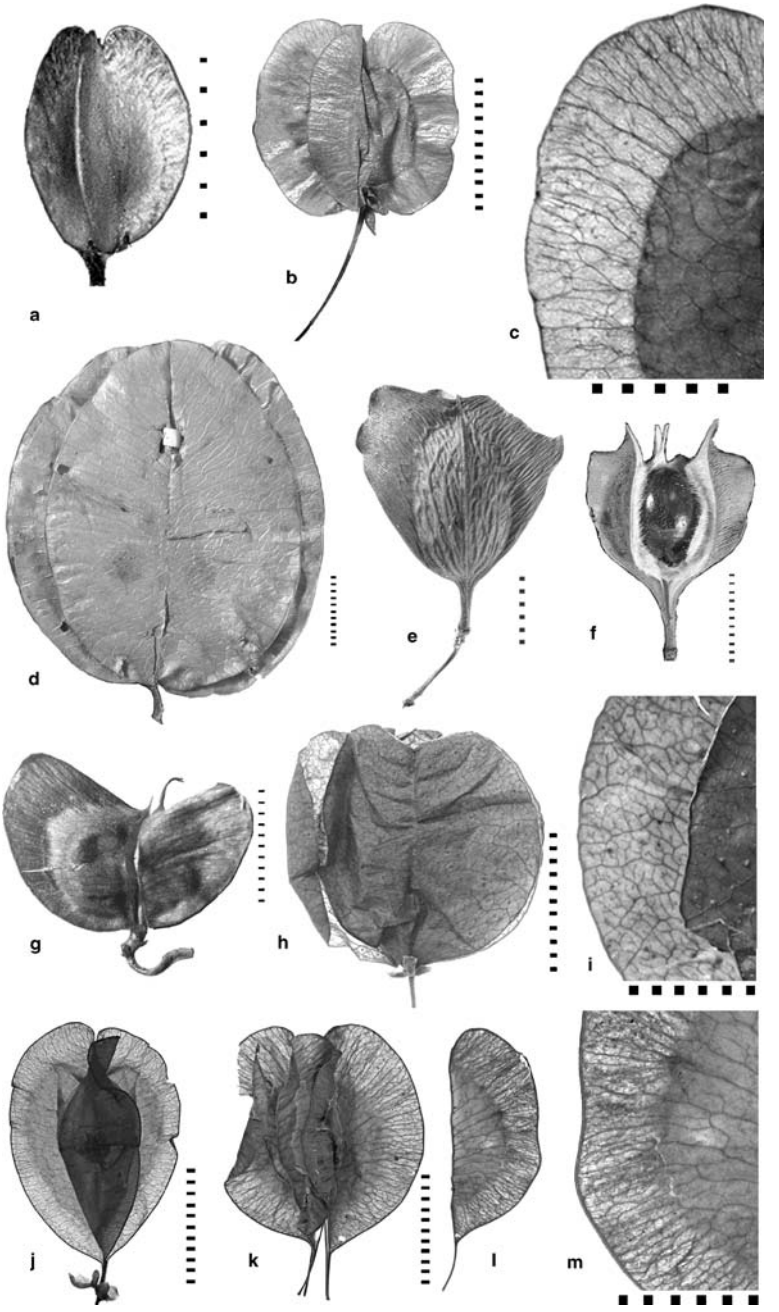


Fig. 17 Salicaceae (**a**) Sapindaceae (**b–m**) **a** *Neopringlea insignis* S. Watson (TEX: Lemke & Bain 012), Tamaulipas, Mexico. **b**, **c** *Dodonaea viscosa* L. (A: Grierson & Long 4187), Cult., Tongsa District, Bhutan. **d** *Koelreuteria integrifolia* Merr. (A: H. Migo, sn), Hangchow, Chekiang Prov., China, Oct. 30 1934. **e**, **f** *Paullinia hispida* Jacq. (GH: J.M. Idrobo & R.E. Schultes 919), Colombia. **g** *Bridgesia incisaefolia* Bert. ex Cambess. (MO 909993), Coqumbo, Chile. **h**, **i** *Boniodendron minus* (Hemsley) T. C. Chen (GH: NM Cuong 183), Vietnam. **j** *Urvillea chacoensis* Hunz. (A: T. Meyer 8829), Argentina. **k–m** Schizocarp and mericarp of *Urvillea filipes* Radlk. (GH: J. Steinbach 8121), Santa Cruz, Bolivia. Scales calibrated in mm

sinuous, craspedodromous to the fimbrial vein; intervening venation is reticulate with irregular polygonal areoles having frequent freely ending veinlets. These fruits are similar to those of *Koelreuteria*, described below but can be distinguished by their smaller size and the presence of complete septa forming a trilocular fruit.

Bridgesia Bertero ex Cambess. (Fig. 17g) has one species of shrub in regions of Mediterranean climate in Chile. The fruits are borne on a thick pedicel and are widely elliptical, wider than high, composed of three wings arising from a central inflated locular area, with a persistent style. The schizocarps split into three mericarps which each retain part of the style. Main veins are straight, subparallel with occasional dichotomies, and anastomoses, craspedodromous to the fimbrial vein. We recognize a fossil species of this genus from the Eocene of Mississippi, USA ("Evaluation of Fossil Fruits," Fig. 24k–m).

Dodonaea Miller (Fig. 17b, c) is a widespread temperate and subtropical genus with about 60 species of shrubs usually in dry areas. The fruits have three membranaceous wings, "eventually breaking into three separate samaras" Gentry (1993). According to van Roosmalen (1985), *Dodonaea* fruits are capsules; seeds are shed when the segments fall apart along the median suture. Main veins form a reticulum with more or less isodiametric areoles over the locular area giving rise to straighter, subparallel veins in the wing that are craspedodromous to the fimbrial vein.

Koelreuteria Laxm. (Fig. 17d), with three species of trees in China, has bladder-like loculicidal capsules, composed of three elliptical to ovate membranous valves which adhere to one another along their margins to form three wings. At maturity the valves split apart, each carrying one or two seeds. The major veins spread from the center line over the septum of each valve and are straight to somewhat sinuous, craspedodromous, joining the fimbrial vein. Intervening veins form a polygonal reticulum. The septum is incomplete, extending from the base approximately to the equator of the unilocular fruit, where the seeds are attached. Complete fossil fruits as well as isolated capsule valves of *Koelreuteria* are known from the Eocene Green River Formation of Colorado (Manchester, 1999).

Paullinia L. (Fig. 17e, f) includes more than 150 species of lianas in tropical America. In *P. hispida*, the fruit is long-stipitate and obovate in outline with an elliptical fruit body and three coriaceous to chartaceous lateral wings. The capsule opens to release a large arillate, seed. Main veins of the wing are subparallel, closely spaced and craspedodromous to the fimbrial vein.

Stocksia Benth. is a genus of one species of rigid spiny shrubs restricted to dry areas in eastern Iran and Afghanistan. The 3-winged fruit is a membranous loculicidal capsule, somewhat inflated like those of *Koelreuteria*. The pedicel shed is with fruit. Venation is reticulate, extending to the fimbrial vein with secondaries interconnecting or freely ending in branched or unbranched veinlets.

Toulicia Aubl. is a genus of trees with 14 species of trees in northern South America. The fruit is a 3-winged schizocarp (Gentry, 1993), elliptical to circular in outline. The overall organization is similar to *Koelreuteria*. Wings are membranous. The main veins are sinuous, extending from the locular area transversely across the wing, craspedodromous to the fimbrial vein. Intervening finer veins dichotomize and form a reticulum with polygonal areoles.

Urvillea Kunth (Fig. 17j–m) includes 13 species of tropical American lianas (Gentry, 1993). The fruits are stipitate elongate–elliptical septifragal capsules with

two to three wings formed from a 3-carpellate ovary (Ferrucci, 2006). Styles persist and the stipitate, fruit is dispersed with the pedicel. Wings are chartaceous, derived from the ovary. Main veins radiate into the wing, subparallel with some dichotomizing. *U. ulmacea* is diagrammed and described by van Roosmalen (1985) as having a narrowly ovoid tricocous schizocarp with a slender stipe, and crowned by a 3-lobed style. Gentry (1993) described the fruits as being composed of three hemielliptic samaras fused along their entire length. *U. chacoensis* (Fig. 17j) and *U. filipes* (Fig. 17k–m) show the stipitate condition and membranous wings with a strong fimbrial vein and a loose transversely oriented reticulum over the locular area which becomes more dense toward the wing margins.

Simaroubaceae This family includes the winged fruit genera *Ailanthus* Desf. and *Soulamea* Lam., the latter of which conforms to the fin-winged configuration.

Soulamea Lam. (Fig. 18a) is a genus of small trees and shrubs with has one species in the Seychelles, one widespread in Malesia and Polynesia, and 12 endemic to New Caledonia. As seen in *S. tomentosa,* the fruit is broadly 2-winged, obcordate indehiscent, samaroid. Fruit body 2-loculed, obcordate with persistent perianth at the base, and a pair of persistent styles. Main veins are subparallel, radiating into the wings from the fruit body, straight to sinuous, rarely dichotomizing or anastomosing, craspedodromous to the fimbrial vein. Vein density is 1.2–1.6 per mm.

Styracaceae This family includes 11 genera, but only *Halesia* has prominently winged fruits. *Pterostyrax* might also be considered fin-winged in organization but the wings (or ribs) are relatively narrow.

Halesia J. Ellis ex L. (Fig. 18b–d), with five extant species of trees in eastern North America and Asia, has 2- or 4-winged indehiscent fruits, depending on the species, developed from an inferior ovary. The fruits are elliptical, with a rounded to cuneate base and cordate apex with a persistent apical beak, surrounded by persistent sepals. Wings are derived from ovary, thick, and semi-opaque. The wings are veinless except for a single prominent intramarginal vein located 1–1.5 mm inside the wing margins.

Halesia Sieb. & Zucc. fruit fossils have been confirmed in the Miocene of western North America (Brown, 1946), and Pliocene of Germany (Tralau, 1965). These fossils show the characteristic intramarginal vein and thus appear to be correctly identified. Fritsch et al. (2001) used these reports, and molecular phylogenies to suggest a North American origin for the genus. Some other North American fossils previously attributed to *Halesia* lack this intramarginal vein and can therefore be dismissed as misidentifications.

Trigoniaceae This family of three genera includes two genera with fin-winged fruits. *Humbertiodendron* Leandri (Fig. 18e), with one species of tree in Madagascar, has indehiscent 3-winged fruits formed from a superior ovary. The fruit is wide-elliptical to circular in outline. Style and perianth do not persist in fruit. The wings are chartaceous, derived from ovary, with main veins radiating into the wings, mostly straight, occasionally dichotomizing in main portion of wing but more frequently near margin, craspedodromous to the margin, entering the fimbrial vein. Long pilose trichomes are present.

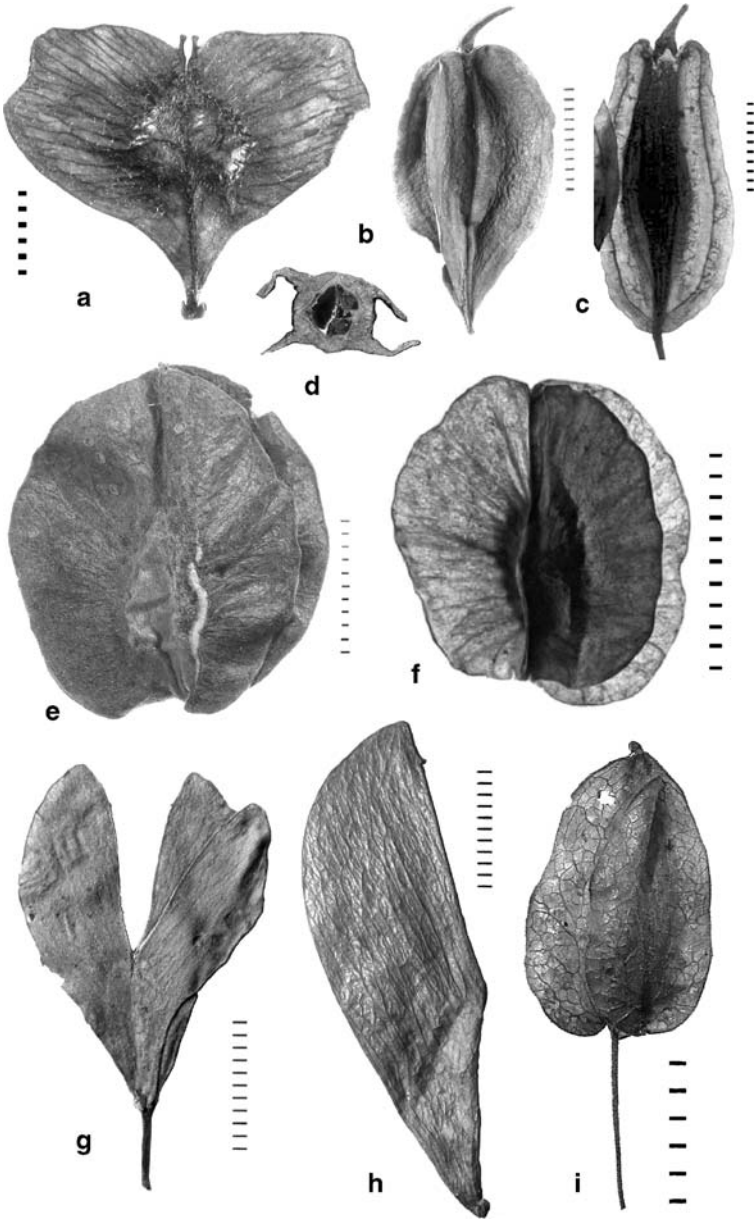


Fig. 18 Simaroubaceae (**a**), Styracaceae (**b**–**d**), Trigoniaceae (**e**, **g**, **h**), Tropaeolaceae (**f**), Verbenaceae (**i**). **a** *Soulamea tomentosa* Brongn. & Gris., showing persistent perianth at base, separate styles at apex and subparallel venation (GH: Vieillard 2414), New Caledonia. **b** *Halesia carolina* L. showing stylar protuberance and three of the four wings, each with a prominent intramarginal vein (CAS 39462: P. Fritsch), Arnold Arboretum Massachusetts. **c** *Halesia diptera* Ellis showing the two wings, each with an intramarginal vein. Note sepal persisting at base of persistent style (A: Chester 1124), eastern North America. **d** Transverse section of the specimen in **b**. **e** *Humbertiodendron saboureaui* Leandri (BARC; K: Capuron 180535F), Madagascar. **f** *Magallana porifolia* Cav. (BARC; K: A. Donat 51), Argentina. **g**, **h** *Trigoniastrum hypoleucum* Miq. (UC 312251: ADE Elmer 21302), Borneo. **i** *Hymenopyramis cana* Craib. (GH: J.F. Maxwell 856), Thailand. Scales calibrated in mm

Trigoniastrum Miq. (Fig. 18g, h) is a monotypic genus of trees in Peninsular Malaysia, Singapore, Sumatra and Borneo. It has 3-winged schizocarpic fruits which at maturity separate into three flat, winged, 1-seeded mericarps.

Tropaeolaceae Tropaeolaceae is a family of Brassicales with about 90 species distributed from southern Mexico to Patagonia. Recently, only a single genus, *Tropaeolum* L., is recognized, following molecular cladistic results (Bayer and Appel, 2003). However, this classification sinks the genus, *Magallana* Cav. which is distinguished by fin-winged samaroid fruits. *Tropaeolum,* as traditionally circumscribed, has schizocarpic fruits with fleshy mericarps. For present purposes it is useful to retain the concept of *Magallana* because of its morphological utility, despite molecular evidence indicating that its recognition renders *Tropaeolum* paraphyletic (Andersson and Andersson, 2000).

Magallana (Fig. 18f) has two species (*M. porifolia* Cav. and *M. trialata* Suess.) of annual or perennial herbs distributed in Argentina (Ruíz Leal and Perez-Moreau, 1964). The tricarpellate superior ovary develops into a 3-winged samara. The fruit is elliptical in outline. The style and perianth do not persist; the pedicel is not dispersed with fruit. The wing is chartaceous, and the margin entire to undulatory. Venation radiates outwards from the central axis, subparallel, and is craspedodromous, joining into a fimbrial vein. The main veins are spaced about one vein per mm, with occasional dichotomies or cross veins.

Verbenaceae This family is characterized by drupaceous and schizocarpic fruits, but winged fruits occur in the genus *Hymenopyramis* Wallich ex Griffith (Fig. 18i) which has six species of scandent shrubs from India to SE Asia. *Hymenopyramis* has 4-winged capsular fruits that may become inflated and balloon-like at maturity. The pedicels are long and moderately thick. The fruits are ovate to elliptical. The chartaceous wings have complex reticulate venation, consisting of multiple orders delimiting more or less isodiametric polygonal areoles. There is a prominent fimbrial vein.

Violaceae This family is characterized by baccate and capsular fruits. The genus *Anchietea* A.St.–Hil. (Fig. 19a, b), with eight species of lianas in tropical South America, may have both winged fruits and winged seeds. *Anchietea selloana* Cham. & Schltd. has 3-valved winged capsular fruits superficially similar to *Koelreuteria*. The fruits are elliptical, with rounded base and rounded to retuse apex, borne on a slender pedicel. Each valve has a prominent midvein to which the seeds are serially attached, with pinnate, complex reticulate venation. There is a fine fimbrial vein.

Zygophyllaceae Fruits of Zygophyllaceae may be capsular or schizocarpic and form from a superior ovary (Beier et al., 2003). Some have fin-winged fruits, including those summarized below. Weyland (1937) recognized a fossil genus, *Zygophyllocarpum* for fin-winged fruits of this family from the late Oligocene of Rott, Germany.

Bulnesia Gay (Fig. 19c) is a genus of eight species of trees and shrubs distributed in mostly arid regions of South America. The fruit is a 5-winged loculicidal capsule,

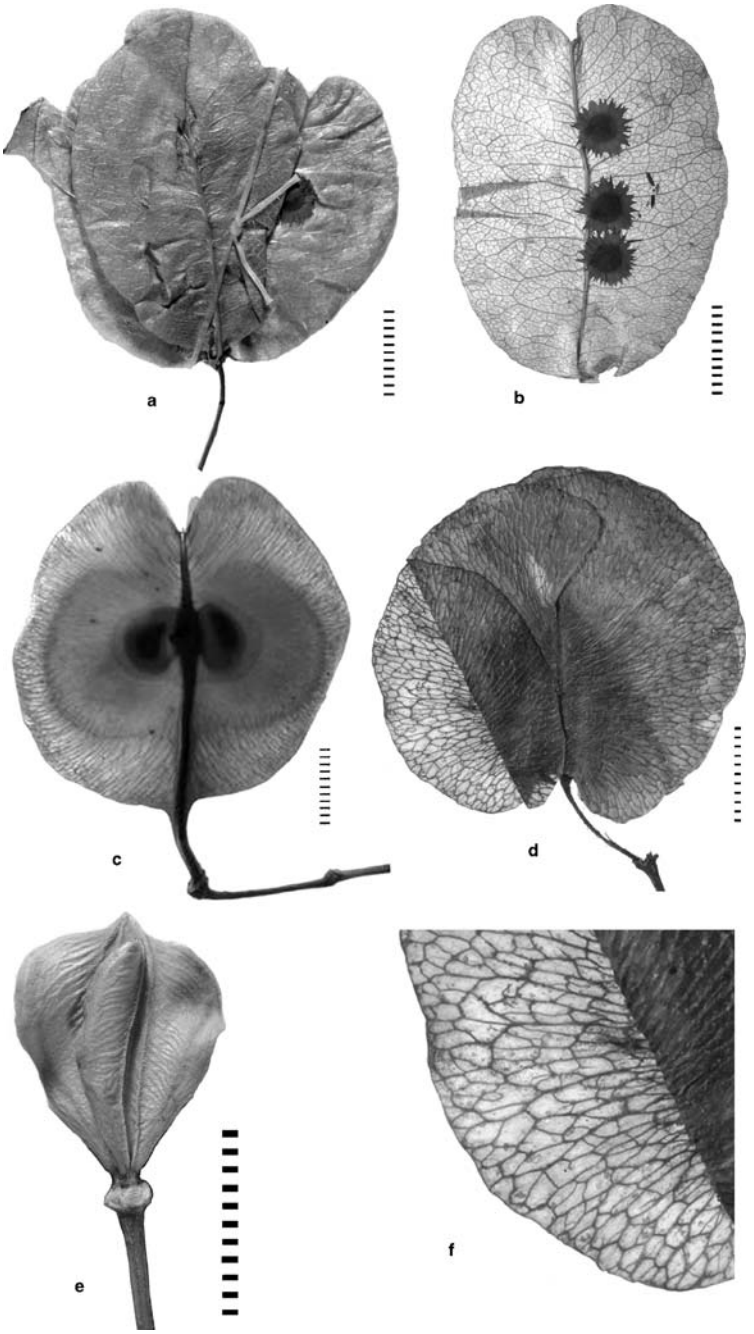


Fig. 19 Violaceae (**a**, **b**), Zygophyllaceae (**c–f**). **a** Fruit of *Anchietea selloana* Cham. & Schltd. (MO 4795524: V.C. Souza 5486), Minas Gerais, Brazil. **b** Isolated valve of fruit from the same collection as **a**. **c** *Bulnesia arborea* Engl. with locules and seeds shown by transmitted light. Note perianth scar at base of stipe (UFPC 1069), cult. Miami Florida. **d** *Zygophyllum morgansa* L. showing wings with reticulate venation (A: R. Marloth 12275), South Africa. **e** *Guaiacum sanctum* L. (A: S.P. Sharplis sn), New Jersey. **f** Detail of venation from **d**; note lack of fimbrial vein. Scales calibrated in mm

or in some species schizocarp, formed from a 5-carpellate ovary and is elliptical to round-elliptical in outline. Style remnants may persist, and a perianth scar is visible at the junction of stipe and pedicel. The pedicel and stipe may be dispersed with the fruit. Wings are chartaceous, derived from ovary. Venation radiates outward from the center line of fruit, dichotomizes and anastomoses, with greater vein density near the margin, and is craspedodromous to the fimbrial vein. Vein density is 1.6–2 per mm. Unbranched trichomes are visible on fruits of *B. foliosa* and *B. rivas-martinezii* (Navarro, 1994).

Guaiacum L. (Fig. 19e) is a genus of six species of trees and shrubs in Tropical America and the Caribbean. The fruit is a (2-)-5-winged septicidally dehiscent capsule (Sheahan, 2007), formed from a 5-carpellate ovary. The fruits are obovate in outline with a prominent perianth scar at junction of pedicel with base of fruit. The wings may be thick and opaque to chartaceous. Venation is subparallel, oriented obtuse to the central axis.

Morkillia Rose & Painter has two Mexican species of shrubs. The fruit is 4-winged, septicidally dehiscent capsule developed from a 4-carpellate ovary. It is elliptical–ovate in outline. The wings are derived from the ovary, coriaceous, and densely hairy. Venation is obscure in the thick tissue, but similar in course to that of *Bulnesia*.

Tribulus L. has 25 species of perennial herbs or subshrubs distributed in tropical and warm regions, especially Africa. Most species have spiny, nonwinged schizocarps, but some species, e.g. *T. platypteris* (Figured by Sweedman, 2006, p. 166) have membranous winged schizocarps. The latter species has elliptical fruits with venation similar to that in *Zygophyllum*.

Zygophyllum L. (Fig. 19d, f) has about 100 species of shrubs distributed in the Mediterranean region of Europe to central Asia, northeastern and southern Africa, and Australia, frequently in arid habitats. The fruit is winged in some of the species. For example, *Z. morgansa* has a 4- to 5-winged loculicidal capsule (Sheahan, 2007) developed from a 4-carpellate. The wings are chartaceous with venation radiating from the central axis dichotomizing, anastomosing and looping to form a reticulum of areoles that are elongate perpendicular to the wing margins, but increasingly isodiametric adjacent the margin. The style persists at apex and the pedicel may be shed with fruit. Vein density is 1.2–1.6 per mm.

Evaluation of Fossil Fruits

The survey of fin-winged fruits presented above is intended to aid in the evaluation of fossil fruits. In the process of preparing this review, we revisited selected examples from the fossil record. We present some examples here to illustrate the utility of fruit characters for identification. Among the oldest fin-winged fruits are the bisymmetrical fruits of *Gurvanella* Krassilov from the early Cretaceous of western Mongolia (Krassilov, 1982) and northeastern China (Sun et al., 2001). These small fruits, with paired wings with reticulate venation remain uncertain as to their affinities. Other examples from the Cretaceous include new records of Combretaceae, Apiaceae and Polygonaceae, treated below. Also considered here are examples from the Tertiary fossil record identified as Hernandiaceae, Polygonaceae, Rhamnaceae, Rutaceae, and Sapindaceae.

Fossil Combretaceae Small fin-winged fruits from the Cretaceous (Albian to Cenomanian) Dakota Formation of Kansas and Nebraska show features characteristic of Combretaceae (Fig. 20a–e). Differentially fractured specimens indicate that the fruits have four symmetrically arranged equal wings arising from a fusiform fruit body. We establish a new genus and species for this taxon:

Dilcherocarpon combretoides gen. et sp. n. Fig. 20a–e.

Etymology. The genus is named for Dr. David Dilcher, who collected many of the specimens and provided helpful discussion about them.
Diagnosis. Fruits bowtie shaped in face view, cordate basally and apically, 4.5–5 mm wide and 4.0–5.0 mm long with four lateral wings. Fruit body fusiform to elliptical in face view, with lateral wings arising in two perpendicular planes of symmetry. Wing veins of a single order, subparallel, very densely spaced and oriented perpendicular to the wing margins. Fimbrial vein absent; wings frequently torn parallel to the venation giving frayed margin. Remnants of epigynous perianth at the apex. The basal end of the fruit, below the position of wings, narrowed into a pedicel-like structure 1.5 to 2.0 mm long, with no obvious scars.
Holotype. UF15709-11023 (Braun Ranch, Cloud Co., Kansas, UF locality 15709) (Fig. 20d, e).
Paratypes. UF15709-5326, 5330, 11024, 11025, 14954, 23764, 25005 (Braun Ranch, Cloud Co., Kansas), UF19025-39054 (Decatur, Nebraska).

Such high density of fine, parallel veins, combined with absence of a fimbrial vein, is rare among the extant families examined in this survey, but is consistent with Combretaceae, as seen in extant *Combretum* (Fig. 6b, c, e), *Pteleopsis* (Fig. 7a–d) and *Terminalia* (Fig. 7e–h). The pedicel-like structure with no obvious scars, corresponds to the elongate receptacle or hypanthium typical of extant Combretaceae and the epigynous perianth remnants indicate that the fruit developed from an inferior ovary. These specimens are from the Albian or Cenomanian localities of the Dakota Group near Braun Ranch, Cloud County, Kansas (Wang & Dilcher, 2006), and Decatur, Nebraska. The presence of Combretaceae in the late Cretaceous has been indicated previously based on well preserved flowers from the Campanian–Maastrichtian of Portugal (Friis et al., 1991) and early Santonian of Japan (Takahashi et al., 1999), but these winged fruits are still older, and provide an additional indication that the syndrome of characters typical of the extant family were established relatively early.

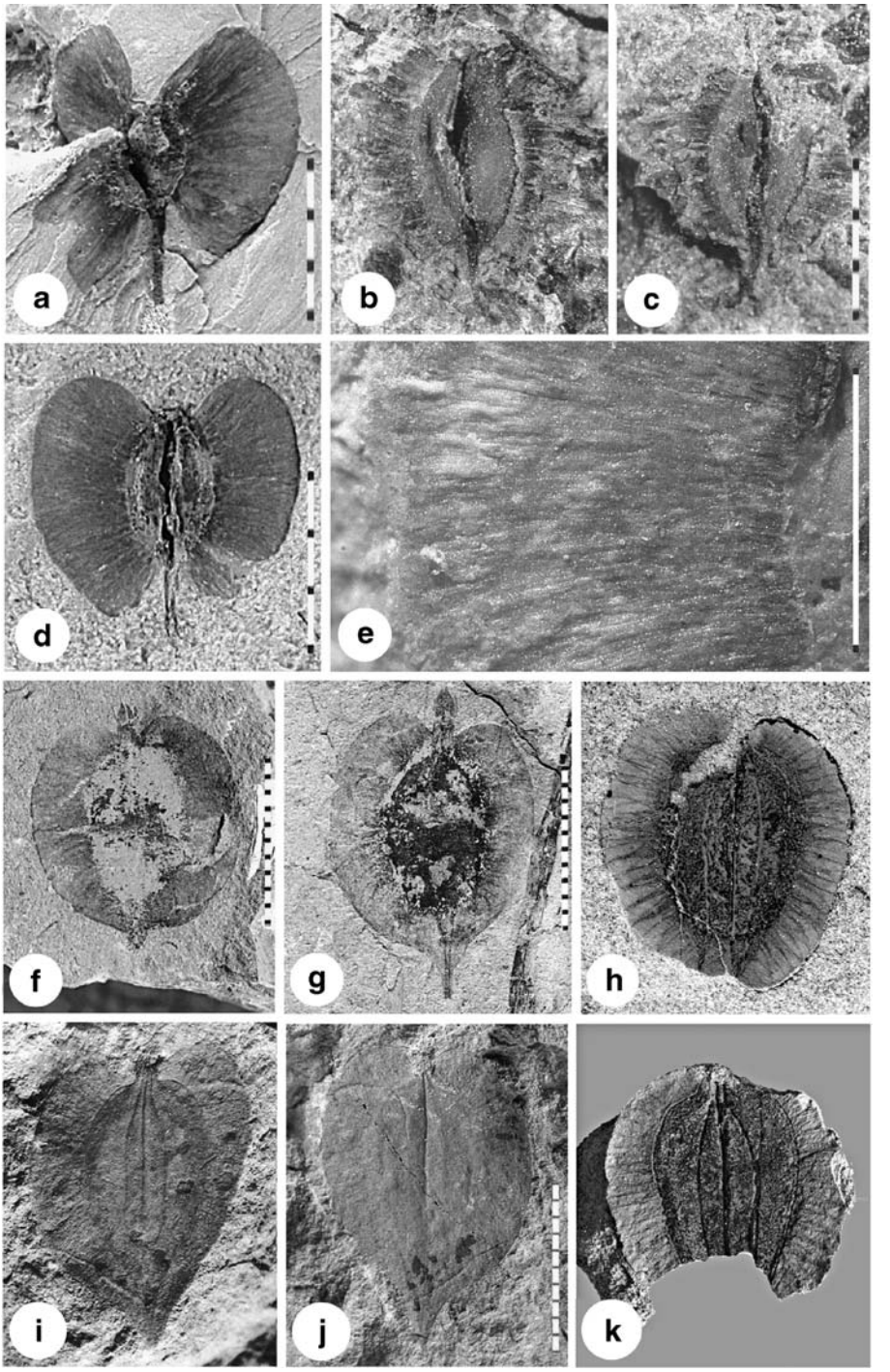
Fossil Apiaceae Compressed fruits of *Carpites ulmiformis* Dorf (1942) from the Late Cretaceous (Maastrichtian) of Wyoming and Montana are likely to represent Apicaceae. They have an obovate–elliptical fruit body with a pair of prominent lateral wings and clearly show a persistent epigynous perianth of several equal tepals fused basally into a short tube that arises the top of the fruit (Fig. 20f, g). A prominent fimbrial vein outlines each wing (Fig. 20f–k), but venation fanning across the wing from the obovate central body is fine and inconspicuous. The fruit body is traversed by a straight median longitudinal vein and four additional longitudinal veins symmetrically placed on either side of the median vein. The outline of the fruit is cordate apically and rounded to cuneate basally. These disseminules resemble the

Fig. 20 Fossil fin-winged fruits of Comrbretaceae (**a**–**e**) and Araliaceae (**f**–**k**). **a–e** Cretaceous (Cenomanian) Combretaceae: *Dilcherocarpon combretoides* gen. et sp. nov. **a** Winged fruit showing three of the four wings, each with very finely striate venation. Dakota Formation: Braun Ranch, Kansas. UF15709-11025. **b**, **c** Counterpart halves of one specimen, showing two wings in the plane of the page, and two additional wings in a perpendicular plane, protruding into the sediment of each counterpart and appearing as a straight longidudinal median groove on both impression surfaces. Note the tearing of wing tissue parallel to the venation due to lack of a fimbrial vein. Dakota Formation, Decatur, Nebraska, UF19025-39054. **d** Holotype, UF15709-11023, Braun Ranch, Kansas. **e** Same, detail of wing venation. **f–k** Cretaceous Araliaceae: *Carpites ulmiformis* Dorf (1942) from the Maastrichtian of Montana and North Dakota. **f**, **g** Specimen from USGS loc. 8557 (Hell Creek Formation, Montana). **f** Showing persistent epigynous calyx, and fine venation of the wing. USNM 455147. **g** Specimen showing apical perianth, longitudinal veins arising from the base. USNM 455149. **h** Specimen from Slope Co., North Dakota. DMNH 20484, locality 568. **i**, **j** Counterpart impressions of specimen from Lance Formation, Crazy Woman Creek, Wyoming. Note multiple longitudinal veins on dorsal side (**i**), single rib on ventral side (**j**), USNM 40260. **k** Counterpart of specimen in h showing deeply impressed longitudinal veins on the fruit body. Scales calibrated in mm

mericarps of Apiaceae (Figs. 2g–l, 3a) in the position and symmetry of wings, epigynous perianth, and straight, well spaced longitudinal veins across the fruit body.

It must be acknowledged that some of these same features are also found in the unrelated Dioscoreaceae; however, *C. ulmiformis* fossils appear to have only two wings rather than three as expected in Dioscoreaceae. Although multiple epigynous tepals are visible in the fossil (Fig. 20f, g), it is not clear from the specimens at hand whether the number of tepals in the fossils were five (consistent with Apicaceae), or six (conforming to Dioscoreaceae). One of the features that helps to distinguish these fossils from Dioscoreaceae is the presence and position of longitudinal veins on the fruit body. Examination of the both counterpart impressions of the same fossil fruit show five veins on one side, but only a single median vein on the opposite side (Fig. 20i vs j, and Fig. 20h vs k). This asymmetral pattern suggests that these disseminules are mericarps of the kind typical for Apiaceae, with three or five longitudinal veins occurring on the dorsal side of each mericarp but only a single vein running medially on the ventral side. This combination of characters provides strong support for the assignment of *Carpites ulmiformis* to the Apiaceae. However, veins of the wings are stronger and more widely spaced than those observed in otherwise similar fruits of the similar extant genera (e.g., Figs. 2g, 3a).

Fossil Brassicaceae Thlaspi primaevum Becker (1961) from the early Oligocene of western Montana was reexamined for this study. The fruit (Fig. 21h–k) is elliptical with a pair of symmetrical wings. The locular area is elliptical to fusiform, and bisected by a vertical septum at right angles to the plane of the wings, and contains the impressions of several seeds ornamented with concentric ridges. The base and apex of the fruit are rounded, except for a pronounced apical notch. The pedicel dispersed with the fruit is 4 mm long, and relatively thin, 0.2 mm. A hypogynous perianth scar occurs at the base of the fruit and a disk-like stigmatic pad is situated at the top of the locular area in the plane of bisymmetry in the apical notch. Venation of the wings extends outward and upward from the locular area, straight to sinuous, occasionally dichotomizing and anastomosing, craspedodromous to a fimbrial vein. Vein density is 1–2 per mm. The locular area shows numerous faint elliptical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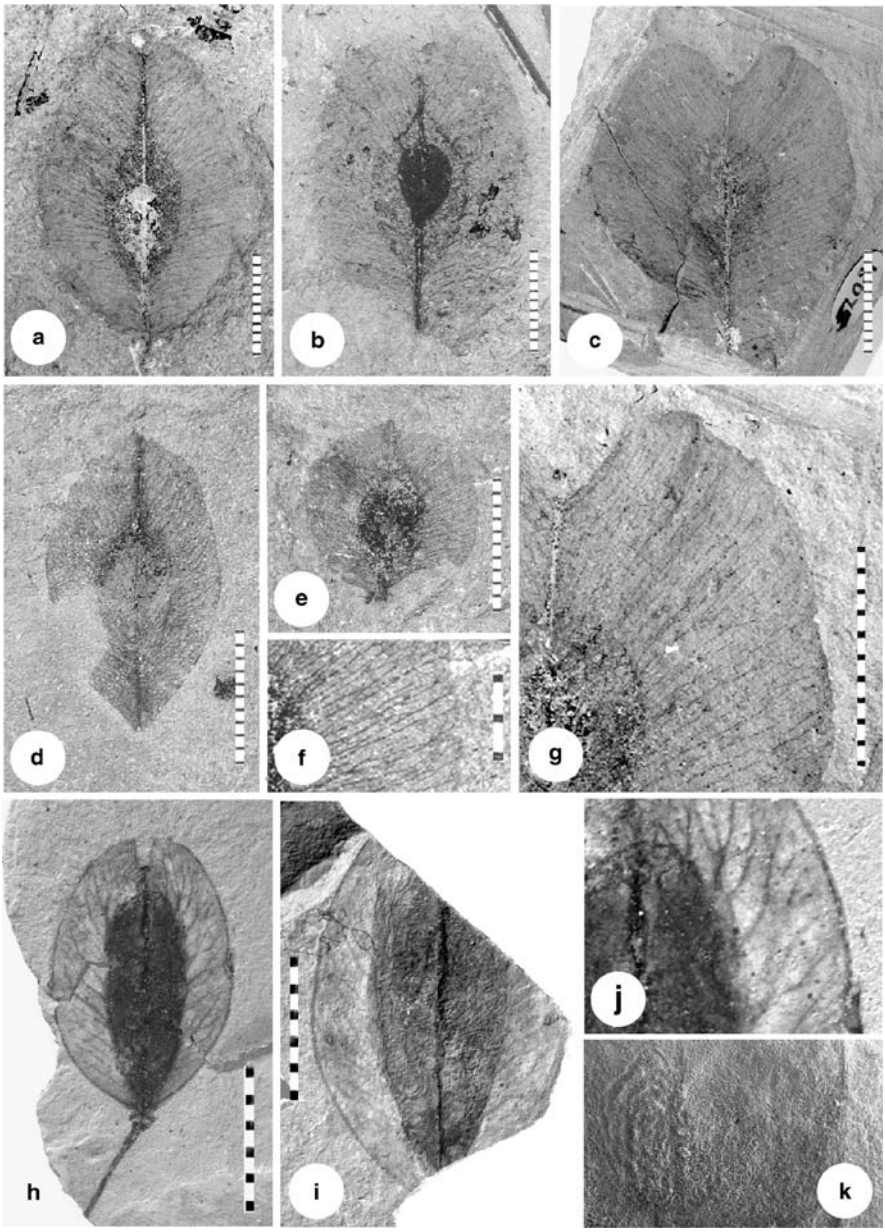


Fig. 21 Fossil Fabaceae (a–g), and Brassicaceae (h–k). **a–g** *Dodonaeites descaisnei* Saporta, a fossil from the Oligocene of France and Hungary. **a** Fruit showing pedicel, paired wings, and the impression of an elliptical seed near the base of the locular area, from Armissan, France, MNHNP sn. **b** Fruit with a single dark seed attached centrally and extending apically within the locule, Armissan, BM 52981-1. **c** Specimen showing retuse apical margin, Armissan, BMv52981-2. **d** Elliptical fruit from Tard Clay, Budapest, Hungary BP 63.1037.1. **e**, **f** Armissan, BMv6652. **g** Detail from **c**. **h–k** Brassicaceae: *Thlaspi primaevum* Becker from Early Oligocene Ruby flora, western Montana. **h** Holotype showing narrow pedicel, hypogynous perianth scar, narrow-obovate locular area and paired wings, UM38256. **i** Larger specimen, UM 38257. **j** detail from **h**, showing subparallel veins and fimbrial vein of the wing. **k** Scanning electron microscopy of the holotype, showing tissue of the wing (*right side*) and a concentrically ribbed elliptical seed within the locule (*left side*). Scales calibrated in mm

impressions suggesting that the fruit bore multiple seeds within the locule. The observed features of fruit morphology are consistent with Brassicaceae, and the distinctive ornamentation of the seeds, taken along with the fruit characters, confirm Becker's assignment of this fossil to extant *Thlaspi*.

Fossil Fabaceae Dodonaeites descaisnei de Saporta (1865), a fossil fruit from the Oligocene of Armissan, France (Fig. 21a–c, e–g) and early Oligocene Tard Clay of Budapest, Hungary (Fig. 21d), appears to represent a fin-winged fruit of Fabaceae, and is almost identical in morphology to *Fissicalyx*. It is unilocular with a single seed, a single straight median rib over the fusiform locular area; it is stipitate, and has a pair of symmetrical wings with fine subparallel veins spaced 3–5 per mm. Features shared between *Dodonaeites descaisnei* (Fig. 21a–g) and extant *Fissicalyx fendleri* (Fig. 9a, b) include presence of a stipe, bisymmetry, indehiscence, two wings, a narrow, fusiform locular area, a single seed per fruit, and no ribs over the locular area, other than the prominent midrib extending the full length of the fruit. Both have an emarginate apex, with protruding persistent style base, and simple, subparallel venation with a single order of relatively thin, somewhat sinuous veins that bifurcate and anastomose occasionally before joining abruptly to a prominent fimbrial vein. The dimensions and proportions also correspond, except that the seed in the modern species is elongate (about four times longer than wide, filling most of the length of the locule, whereas in the fossil species, the seed is ellpsoidal, only about twice as long as wide.

Fossil Hernandiaceae Fruits of *Illigera* occur in the Eocene of western North America but have gone unrecognized until now. We recognize a new species:

Illigera eocenica sp. n. Fig. 22a–e.

Holotype. UF262-17682, Clarno Formation, White Cliffs, Jefferson County, Oregon (Fig. 22c, d).
Paratypes. UF 238-19901, 19905, 19907, 19908, 262-17746 (Clarno Formation, Oregon), DMNH 24518, UCMP PA 20645, 20669, USNM sn, (Green River Formation, Colorado).
Diagnosis. Fruits widely elliptical, about twice as wide as high (23–28 mm wide and 12–13 mm high), with two wings spreading in a common plane. Apex rounded without stylar protuberance, base rounded in some specimens, to attenuate along the pedicel in others, lacking perianth remnant or scar. With a pair of creases forming a V configuration near the apex. Locular area longitudinally fusiform, 2 mm wide, 5 mm high, smooth, bisected by a median longitudinal crease in the axis of bisymmetry. A shorter, narrower, third wing sometimes extends from the midline in a plane opposed to the two main wings. Venation of the wing fanning outward from the locular area, with veins dominantly transverse to the longitudinal axis. The spreading veins extend to the margin and enter into a strong fimbrial vein.

Illigera eocenica is present in Middle Eocene lacustrine shales of the Clarno Formation of Oregon, the Green River Formation in Colorado, Utah, and Wyoming (as *Ptelea cassioides* in MacGinitie, 1969), and is known from a single specimen

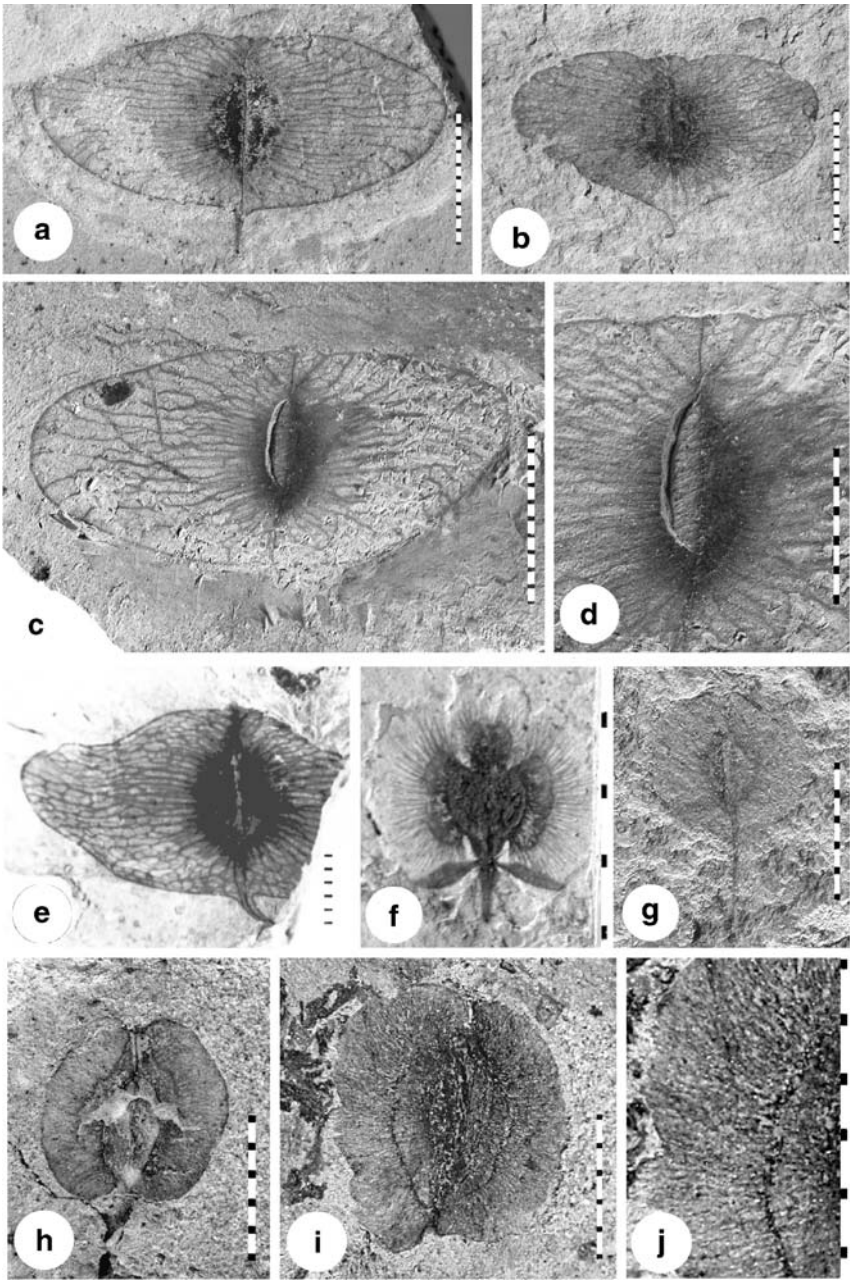


Fig. 22 Hernandiaceae (**a–e**), Polygonaceae (**f–j**). **a–e** *Illigera eocenica* sp. nov. **a** DMNH 24518, loc. 938, Green River Formation, Douglas Pass, Colorado. **b** Specimen showing thin pedicel, White Cliffs, Clarno Formation, Oregon, UF238-19901. **c** Holotype, UF262-17682. **d** Same, enlarged, showing a narrow additional wing flap protruding into the sediment from the central area. **e** Specimen showing pronounced basal protrusion, USNM sn. **f** *Polygonocarpum fimbriatum* Weyland Oligocene of Rott, Germany, RO 11320. **g** *Polygonum antiquum* Heer from the Miocene of Oeningen, Switzerland. BM9440. **h–j** *Polygonocarpum johnsonii* sp. n., Marmarth, North Dakota. **h** YPM 6173, Marmarth, North Dakota. **i** Holotype, DMNH 16608, loc 2087. **j** Detail of wing veination from **i**. Scales calibrated in mm

from Wagon Bed Formation of Wyoming (USGS loc. 9406, mentioned by Brown, 1959, p. 121 as "large two winged seeds"). MacGinitie (1969) described and illustrated this fruit type from the Parachute Creek member of the Green River Formation under the name *Ptelea cassioides*. However, he had earlier established the same binomial (MacGinitie, 1953) based on morphologically distinct specimens from the late Eocene Florissant flora which were subsequently reassigned to the caprifoliaceous genus *Diplodipelta* (Manchester & Donoghue, 1995).

Morphologically similar wide-elliptical winged fruits occur in Combretaceae (*Terminalia argentia*; Fig. 7h, i), Rutaceae (*Spathelia terminalioides*, Fig. 16g) and Hernandiaceae (*Illigera* spp.; Fig. 10f, g). The wide spacing of the veins, lack of fimbrial vein, and straight axial bundle in the axis of bisymmetry rule out affinities with *Terminalia*. These fossils do not show any evidence of hypogynous perianth (which would be expected to persist as a swelling or scars at the junction of the pedicel in specimens like Fig. 22b). If the fruits developed from flowers with epigynous perianth, as suggested by the v-shaped structure at the apex (Fig. 22b) and absence of scars between the pedicel and base of the fruit, then they cannot represent *Ptelea*, *Spathelia*, or other Rutaceae or Sapindales.

This species conforms to extant *Illigera* in general outline, the sinuous wing venation with intervening fine fabric of isodiametric polygonal areoles, the fusiform outline of the locular area, and the median ridge in the plane of bisymmetry. *Illigera* fruits develop from inferior ovaries, as is also inferred for the fossil. In addition, *Illigera* fruits can develop one or two small wings in addition to the two main ones, as has been demonstrated to occur in the fossil species as well (compare small median wing of Fig. 10f, with that exposed in the specimen of Fig. 22d).

Fossil Polygonaceae Fin-winged fruits of Polygonaceae have long been recognized in the fossil record. Heer (1859) named *Polygonum antiquum* based on fin-winged fruits of Polygonaceae as from the Miocene of Oenigen, Switzerland (an example is refigured here, Fig. 22g). *Polygonocarpum fimbriatum* Weyland (1937) from the late Oligocene of Rott, Germany, is confidently placed in the family. The species had small fruits 3.5 mm long and 3 mm wide with at least two lateral wings and a recurved basal pair of sepals (Fig. 22f). It is similar in morphology to fruits of extant *Oxyria* (Fig. 14c) and *Parapteropyrum*. It is now possible to extend the fossil record of Polygonaceae considerably farther back in time based on fossil fruits from the Late Cretaceous and Paleocene of North America.

We recognize a new species of polygonaceous fruit from the late Cretaceous (Maastrichtian) of southwestern North Dakota:

Polygonocarpum johnsonii sp. n. Fig. 22h–j.

Holotype. DMNH 16608 (Fig. 22i, j), Slope County, North Dakota, DMNH locality 2087.

Paratype. YPM 6173 (Fig. 22h), Slope County, North Dakota, DMNH locality 2087.

Etymology. The species is named for Dr. Kirk Johnson, who collected the specimens and made them available for this study.

Diagnosis. Fruit an elliptical to nearly circular samara, 6.5–9.5 mm high, 6.5–8.2 mm wide, with emarginate apex and base. Two (possibly 3?) lateral wings

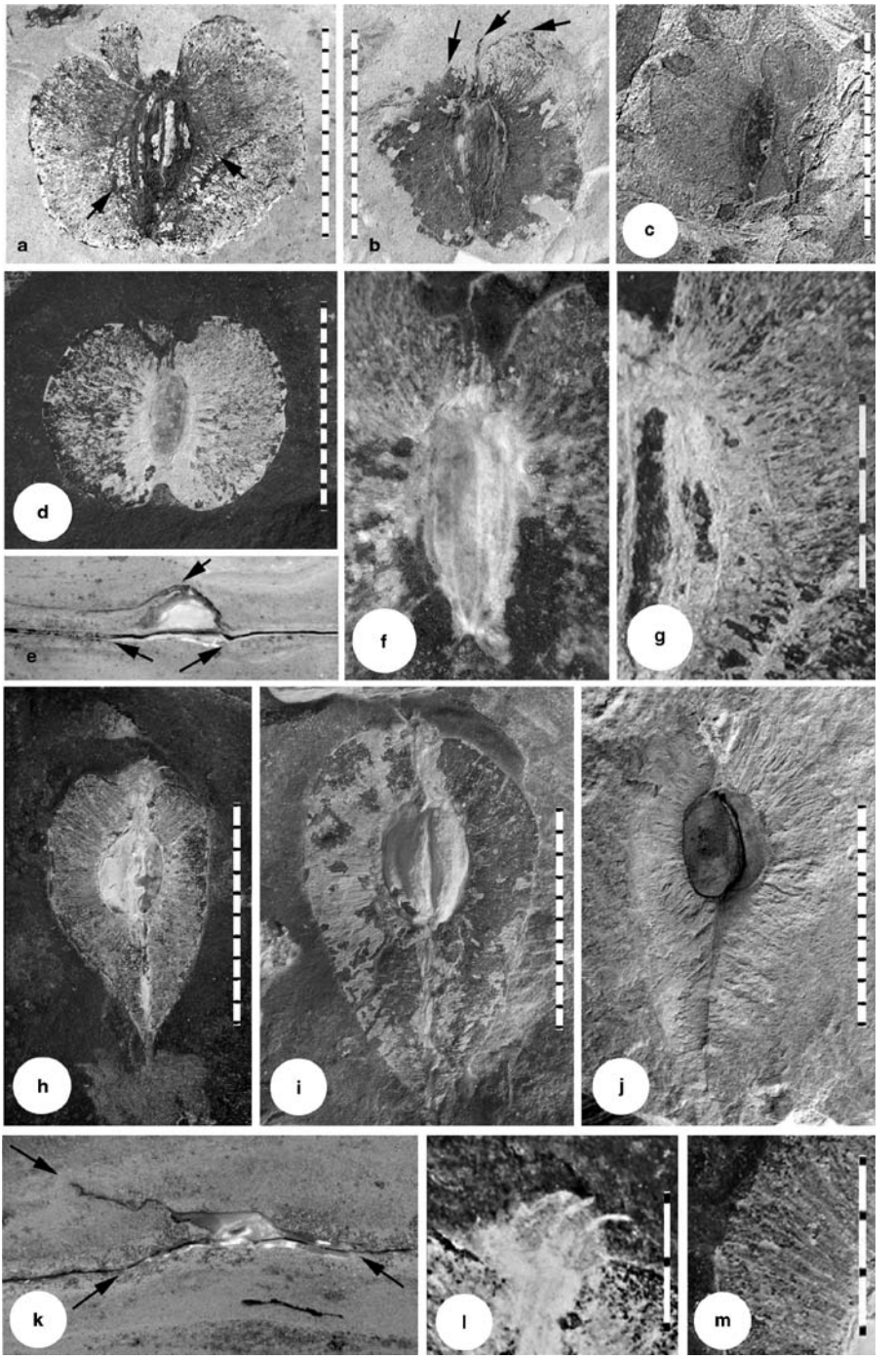
spreading from the central axis. Achene fusiform, pedicel and style unknown. Wings supplied with very fine fusiform-reticulate venation radiating from the central axis with a high vein density of 6 per mm. Fimbrial vein lacking, but with an arched longitudinal intramarginal vein (well inset from the wing margin) in each wing running parallel to the edge of the achene about 1 mm beyond the achene margin.

Polygonocarpum johnsonii is assigned to the Polygonaceae based on the fine fusiform-reticulate venation over the wings, combined with the lack of fimbrial vein and presence of deeply inset intramarginal veins (i.e., a pair of thick veins paralleling the outline of the achene). A similar set of features are seen in extant *Pteropyrum* (Fig. 14e) and *Rheum* (Fig. 15a). In the survey of extant fruits, this type of very fine, fusiform-reticulate venation was observed in only a few other families, including Dioscoreaceae and Nyctaginaceae. However, such venation, in combination with the deeply inset intramarginal vein, is known only in Polygonaceae. We assign this species to the fossil genus *Polygonocarpum*, which Weyland (1937) established to accommodate fossil fruits of polygonaceous affinity that cannot be ascribed to a particular modern genus.

Two additional representives of Polygonaceae are recognized from the Paleocene of North America (Fig. 23). Fruits similar to those of *Polygonocarpum johnsonii* occur in the Paleocene of Wyoming and North Dakota. Numerous specimens are available for study and transverse sections reveal that they are consistently 3-winged and indehiscent. Although it is possible that they could represent a temporal extension of the species *P. johnsonii* into the late Paleocene, these specimens show many details that remain uncertain for the Cretaceous material, including wing number, pedicel, achene morphology and internal anatomy. We treat this as a distinct new species:

Polygonocarpum curtisii sp. n. Fig. 23a–g

Fig. 23 Paleocene Polygonaceae. **a–g** Paleocene fruits of *Polygonocarpum curtisii* sp. nov. **a** Silicified fruit in shale showing narrowly obovate fruit body with longitudinal ribs and two of the wings; note deeply inset intramarginal vein in each of the wings (*arrows*); holotype, negative (inverted) image, UF15722-22554, Almont, North Dakota. **b** Fruit showing three wings (*arrows*), two flattened in the plane of view, another (*middle arrow*) extending back into the sediment; negative (*inverted*) image, UF15722-22558, Almont, North Dakota. **c** Impression specimen in shale with two of the wings exposed in face view, from Alkali Butte, Wyoming; USGS loc. 9207, USNM 356431. **d** Silicified fruit showing two well exposed wings and fragment of a third wing exposed near the apex, photographed prior to transverse section, UF15722-22548, **e** Same specimen as **d**, reassembled and sectioned transversely, enlarged, showing trigonal unilocular fruit body and three wings (*arrows*). **f** Detail from the counterpart surface of the specimen in **d**, moistened with water, showing longitudinal vascular strands over the achene. **g** Detail from **a** showing longitudinal veins over the fruit body, but only fine, fusiform-reticulate subparallel venation in the wing. **h–m** *Podopterus antiqua* sp. n. **h** Silicified fruit showing narrow pedicel, acute base, elliptical endocarp, and two of the wings, each with fine, subparallel venation, photographed prior to transverse section, holotype, FMNH-PP45598. **i** Larger specimen, showing bulging, longitudinally grooved fruit body and two of the wings, Paratype, YPM54383, Almont, North Dakota. **j** Impression specimen in shale, Bayhorse Creek, Montana, USNM 312975. **k** Same specimen as **h**, reassembled and sectioned transversely, enlarged, showing three wings (*arrows*). **l** Apical part of the fruit in **h**, showing bulge of perianth and protrusion of styles or filaments. **m** Detail of fine, fusiform-reticulate, subparallel wing venation from **h**. Scales calibrated in mm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Holotype. UF15722-22554 (Fig. 23a).
Paratypes. UF15722-22548, 22558.
Etymology. This species is named in honor of John Curtis, who collected many of the specimens examined from the locality near Almont, North Dakota.
Diagnosis. Fruits wide-elliptical with emarginate base and apex, 9–10 mm high and 12–14 mm wide, with three radially arranged vertical wings. Fruit body a fusiform, single-seeded endocarp 1.4–1.8 mm wide and 5–7 mm high, triangular in cross section. Several longitudinal veins traversing the full length of the fruit body. Pedicel narrow (0.3 mm), about 4 mm long (Crane et al., 1990, Fig. 23i). Wings chartaceous, with a dense anastomosing network of fine venation. A thick, arched longitudinal vein occurs in each wing parallel to the margin of the achene, 0.5–1 mm outside the achene. Fimbrial vein lacking.

Polygonocarpum curtisii is common in the silicified shales of Almont, North Dakota (Crane et al., 1990, p. 35, 36, Fig. 23a–g). Because the fruits are often preserved flattened in shale, they may at first appear to have only two lateral wings. Brown (1962) attributed one such specimen from the Paleocene of Alkali Butte, Wyoming to *Ulmus* (Brown, 1962, pl. 24, Fig. 17 as *Ulmus rhamnifolia*; refigured here, Fig. 23j). However, transverse sections of permineralized specimens indicate that they bore three wings, one of which often remains hidden in the sediment behind the two wings exposed in the original fracture surface.

This kind of triwinged fruit is superficially similar to those of extant *Wimmeria* (Celastraceae) as noted by Crane et al. (1990). However, the wings in *Wimmeria* and related genera have thicker, more widely spaced subparallel veins, and an intervening very fine reticulum of more or less isodiametric areoles, and a fimbrial vein (Fig. 5h–j). The fine, dense pattern of subparallel reticulate venation with fusiform areoles seen in these fossils, is similar to that observed in some Combretaceae, Dioscoreaceae, some Nyctaginaceae, and Polygonaceae. This pattern, in combination with a thin pedicel, lack of a fimbrial vein, presence of longitudinal veins over the locular area and the well inset intramarginal vein narrows the affinities to Polygonaceae. The well inset intramarginal vein is a feature shared, for example, with extant *Parapteropyrum* and *Pteropyrum* (Fig. 14e). Another example of Polygonaceae from the Paleocene of North Dakota is:

Podopterus antiqua sp. n. Fig. 23h–m

Holotype. FMNH-PP45598 (Fig. 23h, k–m).
Paratype. YPM 54383 (Fig. 23i).
Diagnosis. Fruits obovate with emarginate apex and cuneate base, 13–18 mm high, 8–10.5 mm wide, with three wings. The fruit body is an elliptical, single-seeded endocarp 2.5–3.3 mm wide to 3–4 mm high, subtriangular in cross section. The pedicel is narrow (ca 0.2 mm) and joins the base of the fruit without articulation. Wings chartaceous, with a dense anastomosing network of fine venation. Fimbrial vein lacking. A funnel-like fold of wing tissue representing part of the perianth occurs at the apex with three or more protruding filaments and or style remnants.

This fruit type, which Brown (1962, referring to the specimen reillustrated here in Fig. 23j) considered to represent *Ulmus*, was treated by Crane et al. (1990) simply as "biwinged fruit". More specimens have been collected since those publications, and it is now clear that the fruits were 3-winged rather than just two, as can be seen in obliquely fractured and tranversely sectioned (Fig. 23k) specimens. *P. antiqua* co-occurs with *Polygonocarpus curtisii*, but does not have intramarginal veins and has an acute rather than emarginate base. It corresponds closely in size and morphology and wing venation to extant *Podopterus* (Fig. 14g). Another example that apparently represents this genus is preserved in amber from the Miocene of Chiapas Mexico (Fig. 1.65 in Taylor et al., 2008).

Fossil Malvaceae Fin-winged fruits of *Craigia* were widespread in the Tertiary of the Northern Hemisphere and have been traced to the Eocene in eastern Asia and western North America (Kvaček et al., 2005). We have reexamined the type specimen of the species Berry (1930) assigned to *Ptelea eocenica*, from Grand Junction, Tennessee (Fig. 24a). The pedicel is much to thick to be that of *Ptelea*, however, and appears to have supplied a multivalved fruit. The pedicel is similar in thickness to, and has a similar perianth scar to the fruits of extant *Craigia* (Fig. 11h) and *Maxwellia* (Fig. 12a). The fusiform locular area, and organization of venation is also similar to these genera, but we hesitate to make a formal generic reassignment based on the single available specimen.

Fossil Rhamnaceae Two specimens from the Eocene Green River Formation of Utah appear to represent a fin-winged fruit of Rhamnaceae similar to those of *Gouania*:

Rainbowia gen. n.
Rainbowia rhamnoides sp. n. Fig. 24b, c

Holotype. DMNH 24492 (Fig. 24b).
Paratypes. UF18054-22809 (Fig. 24c).
Etymology. This genus is named for the town of Rainbow, Utah, situtated near the localities from which these fossils were collected. The species refers to the similarity with Rhamnaceae.
Diagnosis. Fruit valves are cordate, with a retuse apex, base obtuse except for the narrowed, stipitate proximal end. Each valve or mericarp with two auriform wings spreading from an obovate thickened central body; veins irregular in course and spacing, with large areoles. One or two prominent intramarginal veins are connected by occasional straight to arched cross veins with the central body.

The venation pattern on the wings of *Rainbowia* is very similar to that observed on those of extant *Gouania*, *Crumenaria* and *Reisseika*. The shape and size are similar to *Gouania* (Fig. 15e, g), however we did not observe any extant species with the sharply protruding base seen in these fossils. That feature could be an indication that these fruits belong to another family, and are only convergent in some of the features with Rhamnaceae, or it could represent an extinct morphological feature for fruits of Rhamnaceae. A more secure placement of this taxon may require a study of more fossil specimens, but currently these are the only two known.

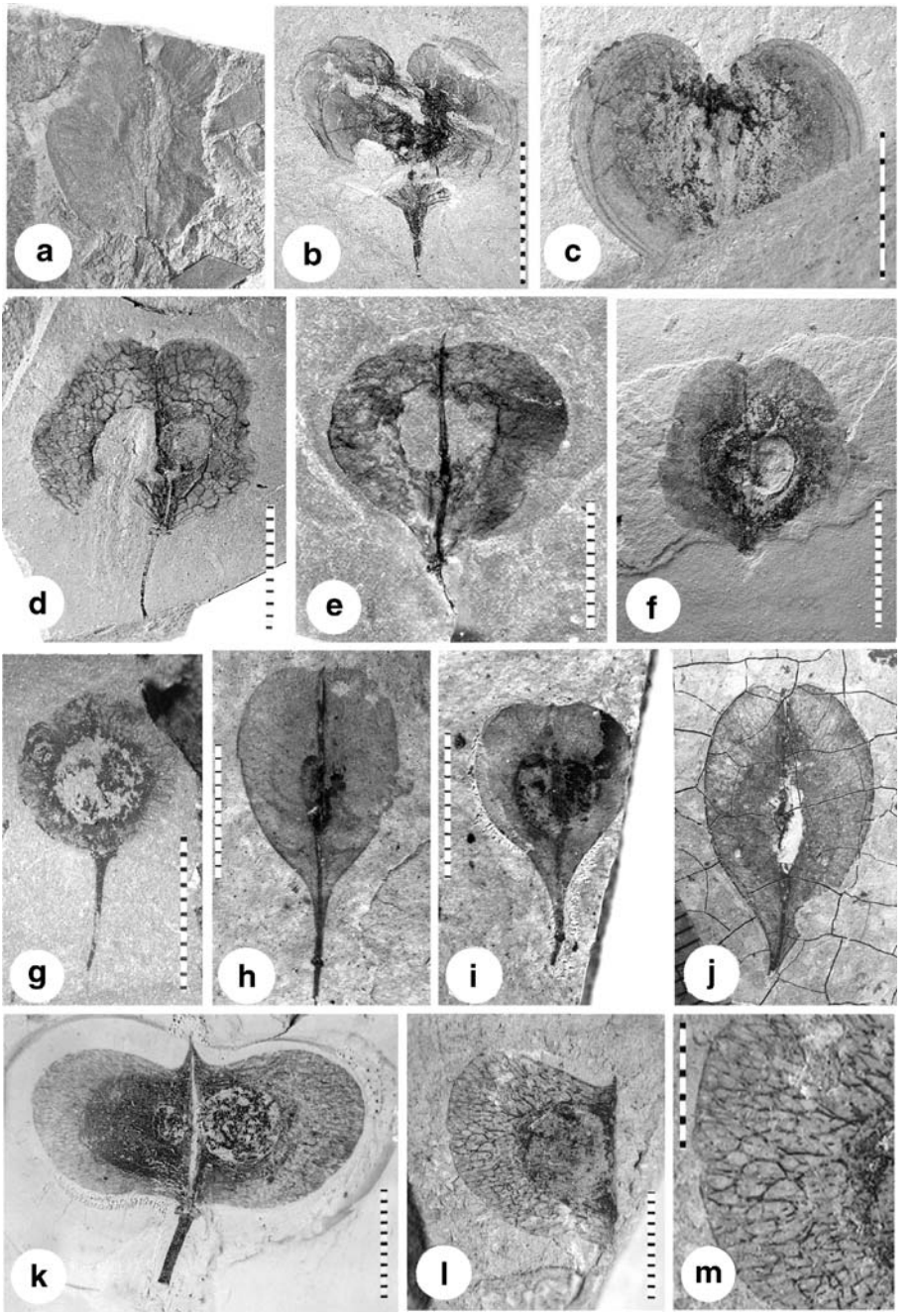
Fossil Rutaceae Although we have rejected some earlier assignments of fossil fruits to the genus *Ptelea*, we infer that the following species from the Eocene of western North America is a valid representative of the genus.

Ptelea paliuruoides (Brown) comb. n. Fig. 24d–g

Basionym. *Carpolithus paliuroides* Brown 1934, p. 67, pl. 15, Fig. 12.
Description. Fruit orbicular to more or less cordate, with a cuneate obtuse to right-angle base and slightly retuse apex, (10–)15–16 mm high and (10–)15–19 mm wide, similar in height and width, with two (or more?) wings symmetrical about the median axis. In face view, a coarse vascular bundle extends straight from the pedicel to the style bisecting the locular area which is positioned near the center of the fruit. Each locule bearing at least one large elliptical smooth rounded seed (Fig. 24f). Pedicel, relatively narrow (0.2 mm thick) and 4–6 mm long. A thickened disk/perianth scar at junction between pedicel and fruit. A thin stylar protrusion, ca 1 mm long, sometimes persisting. A moderately strong, sinuous vein outlining the locular area. Venation across the wing irregularly sinuous, with smaller irregular cross veins forming subangular, more or less isodiametric polygonal areoles (Fig. 24d, e, g). Fimbrial vein present. Wing area dotted with dark spots, 10–20 μm diameter.

This species is based on rare fin-winged fruits from the Middle Eocene Parachute Creek Member of the Green River Formation of Colorado and Utah. The prominent scar at top of pedicel (Fig. 24d, e, g) indicates that this fruit developed from a hypogynous perianth. Candidate families with hypogynous perianth and fin-winged fruits with at least two wings include Zygophyllaceae, Sapindaceae, Malvaceae and Brassicaceae. Because only complete specimens have been found (no mericarps), we infer that the fruits were nonschizocarpic, which would rule out many Brassicaceae, Zygophyllaceae and Sapindaceae. The narrow pedicel distinguishes this fruit from most extant genera in these families, and indicates that this fruit was probably only bicarpellate and two winged, because a thicker pedicel would be required to vascularize a multicarpellate fruit. The fruit is similar to that of *Brossardia* (Brassicaceae, Fig. 4a), but that genus differs in having an inflated locular area that extends from the base of the fruit to near the apex. The locular area in this fossil is confined to the central portion of the fruit (as in extant *Ptelea*) and does not appear to

Fig. 24 Eocene winged fruits of Malvaceae (**a**), Rhamnaceae (**b**, **c**), Rutaceae (**d–g**), Sapindaceae (**h–m**). **a** "*Ptelea*" *eocenica* Berry, USGS 146767 (Berry 1930, Pl. 41 Fig. 4), Grand Junction, Tennessee. **b** *Rainbowia rhamnoides* gen. et sp. n., holotype, DMNH 24492. **c** *Rainbowia rhamnoides*, paratype, UF18054-22809. **d–g** *Ptelea paliuroides* (Brown) comb. n., Middle Eocene Green River Formation. **d** Specimen with slender pedicel and reticulate venation. College of Idaho Museum of Natural History 2381, Rio Blanco County, Colorado. **e** Specimen from Watson Utah, UCMP 390999. **f** UF15753-53132, showing a seed attached to placenta, Watson, Utah. **g** Holotype, Brown, 1934, Roan Creek, Colorado. **h–j** *Brachyruscus alleni* Cockerell from Late Eocene of Florissant, Colorado. **h** Holotype of Cockerell 1922, UCM 38399. **i** Specimen with two seeds developed, UF18557-15040. **j** another specimen showing details of venation, FLFO4532B. **k–m** *Bridgesia bovayensis* sp. n. from Eocene of Bovay Pit, Holly Springs, Mississippi. **k** Holotype showing stout pedicel, hypogynous perianth scar, stylar protrusion, and two intact mericarps each with a large darkened locular area, and reticulately veined wing, UF 15737-30660. **l** Paratype: isolated mericarp, UF 15737-30661. **m** Enlargement from **l**, showing detail of reticulate venation. Scales calibrated in mm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have been inflated. The characters mentioned above led to more detailed comparison with extant *Ptelea*, which also has a thin pedicel and hypogynous perianth. The small dark spots dotting the surface of the fossil appear to represent pellucid dots (resin glands), an important feature in common with Rutaceae. The pair of longitudinal veins typically found on either side of the midline in modern and Miocene species of *Ptelea* (Call & Dilcher, 1995) is not as obvious in this Eocene fossil.

The holotype of this species (Fig. 24g) is smaller and more rounded than the three specimens recovered more recently (Fig. 24d–f), but we believe all of these specimens represent the same species because of the similarities of wing venation, narrow pedicel and prominent perianth scar.

Fossil Sapindaceae
Bridgesia bovayensis sp. n. Fig. 24k–m.

Holotype. UF 15737- 30660 (Fig. 24k).
Paratype. UF 15737-30661 (Fig. 24l, m).
Locality. Bovay Clay Pit, Holly Springs, Mississippi.
Diagnosis. Fruit widely elliptical, 15–16 mm high, 30 mm wide (nearly twice as wide as high), schizocarpic, falling into at least two singly winged mericarps. Locular area, comprising 1/2 to 2/3 the width of the fruit, inflated; the remaining distal portion forms the wings. Each locule contains a single globose seed attached centrally to the median axis of the fruit. The pedicel is stout, articulated with the base of the fruit with a widened scar of perianth and/or disk; a very short stipe is evident between the perianth scar and the remainder of the fruit. Venation consists of main veins spreading into the wings, with frequent dichotomies and anastomoses, craspedodromous to a fimbrial vein.

This species, from the Eocene of Mississippi, is represented by only two specimens, one predehiscent with an intact pedicel and a rounded seed visible within each locule (Fig. 24k), and the other a dispersed mericarp retaining a portion of the stylar projection (Fig. 24l). The combination of superior ovary, stout pedicel, inflated locules and schizocarpy occurs among some genera of Sapindaceae, Brassicaceae, and Zygophyllaceae. The combination of fruit morphology, wing venation, and seed shape are best matched by the extant sapindaceous genus *Bridgesia* (Fig. 17g). This identification has interesting biogeographic implications, because the genus is known today only in South America.

The fossil genus *Brachyruscus* Cockerell was based on the specimen in Fig. 24h from the Late Eocene Florissant beds of Colorado. Cockerell (1922) considered it to be a liliaceous flowering cladode, but closer examination of the type specimen, and other subsequently recovered specimens, shows features characteristic of fin-winged fruits (Fig. 24h–j). The fruit is obovate to cordate, basally decurrent into a short stipe, with a pair of wings symmetrical about the central axis. A single bean shaped seed is observed on each side of the midline, in the middle part of the fruit. A widened scar at junction of pedicel and fruit indicates a hypogynous perianth. The general organization of *Brachyruscus* suggests that affinities might lie with the Brassicaceae, Sapindaceae, Rutaceae, or Zygophyllaceae. Manchester (2001) considered this species likely to represent *Ptelea*, based on similarities with the extant genus including the thin pedicel, hypogynous perianth scar, a slight stylar

protuberance at the apex of the fruit; indehiscence, elongate, elliptical seeds in each carpel, and reticulate wing venation. He noted, however, that in the fossil specimens, the wing is obovate, narrowing basally and broadest in the apical one-half, whereas the extant species of *Ptelea* have a broadly elliptical outline and that the fossil fruits lack the two subsidiary veins seen on either side of the central axis that diverge from the pedicel and extend to the base of the locules in *Ptelea* (Call & Dilcher, 1995). In addition, the single, rather than double scar at base of the fruit is a distinction from the fruits of Rutaceae. Among the extant fruits that we examined *Brachyruscus* most resembles *Urvillea* (Sapindaceae, Fig. 17j–m).

Conclusions

These examples indicate that the survey of extant fin-winged fruits presented here can provide an improved basis for evaluating fruits from the fossil record. Some of the fossils are readily identified to extant families and/or genera, but in other cases the characters studied are not sufficiently diagnostic to achieve confident identification. Given the numerous cases of convergent evolution of fin-winged fruits, which occur in many different extant families (Table 1), it would not be surprising that some fossils may represent additional cases in which this fruit type evolved, for which there is no living representative. Special attention to details of venation as well as features of persistent perianth, bracts, disks, when present, can facilitate confident identification of extant genera, and also help to recognize extinct taxa. For improved confidence, tentative identifications achieved based on the characters presented here should also be checked with additional characters, including placentation, seed morphology and epidermal structure.

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