TAXONOMIC DISTRIBUTION OF MODERN FIN-WINGED FRUITS AND THE FOSSIL HISTORY OF THE COMBRETACEAE IN THE UNITED STATES BASED ON FIN-WINGED FRUITS

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
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To Craig Greene

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Abstract of Thesis Presented to the Graduate School
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Angiosperms have evolved wind dispersed fruits and seeds many times. The wings of fruits may be formed from different structures including outgrowths of the ovary or hypanthium, perianth parts, and bracts or bracteoles. The wings may also form various morphological and biomechanical shapes. One such of these fruits is "fin-winged" that is, having a longitudinal central axis from which several longitudinally oriented wings radiate. This form can be found in capsules, samaras, as well as in other fruit types where the wings may be formed from accessory structures. This thesis examines the diversity of these fin-winged fruits at the generic level within modern Angiosperms and gives brief descriptions of these fruits to aid in identification of dispersed fin-winged fruits. These descriptions are applied to determine if three fruit fossils, described as the genus *Terminalia* (Combretaceae), have sufficient characters to be differentiated from other fin-winged genera, and if they truly belong in the Combretaceae. The descriptions are also be used to make inferences about the evolution of these fruits. This survey indicated that fin-winged fruits are present among 23 families of angiosperm and are particularly well represented in the rosids.

CHAPTER 1
INTRODUCTION

Modern Fruits

Winged fruits are found in many Tertiary fossil localities and are commonly preserved together with fossil leaves and other debris in lake and pond deposits (e.g. Tidwell 1975, Wilde and Frankenhäuser 1997, Manchester 2001). The emphasis in many paleobotanical studies has been on the leaves, and the co-occurring winged fruits and seeds are often mentioned only in passing. Nevertheless, fruits and seeds are especially useful in taxonomy because they are part of the reproductive structures, which often have diagnostic features in angiosperms (Tiffney 1990). Winged fruits also 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 characters (Spjut 1994).

Despite this, it is only in the past few decades that fossilized winged fruits have been treated in more detail. Some examples of recent treatments are Acer (Wolfe and Tanai 1987), Fraxinus (Call and Dilcher 1992), Eucommia (Call and Dilcher 1997), Ceratopetalum (Barnes and Hill 1999), Dipteronia (McClain and Manchester 2001) and Ailanthus (Corbett and Manchester 2004). Recent treatments of extinct genera include Chaneya (Wang and Manchester 2000), Cedrelospermum (Manchester 1989), and Diplodipelta (Manchester and Donoghue 1995). In these instances, the fruits were more informative than leaves for the taxonomic determinations.

Many additional kinds of winged fruits are known from the Tertiary of North America that have not been identified. The difficulty in identifying their familial and generic affinities is largely due to the inaccessibility of comparative data on modern genera with winged fruits

(Tiffney 1990). An important recent contribution was published on asymmetrically winged fruits of the Americas (Mirle and Burnham 1999). It was accompanied by some line diagrams to aid in keying out unknown specimens, but did not include photographic images of the many different genera surveyed.

There are at least 30 extant genera of winged fruits that are popularly known and readily accessible in western North America, including Acer, Fraxinus, Ulmus, Carpinus, and Halesia (Schopmeyer 1977). If a fossil fruit does not match one of these familiar types, the comparative work for identification becomes a more daunting challenge because winged fruits occur in numerous genera scattered through at least 93 families of flowering plants (Dallwitz et al. 2000 onwards). There is no single source for comparative data on modern winged fruit genera and not even a comprehensive worldwide list. If a fossil winged fruit does not match a known living fruit type, it may be extinct, or it may correspond to an extant genus with which the investigator is unfamiliar. This lack of familiarity may occur more often when a genus has a fossil record across several continents, but has a limited distribution in modern times, as in the case of the extant Asian genus Craigia, whose fossil fruits in Europe and North America were formerly thought to represent an extinct genus Pteleaecarpum Weyland (Buzek et al. 1989), until their common identity was discovered (Kvaček et al. 1991).

Various morphological categories of winged fruits can be recognized, such as those with an apical or basal whorl of propeller-like wings, those with a single surrounding wing, and they vary in aerodynamic efficiency and mode of falling (Augsburger 1988). In this treatment, I focused on fruits which have two or more wings radiating from the vertical central axis as in the case of the anthocarps of the Nyctaginaceae (Galloway 1975). These fruits were referred to as "tumblers" (Augsburber 1988) in relation to flight pattern, as "finned" (Matlack 1987) and

"cyclically winged" (Wurdak et al. 2004). I use the term "fin-winged" because "tumblers" refers to flight pattern and some of these fruits do not fly; "finned" could refer to ribs and does not fully convey that they are winged; and "cyclically winged" could refer to fruits with wings radiating laterally. In some cases the entire fruit is the unit of dispersal and in others, the wings are on mericarps which fall off to disperse the seed. Some are capsular and dehisce entirely and others remain attached to the twig and dehisce their seeds as the fruit is shaken by the wind. To aid in systematic work, descriptions of many genera with the fin-winged morphology will be presented. These descriptions will allow comparisons to be made and will help determine if it is possible to distinguish between different families and genera based solely on the morphology of their fruit. The family Combretaceae is one in which fin-winged fruits occur in several genera with some genera more similar than others. This makes it an ideal family to study in detail.

Combretaceae

Some fossils of interest are those that have been assigned to the white mangrove family (Combretaceae) from the Eocene of the United States. Today this family is distributed pantropically, and can be found in the state of Florida. Many of the reported fossils are leaves, but because the entire-margined, pinnately veined leaves of this family are of a common morphology encountered in many angiosperm families, additional features are needed to confirm their identity. The family has diagnostically useful features such as combretaceous hairs and extrafloral nectaries on the leaves, but these have not been found on these impression fossils.

The Combretaceae were revised in 1965 by the two main workers in this group, A.W Excell and C.A. Stace (Excell and Stace 1965). They recognized two subfamilies, the Strephonematoideae and the Combretoideae. Strephonematoideae contains the genus *Strephonema* which is distinct in its semi-inferior ovary, two-armed hairs, paracytic stomata, and revolute domatia. The Combretoideae in turn have a fully inferior ovary and convolute or plicate

cotyledons and the stomata are cyclocytic or anomocytic. The fruits of *Stephonema* are drupaceous and do not have any specialized dispersal mechanism (Jongkind 1995), and are not considered here.

The Combretoideae have been studied phylogenetically by Tan et al. (2002). The study included 18 taxa and was based on ITS, rbcL, PY-IGS but included no morphological data. *Strephonema* was used as the outgroup and the results were similar to what would be expected from the traditional taxonomy. The subfamily split into the tribe containing *Laguncularia* and *Lumnizera* (Laguncularieae) and the tribe Combretaeae which further divided into two clades; Combretinae and Terminaliinae. Traditionally, there is a third subtribe the Pteleopsidinae, but this was not included in Tan's analysis. All of these groups contain species with winged fruits.

The genera of Combretaceae that contain species with winged fruits are *Calycopteris* , *Combretum*, *Pteleopsis*, *Meiostemon*, *Terminalia,* and *Thiloa*. Wings may be derived from ovary tissue, bracteoles or perianth (Excel and Stace 1965).

There are three unique synapomorphies for the Combretaceae; anauxotelic inflorescences (inflorescence not ending in flower and growth not extending beyond inflorescence), "combretaceous" hairs (long, straight, sharply pointed, unicellular, very thick walled, with conical internal component at base), and a "combretaceous" ovary (ovary inferior and unilocular; ovules few, pendulous on elongate funiculi from the tip of locule) (Johnson and Briggs 1984, Conti et al. 1997). Any of these features could be preserved in the right conditions, but none of the fossil fruit species considered here are common and all are preserved as either compression or impression fossils unattached to branches or leaves.

Fossil fruits have also been attributed to this family. Three North American fossil species have been identified as belonging to this family. Fossil fruits assigned to *Terminalia vera* are

found in Eocene claypits in Tennessee and Kentucky and were first described by Edward Berry in 1930. This fruit was described as similar to *T. brownii* and *T. darlingii*. *Terminalia estamina* was described by MacGinitie (1941) based on leaves and associated winged fruits from the Eocene Chalk Bluffs flora of the Central Sierra Nevada, California, and was compared to extant *T. hainensis* and *T. triflora*. *Terminalia oregona* was described from the Oligocene of Oregon by Meyer and Manchester (1997). It was compared to extant *T. paniculata*, and to MacGinitie's fossil fruits of *Terminalia estamina*.

Characters for identifying combretaceous fruits have not been clearly presented before, nor have rigorous morphological comparisons been made between the winged fruits borne by different genera of the family. Most of the fruits in this family are dispersed abiotically either by water or wind, and fin-winged fruits are also present in several genera. Without detailed morphological information on the fruits of extant taxa, it is difficult to have confidence in the diagnosis of these fossiliferous fruits. MacGinitie (1941) reported that the seed cavity of *Combretum* is typically longer relative to the wing than those of *Terminalia*, but he did not make a full comparison or mention the status of the other genera.

Study of the morphology of these fossils and comparison with the modern genera of this and other families with fin-winged fruits will provide more characters to evaluate whether these fossils belong to the family, and if so, will give a strong record for the family in the United States during the Eocene.

CHAPTER 2
MATERIALS AND METHODS

Modern Fruit Descriptions

A list was made of fruits known to have the fin-winged fruit type from internet and literature searches that I made. The fruit morphology of genera in this list was verified when possible by examination of specimens in herbaria. The taxonomy was updated to the APG system (Angiosperm Phylogeny Group 2003).

Extant fruits were examined and photographed with a Nikon Coolpix 5400 digital camera at the Gray (GH) and Arnold Arboretum (A) Herbaria at Harvard University, Cambridge, MA, at the US National Museum at the Smithsonian Institution, Washington DC (US), and the United States National Seed Herbarium, Beltsville, MD (USNSH). Photographs taken of specimens at the Harvard Herbaria for which the source was unclear (A or GH) are provisionally marked HARVARD or HARVARD SEED COLLECTION (if they came from the seed collection). The lighting, both transmitted, and reflected, was adjusted to best show characters such as venation and trichomes.

The photographs were then used to determine important characters for these genera. Taxonomic literature (e.g. Goldberg 1986, Hutchinson 1964, and Judd 2006) was consulted to help interpret the photographs. The fruits were characterized by number of wings, number of carpels, dehiscence, ovary position, overall shape, wing texture, venation, vein spacing, accessory parts (such as disk scar), and presence of a marginal vein. In some cases, the state was not observable in the photographs nor available in the literature. Parentheses are included around characters for which information is given from familial descriptions, when the details for the particular genus were not available. Fruit type is given when clear, but indehiscent fruits are often simply marked “indehiscent” to avoid confusing terms such as samara/samarium. Length

and width are recorded for individual specimens with slashes between different measured specimens or, in the case of some of the genera in Combretaceae are given as ranges.

Fossil and Modern Combretaceae

Comparisons were made with extant genera of all angiosperm families known to possess plants with the fin-winged fruit type. Specimens were examined and photographed at the herbaria mentioned above. Fossil fruits were studied from collections of the Florida Museum of Natural History, Gainesville (UF), the Smithsonian Institution [United States National Museum], Washington, D.C., (USNM), the University of California, Museum of Paleontology, Berkeley (UCMP), and the Field Museum of Natural History, Chicago (FMNH).

The Eocene fruits from western Tennessee and Kentucky were collected along with fossil leaves, fruits, flowers and pollen from clay pits in the middle Eocene Claiborne Formation of Tennessee and Kentucky. Large portions of the flora, including the species considered here, were monographed by Berry (1916, 1930), but many of the determinations are still undergoing revision (Dilcher and Jones 1980, Jones and Dilcher 1980, Herendeen et al., 1990, Herendeen and Dilcher 1990). The age estimate is based on palynological correlations.

A total of 25 specimens were examined, including ten from Lamkin clay pit, one from Warman, five from Grable, ten from Puryear, two from Wilbank, and one each from Powers localities. A dissecting microscope was used to examine details of the fruits, and sediment was chipped with needles to expose details of the wings. Each specimen was photographed with a Nikon Coolpix 955 digital camera.

The fossils were initially exposed by splitting the clay with chisels, revealing the fruits in longitudinal section. Because the plane of fracture usually exposes only two of the wings, more detailed preparation was necessary to demonstrate the full number of wings. To reveal the complete complement of wings, both counterpart halves of the same specimen were reassembled

and then fractured transversely. To control the orientation of the transverse fracture, we used a dry circular diamond saw to pre-cut the surrounding clay in the desired plane.

Wing venation was studied under magnification and a camera lucida was used to record details of venation. Line drawings were used to determine if each wing was a composite of two fused laminae or if it was a single structure. Venation patterns of part and counterpart were traced and overlaid to determine if the venation was the same on each side.

The Eocene specimens from California, from the Chalk Bluffs flora of the Sierra Nevada Mountains were previously described by MacGinitie (1941) under the name Terminalia estamina. Specimens were studied from the UCMP and USNM collections

The Oligocene specimens from Oregon were previously treated by Lakhanpal (1958), Brown (1959) and Meyer and Manchester (1997). We studied the original specimens deposited at UF, USNM, and UCMP.

The fossils were then compared to the modern genera of fruit with fin wings and genera with similar features were compared to determine whether the fossils could be confidently identified to a particular taxonomic group.

Table 2-1. Modern fin-winged fruits

Family	Genus	wing num.	carpel num.	dispersal mode	ovary position	marginal vein	Persistance of parts	Longer/ Wider/ (roughly) equal (Q)
Achariaceae	Carpotroche	6-20+	4-8	fruit	Sup.	No	disk	Q
Apiaceae	Prangos	5	5	finned mericarp	Inf.	No	Perianth	L
Apiaceae	Steganotaenia	2	5	finned mericarp	Inf	No	Perianth	L
Begoniaceae	Begonia	3	3/5	anemoballisty	Inf	Yes	Stamenal disk	L/W/Q
Burmanniaceae	Burmannia	3	3	?	Inf	?	?	?
Cardiopteridaceae	Cardiopteris	2	2	fruit	Sup.	Yes	Style	L
Celastraceae	Stackhousia	3	3--5	mericarp	Sup.	Yes	Style, perianth	L
Celastraceae	Tripterigium	3	3-loc	fruit	Sup.	Yes	Style, Perianth	L
Celastraceae	Wimmeria	2-3-(4)	2-3-loc	fruit	Sup.	Yes		L/W
Combretaceae	Combretum	2-5	4--5	fruit	Inf.	No	(style)	L/W/Q
Combretaceae	Macropteranthus	4	2	fruit	Inf.	No	Perianth	L/W
Combretaceae	Meiostemon	2		fruit	Inf.	No	apical protrusion	L
Combretaceae	Pteleopsis	2	2	fruit	Inf.	No	No	L
Combretaceae	Thiloa	4	2	fruit	Inf.	No	No	Q
Combretaceae	Terminalia	2,4,5	4--5	fruit	Inf.	No	No	L/W/Q
Cunoniaceae	Gillbeea	3	3	?	Sup.	Yes	No	L
Cyrillaceae	Cliftonia	1--2	3-4 locules	fruit	Sup.	?	Perianth	Q
Dioscoreaceae	Dioscorea	3	3	anemoballisty	Inf.	suture	Perianth	L/W
Fabaceae	Fissicalyx	2	1	fruit	Sup.	No	No	L
Hernandiaceae	Illigera	2	1	fruit	Inf.	No	No	W
Lophopixidaceae	Lophopyxis	5	5	fruit	Sup.	No	Style, perianth	L
Lauranthaceae	Nuyitsia	3	3--4	fruit	I	No	No	L
Malvaceae	Cavanillesia	4	5	fruit	S	No	apical protrusion	W
Malvaceae	Abroma	5	5	capsule	S	suture	Perianth	W
Malvaceae	Kleinhovia	5	5	capsule	S	suture	Perianth	W
Malvaceae	Pentace	5	2--10	?	S	No	Perianth	L
Malvaceae	Pterostyrax	5	5	?	Sup.	No	P	L

Table 2-1. Continued

Family	Genus	wing num.	carpel num.	dispersal mode	ovary position	marginal vein	Persistance of parts	Longer/ Wider/ (roughly) equal (Q)
Malvaceae	Berrya	5	5	capsule	Sup.	No	?	W
Malvaceae	Burretiodendron	5	5	capsule	Sup.	Yes, suture	S	L
Malvaceae	Colona	3/4/5	?	capsule	Sup.	No	S	W
Malvaceae	Craigia	5	3/4	capsule	Sup.	Yes	No	L
Malpighiaceae	Tetrapterys	?	?	?	?	?	?	?
Malpighiaceae	Aspidopterys	3	3	fruit	Sup.	No	No	L
Nyctaginaceae	Phaeoptilum	4	1	fruit	Sup.	No	No	L
Onagraceae	Megapterium	4	4	anemoballisty	Inf.	suture	No	Q
Onagraceae	Oenothera	4	4	anemoballisty	Inf.	suture	No	L/Q
Pedaliaceae	Holubia	4	2	fruit	Sup.	Yes	No	Q
Pedaliaceae	Pterodiscus	4	(2-4)	fruit	Sup.	No	Perianth	Q
Phyllanthaceae	Hymenocardia	2	3	fruit	Sup.	Yes	No	L
Polygalaceae	Polygala		(2-3)	fruit	Sup.	No	apical protrusion	L
Polygonaceae	Atraphaxis	3	(2-3)	fruit	Sup.	No	Perianth	W
Polygonaceae	Rheum	3	(2-3)	fruit	Sup.	No	No	L
Polygonaceae	Rumex	3	(2-3)	fruit	Sup.	No	No	L/W
Polygonaceae	Polygonum	3	(2-3)	fruit	Sup.	No	No	L
Polygonaceae	Antigonon	3	(2-3)	fruit	Sup.	No	No	Q
Rhamnaceae	Gouania	3	3	capsule	Sup.	I. marginal	apical disk	W
Rhamnaceae	Chaydia	3	3	capsule	Sup.	I. marginal	No	L
Rhamnaceae	Reissikia	3	3	mericarp	Sup.	I. marginal	No	W
Rutaceae	Balfourodendron	4	4--5	fruit	Sup.	No	No	W
Rutaceae	Ptelea	2--3	2-3 loc	No	Sup.	No	No	L/Q
Sapindaceae	Dodonaea	3	?3	?	Sup.	?	?	?
Sapindaceae	Urvillea	2	(2-3)	capsule	Sup.	Yes	basal disk	L
Sapindaceae	Majidea	2?	(2-3)	capsule	Sup.	Yes	basal disk	?
Sapindaceae	Stocksia	?	(2-3)	capsule	Sup.	Yes	basal disk	?
Sapindaceae	Thouindium	3	(2-3)	capsule	Sup.	Yes	basal disk	L

Table 2-1. Continued

Family	Genus	wing num.	carpel num.	dispersal mode	ovary position	marginal vein	Persistance of parts	Longer/ Wider/ (roughly) equal (Q)
Sapindaceae	Toulicia	3	(2-3)	capsule	Sup.	Yes	basal disk	?
Styraceae	Halesia	2 or 4	2	fruit	Inf.	Yes	Perianth	L
Trigoniaceae	Humbertiodendron	3	3	fruit	Sup.	Yes	No	Q
Tropeaeoceae	Tropaeolum	3	3 (1 locule)	mericarp	Sup.	Yes	?	L
Zygophyllaceae	Bulnesia	5	5	mericarp	Sup.	Yes	?	?
Zygophyllaceae	Guiacum	?	5	Yes	Sup.	?	?	?
Zygophyllaceae	Morkillia	4	(2-5)	capsule	Sup.	No?		L
Zygophyllaceae	Porleria	3	(2-5)	mericarp	Sup.	?	?	?
Zygophyllaceae	Zygophyllum		(2-5)	mericarp	Sup.	?	?	?

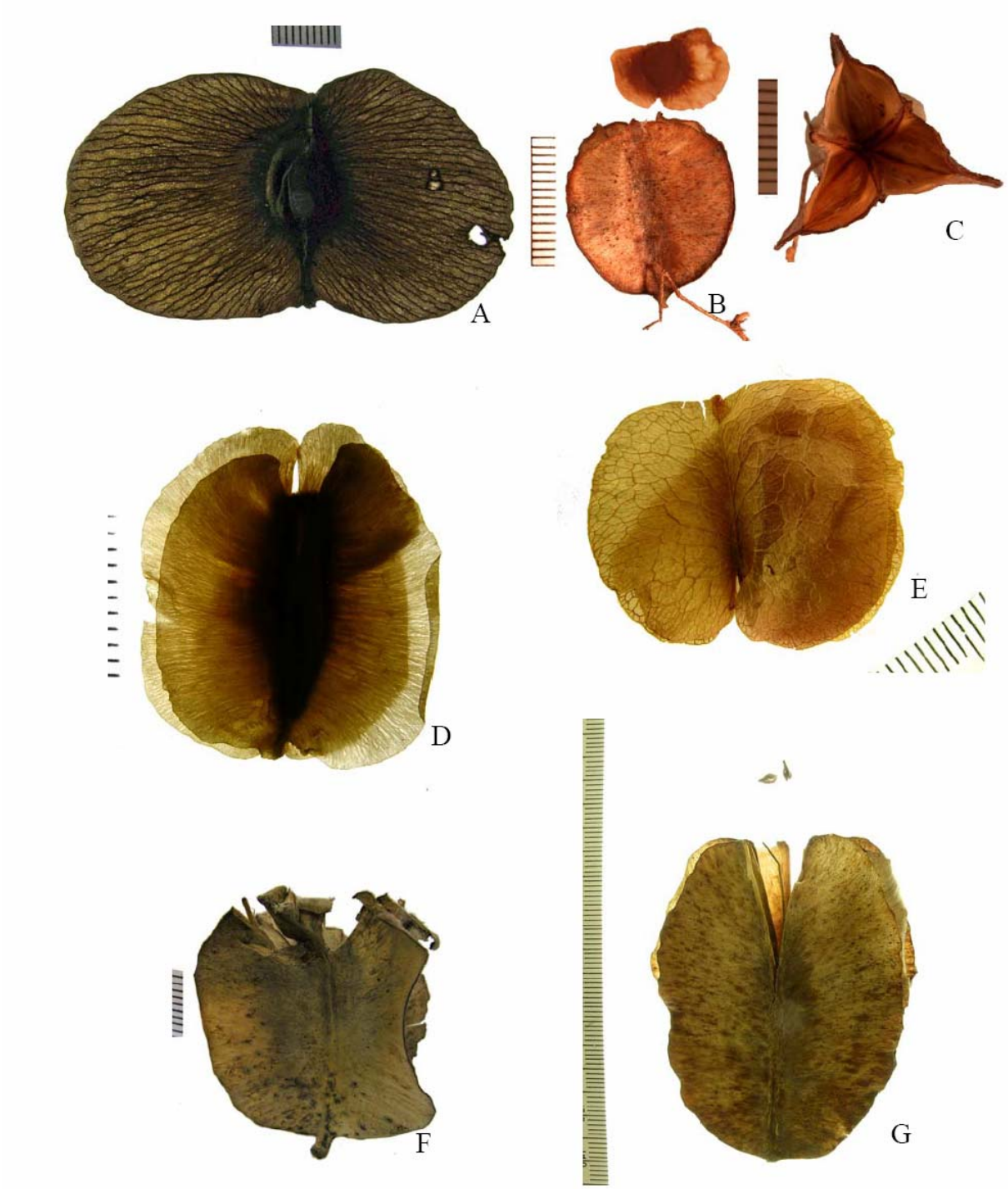

Figure 2-1. Hernandiaceae—Onagraceae. A) *Illigera grandiflora* (Heng 11446, A). B) *Dioscorea* (McPherson 43, FLAS). C) *Dioscorea* (McPherson 43, FLAS). D) *Phaeoptilum. spirosum* (R. Srydel "≥ 199", USNSH). E) *Rumex venosus* (77, USNSH). F) *Oenothera missouriensis* (Stevens 561, GH). G) *Megapterium missouriense* (L.E Wham, USNSH).

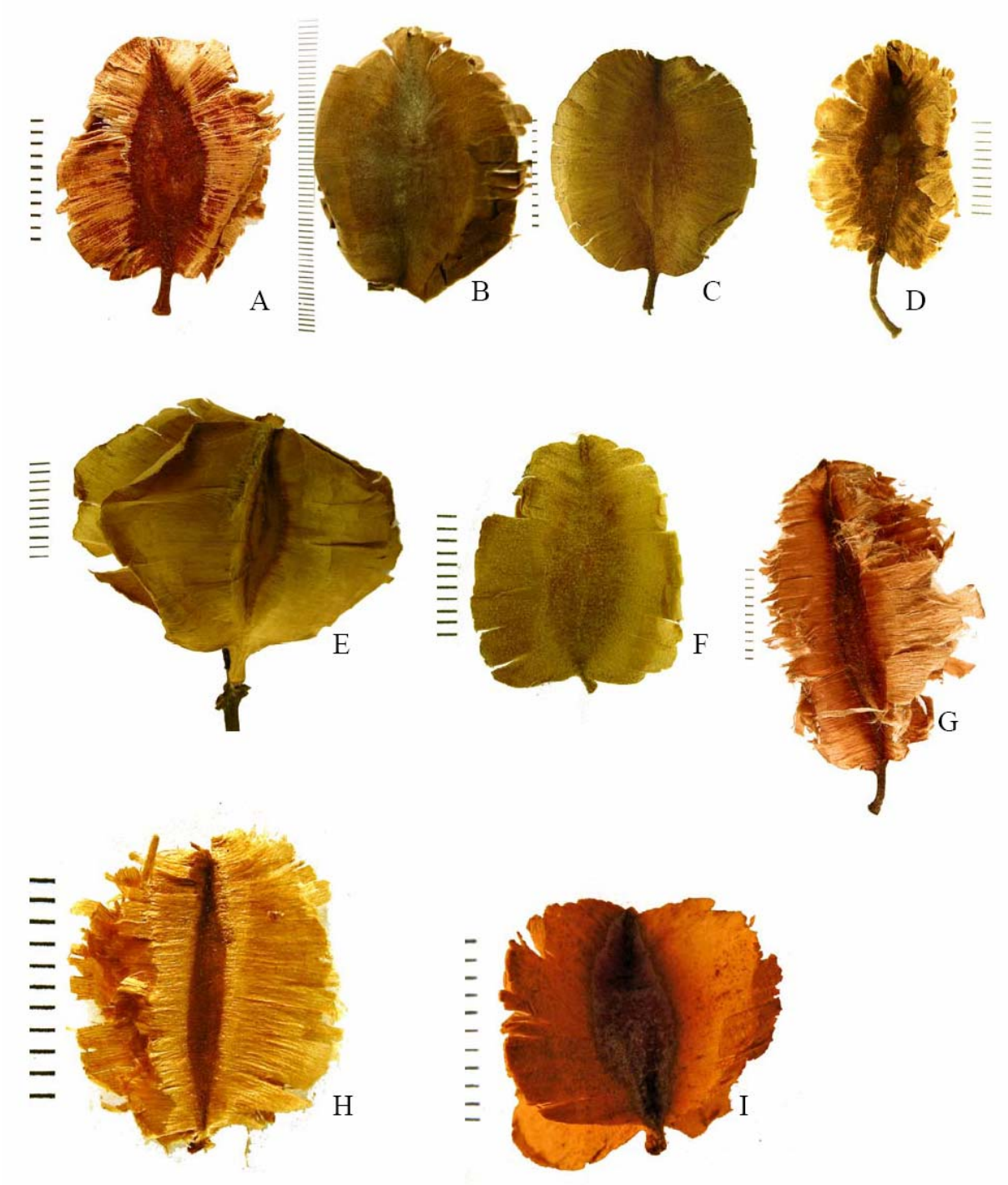

Figure 2-2. Combretaceae (Combretum). A) *Combretum apiculatum* (SPI 28342, USNSH). B) *Combretum gazense* (PIG 13469, USNSH). C) *Combretum fruticosum* (PI 104111,USNSH). D) *Combretum rhodesicum* (SPI 48244, Harvard). E) *Combretum grandiflorum* (SPI 72993, USNSH). F) *Combretum primigenum* (SPI 61642, USNSH). G*) Combretum paniculatum* (PI s.n., USNSH). H) *Combretum smeathmanii* (PI 73930, USNSH). I) *Combretum imberbe* (SPI 48243, USNSH).

Figure 2-3. Combretaceae (Terminalia). A) *Terminalia argentea* (PI 300640, USNSH). B) *Terminalia superba* (Harris and Fay 781, Harvard). C) *Terminalia macroptera* (221-9, Harvard). D) *Terminalia tomentosa* (Hara et al. 630075, A). E) *Terminalia tomentosa* (Butterwick 2, A). F) *Terminalia virens* (Maguire 30764, USNSH). G) *Terminalia sericera* (Parker 1428, Harvard). H) *Terminalia amazonia* (Steinbach 6617, A). I) *Terminalia browneii* (Harvard from Flora Uganda). J) *Terminalia pedicellata* (Maxwell 01-461, A)

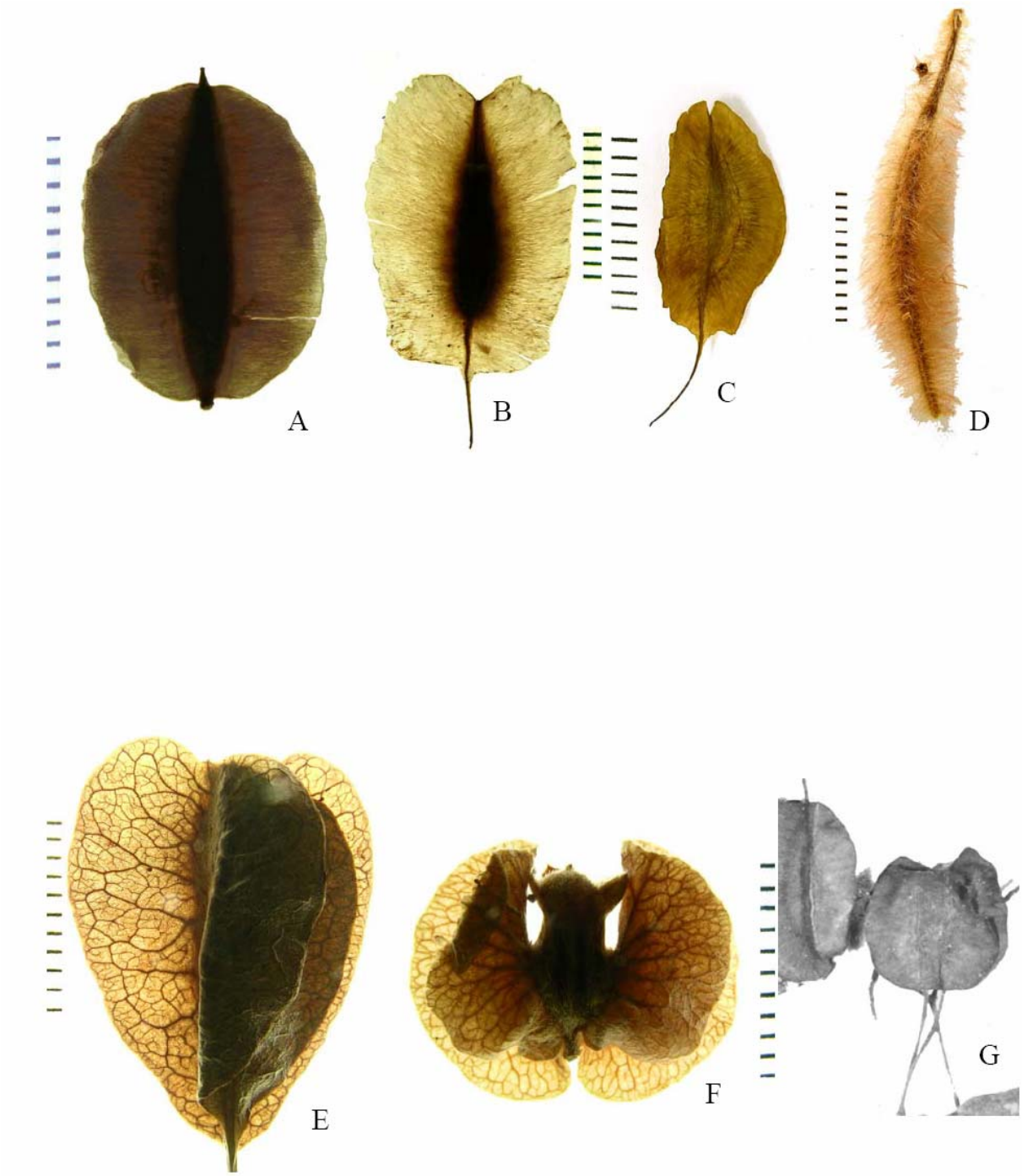

Figure 2-4. Combretaceae (other). A) *Meiostemon tetrardra* (Grosuenor sn1966, USNSH). B) *Pteleopsis hylodendron* (Claesaers 401, USNSH). C) *Pteleopsis sp.* (Gossweiler 13550, USNSH). D) *Guiera sp* (Bamps 2477, USNSH). E) *Macropteranthus fitzalani* (Francis SN 1920, USNSH). F) *Macropteranthus kekwickii* (N.Byrnes 1592, USNSH). G) *Thiloa sp.* (photo of a photograph from "Types from Munich Herbarium").

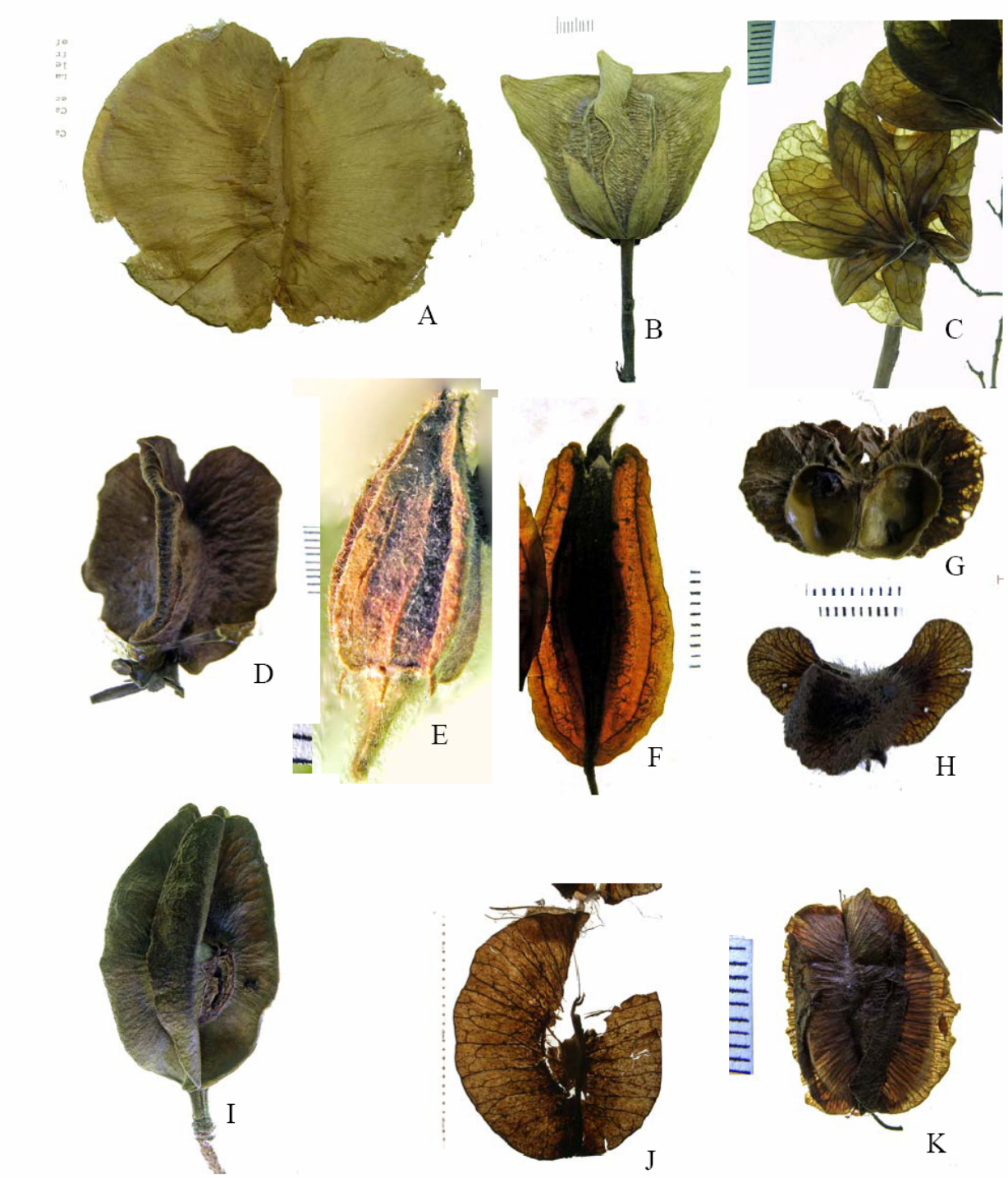

Figure 2-5. Malvales. A) *Cavanellisia platanifolia* (Foster 2247, GH). B) *Abroma angusta* (Wang 41264, A). C) *Kleinhovia hospita* (Huang et al 16132, A). D) *Maxwellia lepidota* (Hurliman 13129, A)). E) *Pterostyrax corymbosa* (Mie Min-Xiang 92250, A). F) *Halesia diptera* (Chester 1124, A). G) *Berrya javanica* (KK and SS 11, A). H) *Colona sp*. (Suejarto 59, A). I) *Burretiodendron esquirolli* (Malelen et al. 1160, A). J) *Cragia yunnanensis* (1124, UF). K) *Pentace laxiflora* (San 78602, A).

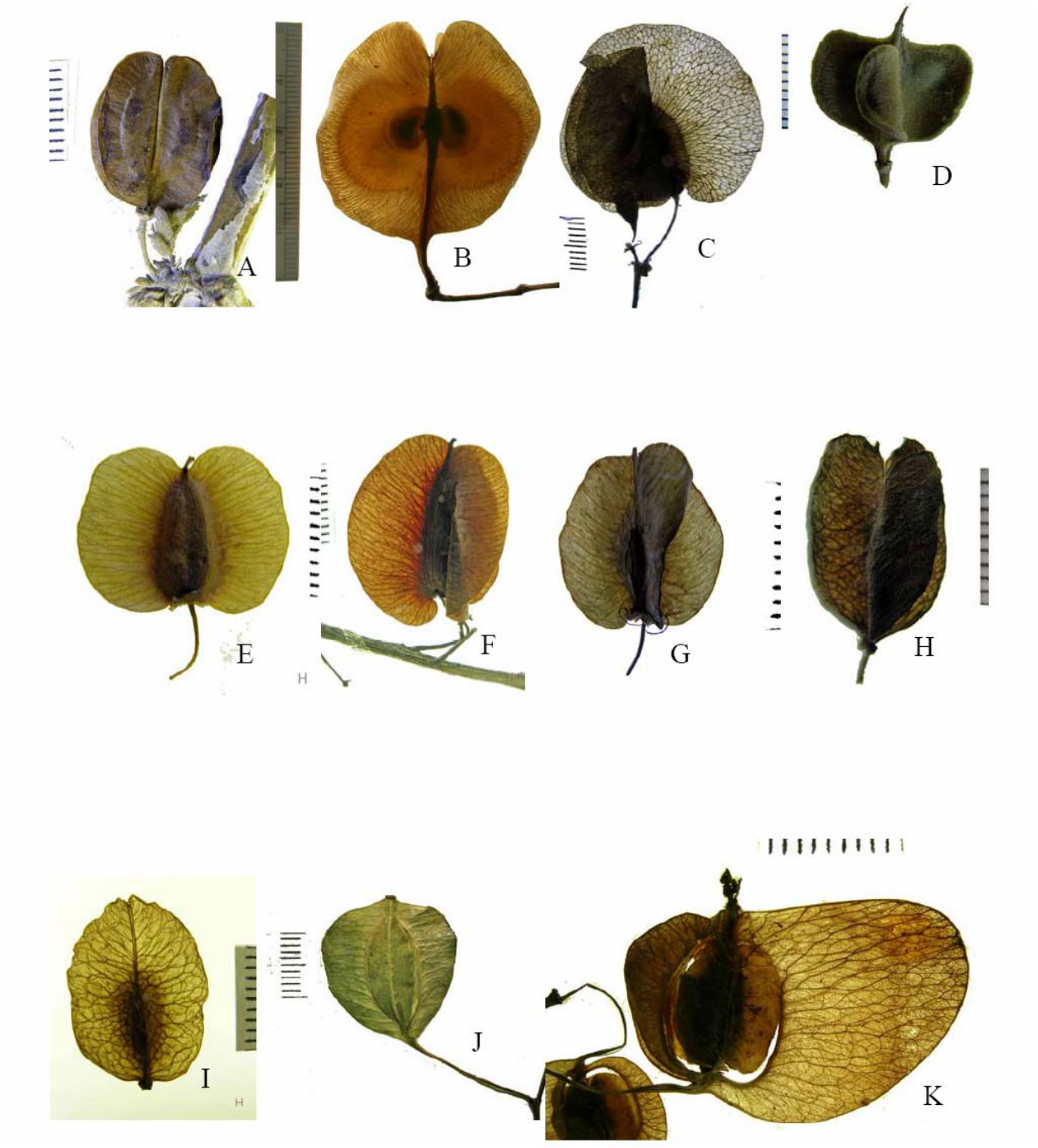

Figure 2-6. Zygophyllaceae—Begoniaceae. A) *Bulnesia chilensis* (Weidermaum 429, GH). B) *Bulnesia arborea* (1069, UF). C) *Zygophyllum morgansa* (Marloth 12275, A). D) *Porleria angustifolia* (Moore and Steyermark 3288, Harvard). E) *Wimmeria mexicana* (Clevinger July 1999, GH). F) *Wimmeria concolor* (Goldman 227, GH). G) *Tripterigium regelii* (USNSH Togashi 531). H) *Gillbeea papuana* (Brass 31815, A). I) *Gillbeea papuana* (Takeuchi 6084, A). J) *Begonia sp.* (Kosterman 6022, A). K) *Begonia nelubifolia* (Poropus 8543, GH).

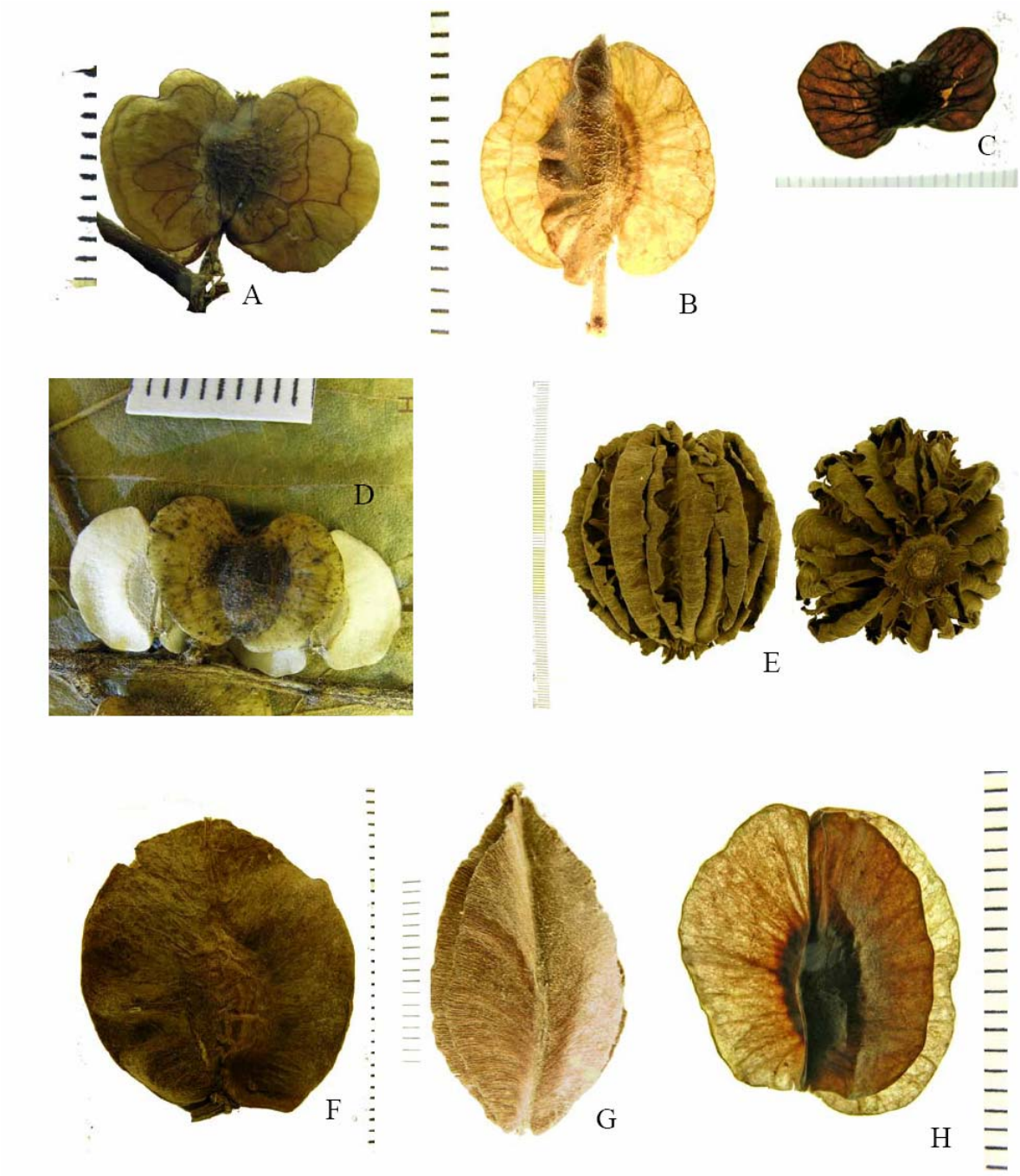

Figure 2-7. Rhamnaceae—Tropaeolumaceae. A) *Gouania domingensis* (Rodriguez 2566, A). B) *Chaydaia* (Huder 601, USNSH). C) *Reisseika* (L.O. Williams 6834, USNSH). D) *Gouania lupuloides* (Brumbach 9537, GH). E) *Carpotroche amazonica* (No. 9001, USNSH). F) *Humbertodendron* (Capman 180535F, USNSH). G) *Lophopyxis* (Buderus NGF 23932, USNSH). *Tropaeolum* (Donat 51, USNSH).

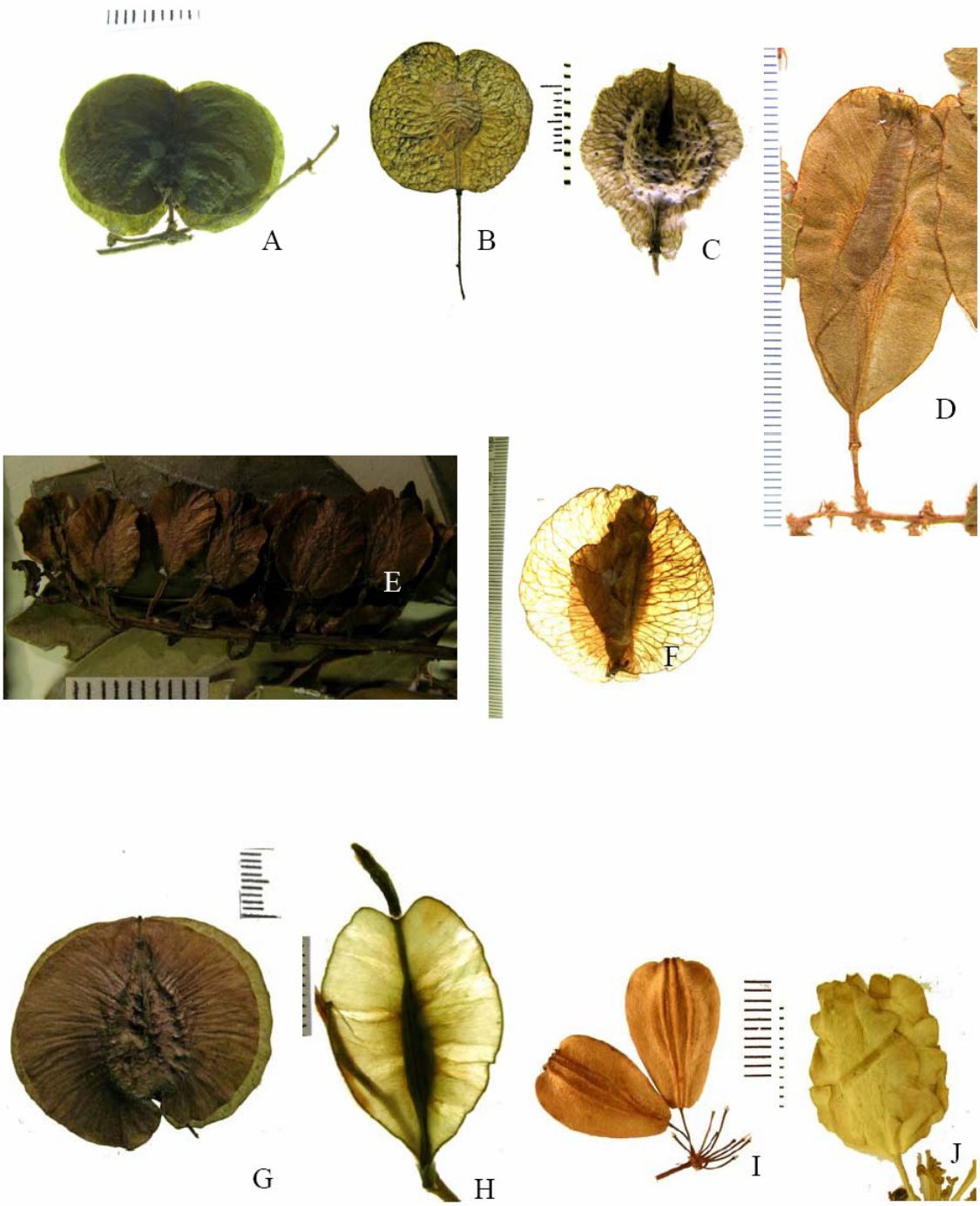

Figure 2-8. Rutaceae— Apiaceae. A) *Balfourodendron riedelanum* (Fiebrig 6104, GH). B) *Ptelea trifolata* (Harvard Seed Collection). C) *Ptelea crenulata* (Harvard Seed Collection). D) *Urvillea andersonii* (Anderson 9150, NYBG). E) *Cliftonia monophylla* (Rhoades 5a203, GH). F) *Holubia saccata* (AOD Mogg 24419, USNSH) G) *Pterodiscus sp.* (Dinker 4935, A). H) *Cardiopteris moluccanum* (Wang 81070, A). I) *Steganotaenia araliocea* (Meyer 7962, USNSH). J) *Prangos odotoptera* (Reckingerf 997, USNSH).

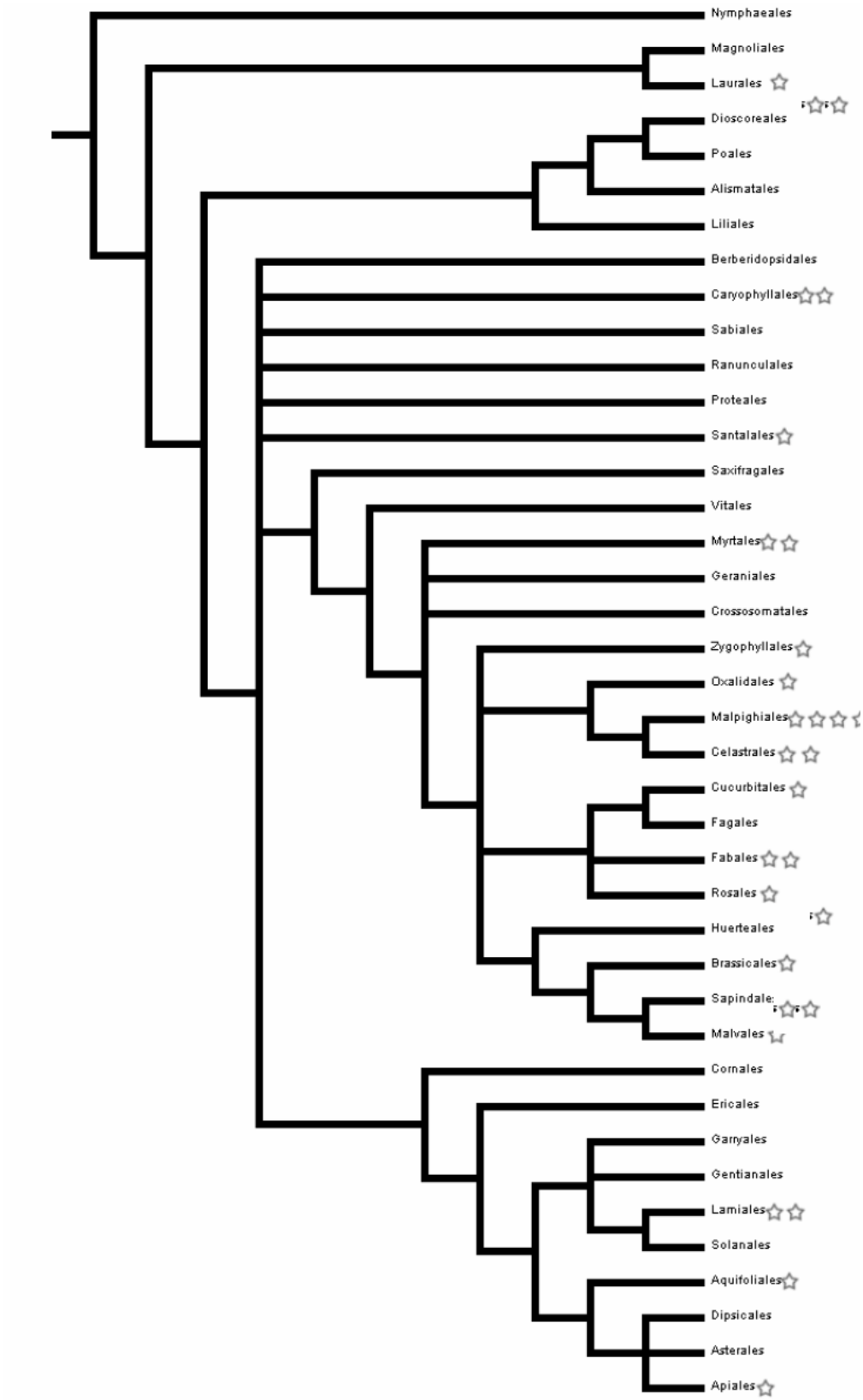

Figure 2-9. Distribution of fin winged fruits on Angiosperm phylogeny. Each star represents a family that contains at least one species with fin winged fruits. Topology taken from (Stevens, 2001 onwards).

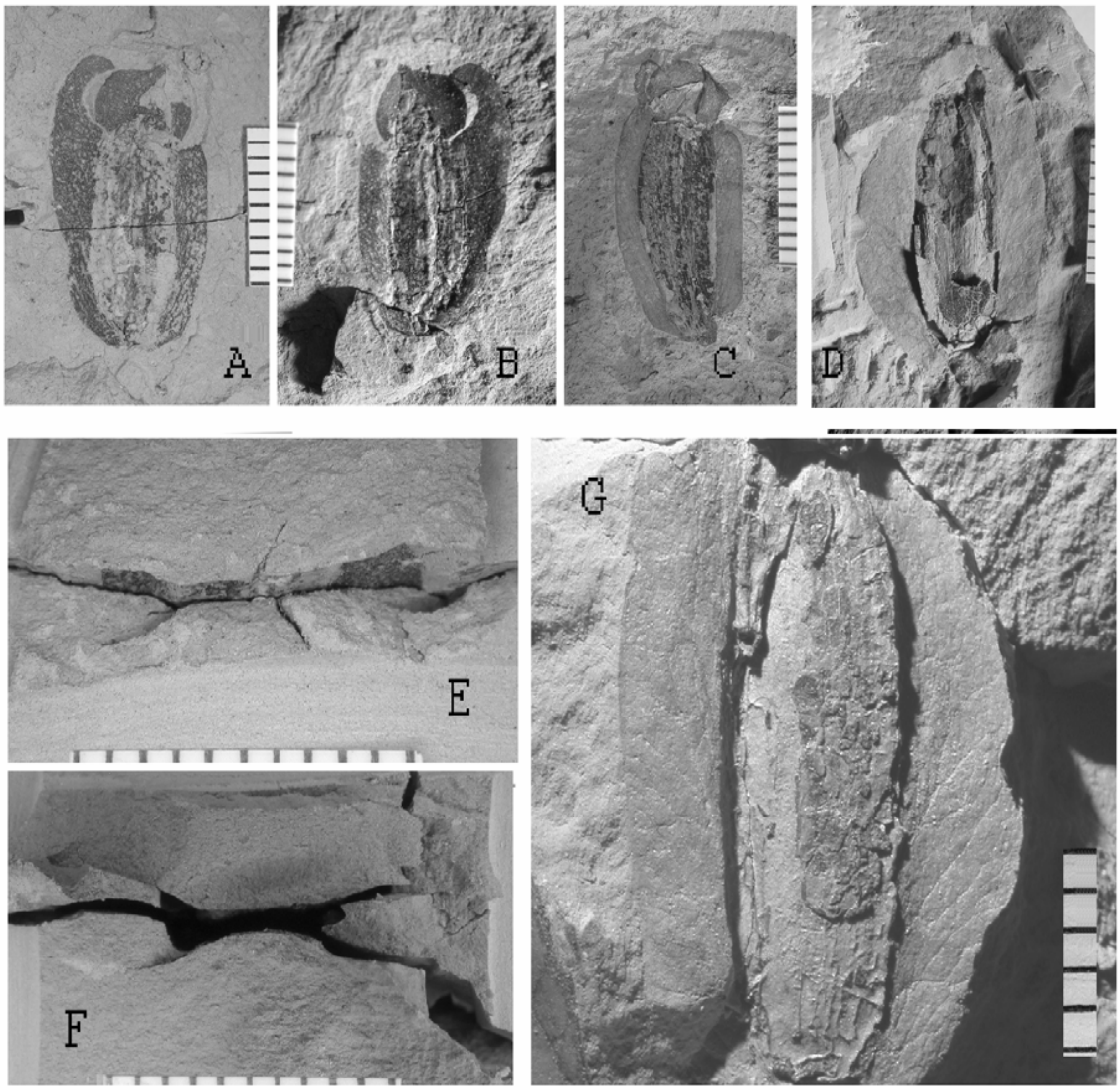

Figure 2-10. *Terminalia vera*. A) (FLMNH 15815-48329). B) (FLMNH 15815-48329). C) (FLMNH 15815-48326). D) (UF 15875-48329). E) (UF 15875-48329). F) (UF 18884-32723) G. (UF 18884-32723).

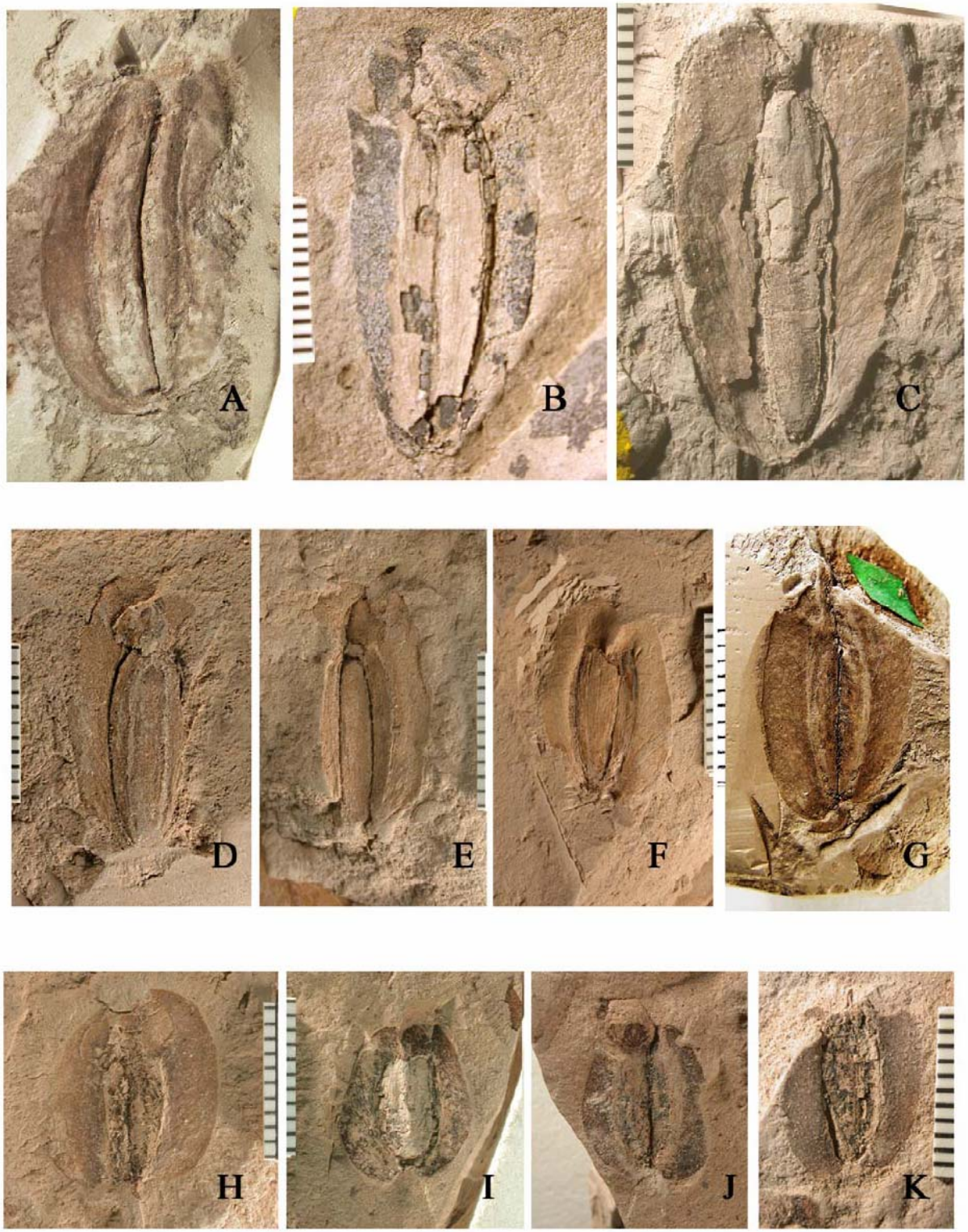

Figure 2-11. *Carpolithes prangosoides*. A) (USNM 36005). B) (FLMNH 15815-48328). C.) (FLMNH 15820-48318). D) (FLMNH 18884-32781). E) (FLMNH 18884-32781). F) (UF15820-48332) G) (FLMNH 18952-46057). H) (FLMNH15826-48331). I) (FLMNH). J) (FLMNH). K) (FLMNH 15815-48325).

Figure 2-12. *Terminalia vera* and *Macropteranthus fitzalani*. A) (USNM). B) (USNSH Francis SN 1920).

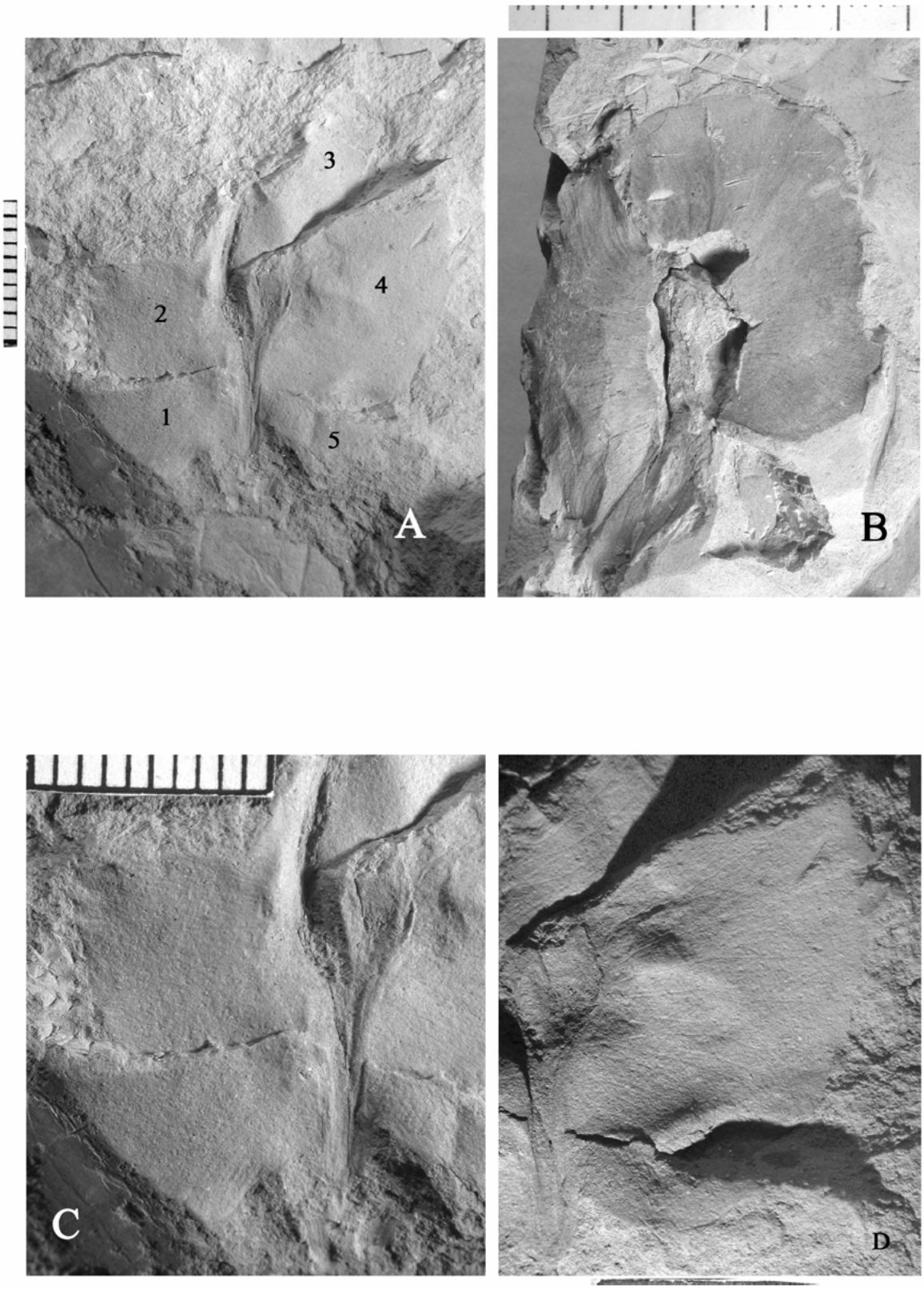

Figure 2-13. *Terminalia estamina*. A) (UCMP 2321). B) (USNM 313946). C) (UCMP 2321). D) (UCMP 2321).

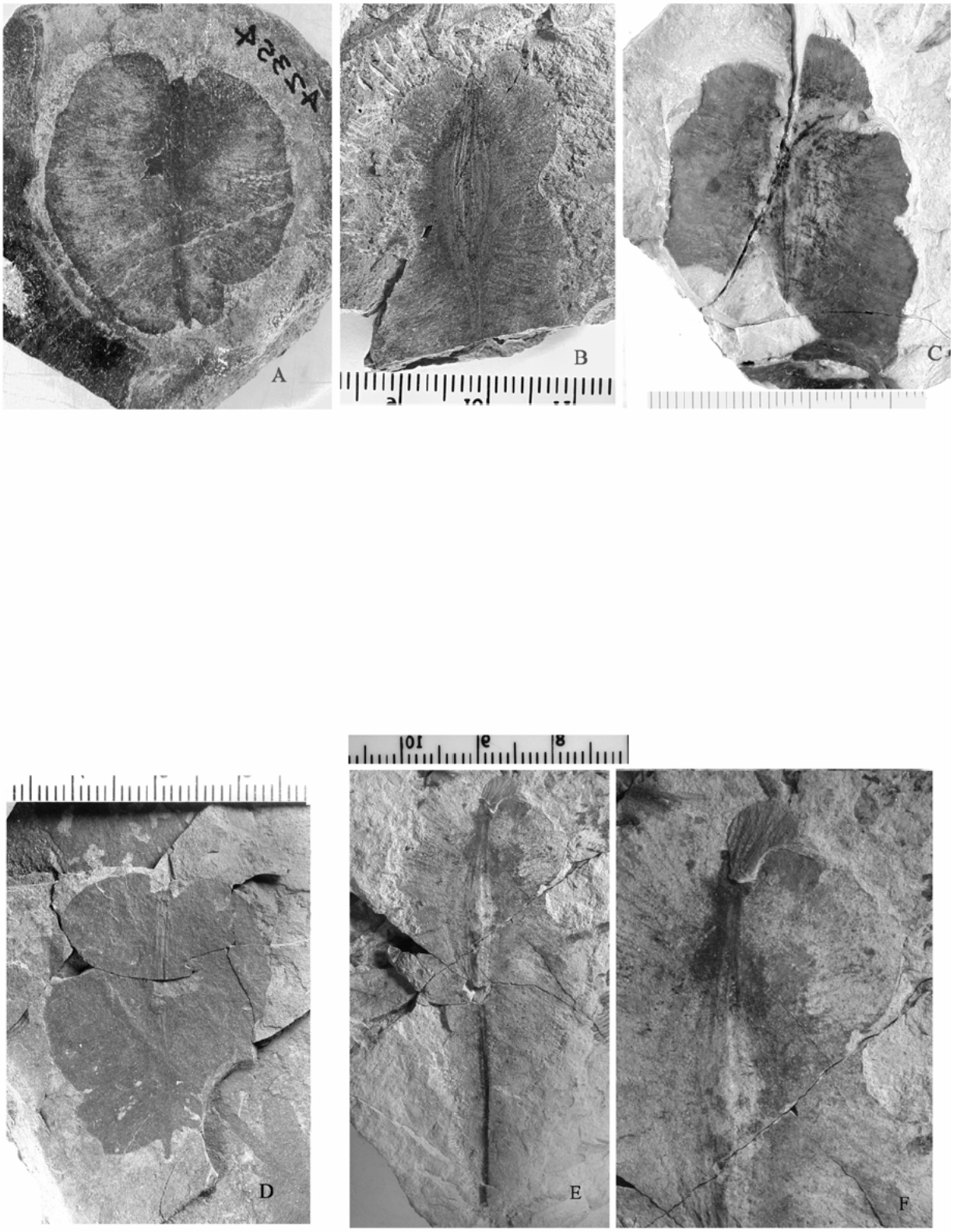

Figure 2-14. *Terminalia estamina*. A) Willemette flora (USNM42334). B) Fossil Oregon (UF 15842-7032). C) Lyons flora (USNM 42353). D) (UF 250-10497). E) (UF 250-10497). F) (UF 250-10497).

CHAPTER 3
MODERN FRUIT SURVEY

As a result of this survey, I became aware of at least 87 genera in which radially finned fruits are present. Each genus is described below (arranged alphabetically by family). These data serve as the basis for the comparative analyses presented in Chapter 5.

Achariaceae
Carpotroche (Figure 2-7E)
Species examined: C*arpotroche amazonica* Mart. (No. 9001, USNSH)
Type of fruit: Indehiscent
Length: 7.8 cm
Width: 7.1 cm
Shape in outline: Globose
Ovary condition: Superior
Persistence of styles/perianth: Disk on basal surface
Persistence of pedicel/stipe: No
Carpels: 4-8
Number of wings: 6 to many (~20); often dissected
Margins: Entire/undulate
Wing derivation: Ovary
Wing thickness: Coriaceous
Trichomes: None observed
Venation: Wing was too opaque to observe venation
Distribution: Tropical America

Apiaceae

Anatomy and morphology of fin-winged fruit genera of Apiaceae and Araliacaeae (*Annesorhiza, Asteriscium, Astrotricha, Choritaenia, Dasispermum, Elaeoselinum, Heptaptera, Hermas, Heteromorpha, Laretia, Molopospermum, Myodocarpus, Pachypleurum, Peucedanum, Polemanniopsis, Polylophium, Rouya,* and *Tordylium)* has been recently studied in detail (Liu et al. 2006). They found that fruit characters including developmental origin of the wings, the shape of the carpel, presence of vittae, and other anatomical features to correspond with molecular cladograms, which suggests that in this group at least, fruits have great taxonomic value. Described below are two genera which were not included. *Prangos* is obviously winged

but the species of Steganotaenia I observed appeared only slightly finned although they can be winged (Hyde and Wursten 2002-7).

Prangos (Figure 2-8J)
Species*: Prangos odontotlera* Boiss. (K.H Beckinguif 997, USNSH)
Type of fruit: Schizocarp
Length: 2 cm. (+0.5 pedicel)
Width: 1 cm
Shape in outline: Elliptical
Ovary condition: Inferior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Carpels: 5
Number of wings: 5
Margins: Entire
Wing derivation: From ribs on ovary
Wing thickness: Papery
Trichomes: None observed
Venation: None apparent

Steganotaenia (Figure 2-8I)
Species examined: S*teganotaenia araliacea* Hochst. (F.G. Meyers 7962, USNSH)
Type of fruit: Schizocarp
Length: 1.6 cm. (+.4 pedicel)
Width: 1 cm
Shape in outline: Elliptical
Ovary condition: Inferior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Carpels: 5
Number of wings: This species is more ridged than winged, but other species prominently 2 winged
Margins: Entire
Wing derivation: Ovary
Wing thickness: Coriaceaous
Trichomes: No
Venation: N/A

Begoniaceae

Begoniaceae have 2 genera with the prominent winged ovaries *Begonia* and *Hillebrandia*. Begonias have many stamens, and there is a disk at the apex of the fruit where these stamens, along with petals and stigma were attached. Begonias may be wind dispersed, animal dispersed, or rain dispersed. Different fruit morphologies are associated with each of

these different dispersal syndromes. Wind dispersed begonias tend to have three locules with three equal or close to equal sized wings while rain dispersed begonias have one large wing and two smaller wings. Ecologically, wind dispersed begonias are more often found in open forest habitat while rain or animal dispersed begonias are found in humid closed forest habitats (Tebbitt et al. 2006).

Begonia (Figure 2-6JK)
Species examined: B*egonia sp*. (Hoover et al. 988, A), *Begonia nelumbiifolia* Cham. & Schltdl. (Porpus 8543, GH), *Begonia sp.* (Kosterman 6022, A)
Type of fruit: Dehiscent/Indehiscent. capsule splitting along sutures and releasing seeds via anemoballisty
Length: Variable
Width: Variable longer than wide or wider than long
Shape in outline: Variable
Ovary condition: Inferior
Persistence of styles/perianth: Yes- staminal disk
Persistence of pedicel/stipe: Yes stipe
Carpels: 3-5
Symmetry: Often with one locule and wing larger than the others
Number of wings: 3
Margins: Entire
Wing derivation: Ovary outgrowth
Wing thickness: Membranous
Trichomes: No
Venation : Transverse; no marginal vein; some looping; areoles transverse elongate

Burmaniaceae are closely related to Dioscorea and some have similar fruits. Three winged with minute seeds. The three carpels are sometimes basally affixed.

Cardiopteridacerae

Cardiopteris (Figure 2-8H)
Species examined: C*ardiopteris moluccana* Blume (Wang 81070, A)
Type of fruit: Indehiscent
Length: 3.5 cm
Width: 2.8 cm
Shape in outline: Transversely Elliptical
Ovary condition: Superior
Persistence of styles/perianth: One large stylar protrusion and calyx present at base
Persistence of pedicel/stipe: maybe very small stipe
Carpels/Locules: 2 carpels, 1 locule
Number of wings: 2
Margins: Entire, smooth

Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Marginal vein only

Celastraceae

Stackhousia. These herbs are found in Australia/Malesia (Mabberly 1989). The plants accumulate nickel in various organs including the fruits (Bhatia et al. 2003). Their fruits are Schizocarpic and readily identifiable by their wings with radiating veins completely free from interconnections and dichotomizations and with a marginal vein. Interestingly, the germination of the seeds is increased in the presence of smoke (Vigilante et al. 1998).

Species examined: S*tackhousia brunonis* Benth. (A. Travers 19, A)
Type of fruit: Schizocarp
Length: 2.4 cm
Width: 1.7 cm
Shape in outline: Ovate
Apex: Acuminate
Base: Cordate
Ovary condition: Superior
Persistence of styles/perianth: Calyx at base and apical protrusions
Persistence of pedicel/stipe: Very small stipe
Carpels: 3-5
Number of wings: 3
Margins: Entire with marginal vein
Wing derivation: Pericarp
Wing thickness: Chartaceous
Trichomes: Yes, unbranched
Venation: Radiating out and arcing slightly upward; thicker at central body and thinning towards margin; joining marginal vein.

Tripterygium (Figure 2-6G). *Tripterygium* is a liana or scandent shrub which is used in herbal medicine. The ovules are epitropous.

Species examined: T*ripterigium regelii* Sprague & Takeda (Togashi 531, A); *Tripterigium wilfordii* Hook.f. (Cavaderic 3316, A)
Type of fruit: Indehiscent
Length: 1.2 cm
Width: 1.1 cm
Shape in outline: Longitudinally Elliptical
Apex: Rounded/cordate
Base: Lobate

Ovary condition: Superior
Persistence of styles/perianth: Apical protrusion and floral remnants at base
Persistence of pedicel/stipe: Pedicel
Carpels: 3 locules
Number of wings: 3
Margins: Entire (marginal vein)
Wing derivation: Ovary?
Wing thickness: Chartaceous
Trichomes: No
Venation: Arching upwards subparrallel and only occasionally dichotomizing; central body with longitudinal veins and some transverse crossveins (marginal vein)
Distribution: East China to Taiwan

Wimmeria (Figure 2-6 E F)
Species examined: W*immeria concolor* Cham. & Schltdl. (Goldman 227, GH), *Wimmeria confusa* Hemsl. (Lundell 1938, GH), *Wimmeria mexicana* (DC.) Lundell (Clevinger July 1999, GH)
Type of fruit: Indehiscent samara
Length: 1.4/ 2 cm
Length: 1.8/ 1.6 cm
Shape in outline: Elliptical
Ovary condition: Superior
Persistence of styles/perianth: Styles at apex, perianth at base
Persistence of pedicel/stipe: Pedicel
Carpels: 2-3 locules
Number of wings: Usually 3, but may be 2 or 4 (Lundel, 1938)
Margins: Entire
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Radiating subparallel dichotomizing and anastomosing
Fruit may have silvery cottonlike filaments when breaking open

Combretaceae

Combretaceae are a family with fruits that are water dispersed, animal dispersed, and wind dispersed. Wind dispersal occurs in many clades within the family. This family is discussed in greater detail in Chapter 3.

Combretum (Figure 2-2)
Species examined: C*ombretum apiculatum* Sond. (SPI 28342, USNSH); *C. erythrophyllum* Sond. (PI112639, USNSH); *C. farinosum* H.B. & K. (FPI 81266, USNSH); *C. fruticosum* Stuntz (PI 104111, USNSH); *C. gazense* Swynn. & Baker f. (PIG 13469, USNSH); *C. grandiflorum* G. Don (SPI 72993, USNSH); *C. imberbe*

Wawra(SPI 48243, USNSH); *C. paniculatum* Vent. (PI s.n., USNSH): C. *primigenum* Marloth. (SPI 48244, USNSH); *C. smeathmannii* G.Don (PI 73930, USNSH)
Type of fruit: Indehiscent. diclesium (Spjut, 1994)
Length: 1-5 cm
Width: 1-4 cm
Shape in outline: Variable from widely elliptical, ovate, to narrowly elliptical
Ovary condition: Inferior
Persistence of styles/perianth: Sometimes stylar protusion at apex
Persistence of pedicel/stipe: Usually a pedicel
Carpels: 4-5 (one locule)
Number of wings: 4-5
Margins: Usually tattered
Wing derivation: Perianth
Wing thickness: Chartaceous
Trichomes: Not observed
Venation: Generally radiating subparallel

Macropteranthes (Figure 2-4 E F)
Species examined: *M. fitzalani* F. Muell (SN 1960, USNSH); *M kekwickii* Benth. (W. Byrnes 1592, USNSH)
Type of fruit: Indehiscent
Length: 1 cm/ 2 cm+
Width: 1.5 cm/ 1.5 cm
Shape in outline: Wide elliptical. to elongate obovate
Ovary condition: Inferior
Persistence of styles/perianth: Calyx lobes at apex
Persistence of pedicel/stipe: Pedicel on fruits of *M. fitzalani*
Carpels: 2 but pseudomonomerous
Number of wings: 4 each (composed of 2 lamina)
Margins: Entire
Wing derivation: Bracteoles
Wing thickness: Chartaceous
Trichomes: Not observed but presumably there may be combretaceous hairs.
Venation: Primaries looping or not with secondaries interconnecting and looping at margins (or not), and tertiaries when present interconnecting or forming blind ended branched veinlets

Pteleopsis (Figure 2-4 B C)
Species examined: *P. hylodendron* Mildber. (J. Classens 401J, USNSH) *P. sp* (Gossweiler 13530, USNSH).
Type of fruit: Indehiscent
Length: 1.5-2.5 cm
Width: 0.5-1.5 cm
Shape in outline: Elliptical., sometimes with v-shaped notch at apex or stylar protrusion, base truncate
Ovary condition: Inferior
Persistence of styles/perianth: Sometimes stylar protrusion
Persistence of pedicel/stipe: Pedicel

Carpels: 2, but appearing as one
Number of wings: 2
Margins: Entire
Wing derivation: Perianth
Wing thickness: Chartaceous
Trichomes: Not observed but presumably there may be combretaceous hairs
Venation: Radiating subparallel

Thiloa (Figure 2-4 G)
Species examined: T*hiloa glaucocarpa* (Mart.) Eich. Image was observed at Harvard from "Types of the Munich Herbarium"
Type of fruit: Indehiscent
Length: ?
Width: ?
Shape in outline: Rounded
Ovary condition: Inferior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Carpels: 2, but appearing as one
Number of wings: 4
Margins: Entire
Wing derivation: Perianth
Wing thickness: Chartaceous
Trichomes: Not observed but presumably there may be combretaceous hairs
Venation: Not observed

Terminalia (Figure 2-3)
Species examined: T. *argentea* Mart. (PI 300640, USNSH); *T. virens* (Spruce ex Eicheler) Alwen & Stace (B. Maguire et al. 30764, USNSH); *T. alata* Herb.Madr. ex Wall. (Maxwell 92-19, A); *T. amazonica* Excell (Steinbach 6617, A); *T. argentea* Mart. (Mello et al. 608, GH); *T. glaucescens* Planch. Ex Benth. (Bretleler 248, A); *T. macroptera* Mart. (221-9 Harvard); *T. pedicellata* W.Nanakorn (Maxwell, 01-461, A); *T. pyrifolia* Kurz. (Burma Forest School Herbarium 61, A); *T. tomentosa* Mart. Ex Eichl. (Hara 100014, A).
Type of fruit: Indehiscent diclesium (Spjut, 1994)
Length: 0.5- 7 cm
Width: 1- 6cm
Shape in outline: Variable from elongate to elliptical to very wide elliptical
Ovary condition: Inferior
Persistence of styles/perianth: Stylar protrusion sometimes; diclesium.
Persistence of pedicel/stipe: Sometimes stipe or pedicel
Carpels: 2 but appearing as one
Number of wings: 2, 4, 5
Margins: Entire, may be tattered or reinforced by increased dichotomizations near margin
Wing derivation: Perianth
Wing thickness: Chartaceous to coriaceous
Trichomes: Combretaceous hairs present or absent

Venation: Usually radiating subparrallel but may dichotomize and anastomose either occatinally or as a reinforcement to the margin

Cunonaceae

Gillbeea (Figure 2-6 H I)
Gillbeea is found in New Guinea and Queensland and has a three winged one seeded fruit. Anatomical information for the flowers of this genus can be found in Matthews et al. (2001). The broken pieces had two distinctive veins from the central body to the apex.
Species examined: G*illbeea papuana* Schltr. (Takeuchi 6084, A) (Brass 31815, A)
Type of fruit: Described as Indehiscent., but I found pieces broken apart
Length: 1.6 cm
Width: 1 cm
Shape in outline: Longitudinally Elliptical
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Carpels: 3
Number of wings: 3
Margins: Wavy/entire with marginal vein
Wing derivation: Ovary wall outgrowths
Wing texture: Chartaceous
Trichomes: Yes
Venation: Radiating reticulum with midveins running apically from central axis and a marginal vein present

Cyrillaceae

Cliftonia (Figure 2-8E)
Species examined: C*liftonia monophylla* Britton (Rhoades 5a203, GH).
Type of fruit: Indehiscent
Length: 0.5 cm
Width: 0.5 cm
Shape in outline: Longitudinally Elliptical
Apex: Emarginate
Base: Rounded
Ovary condition: Superior
Persistence of styles/perianth: Persistent sepals at base of fruit
Persistence of pedicel/stipe: Pedicel?
Carpels: 3-4
Number of wings: 2-3
Margins: Entire
Wing derivation: Ovary
Wing thickness: Coriaceous
Trichomes: No

Venation: Unknown

Dioscoreaceae

Dioscorea (Figure 2-1 B C)
Species examined: *Dioscorea alata* L. (McPherson 43, FLAS)
Type of fruit: Apically opening capsule (dispersing via anemoballisty)
Length: Variable 4.3 cm
Width: Variable 4.3 cm
Shape in outline: Variable from longer than wide to round to wider than long
Ovary condition: Inferior
Persistence of styles/perianth: Sometimes perianth persists at apex
Persistence of pedicel/stipe: Small pedicel
Carpels: 3
Number of wings: 3
Margins: Thick marginal suture
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Striations radiating outward to true venation
Seeds: Often with winged seeds

Fabaceae

There are several genera in the Fabaceae that have winged fruits. Of these, at least three are known to have the fin-winged morphology. Much has been published about the fruits of this family (Kirkbride et al. 2003; Stirton and Zarucchi 1989, Gunn 1984) including the morphology and aerodynamics of wind dispersed legumes. At least four genera have fin-winged fruit (*Fissicalyx, Piscidia, Sesbania*, and *Tetracarpon*). *Piscidia* is found from Florida to Venezuala and was figured in Flora of Panama (Dwyer 1965). The fruits are pedicellate and stipitate, four winged, both apex and base are truncate, with pinnate venation. *Fissicalyx* is described below.

Fissicalyx. *Fissicalyx* is a member of the Dalbergioid legumes, a group which has at least 16 genera with wings (Lavin et al. 2001). The wings of *Fissicalyx* are derived from expansion of the ovary wall, but in other winged genera the wings are formed from expansion of ovary sutures or from the stipe. This genus is figured in (Dwyer 1965).

Species examined: Image of *Fissicalyx* taken from USNSH website
Type of fruit: Indehiscent pod
Length: 6 cm
Width: 5.3 cm
Shape in outline: Elliptical with an acuminate apex
Ovary condition: Superior
Persistence of styles/perianth: Style at apex
Persistence of pedicel/stipe: No
Carpels: 1
Number of wings: 2
Margins: Entire
Wing derivation: Expansion of ovary wall
Wing thickness: Chartaceous?
Trichomes: No
Venation: Radiating

Hernandiaceae

Illigera (Figure 2-1 A)
Species examined*: Illigera celibica* Miq. (How 73378, A), *Illigera cordata* Dunn (Delaway 4 Sept. 1883, A), *Illigera grandiflora* W.W.Sm. & Jeffrey (Heng 11446, A) (Heng 10346, A)
Fruit type: Indehiscent., coded as a drupe (Renner, 1999)
Length: 3.6/3.6 cm
Width: 6.9/3.7 cm
Shape in outline: Laterally elliptical or rounded
Apex: Cordate
Base: Cordate/ cuneate
Ovary condition: Inferior
Persistence of styles/perianth: Perhaps sometimes style
Persistence of pedicel/stipe: No
Carpels: One
Symmetry: 2 wings larger than third
Number of wings: 2 or 3
Margins: Entire slightly wavy
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Veins radiating to margin very sinuous all of a single order

Lophopyxidaceae

Lophopyxis (Figure 2-7 G). *Lophopyxi*s is the only genus in the Lophopyxidaceae, it is sometimes placed in Celastraceae but has characters such as tomentose ovaries which are different from the Celastraceae (Simmons et al. 1999)

Species examined: L*ophopyxis combretocarpa* Engl. Ex Pax (Abrahia 3405, USNSH)
Lophopyxis maingayi Hook.f. (Schode 5063, USNSH)
Type of fruit: Indehiscent samara
Length: 3 cm
Width: 1.5 cm
Shape in outline: Elongate obovate
Ovary condition: Superior.
Persistence of styles/perianth: Stylar remnants at apex and perianth remnants at base
Persistence of pedicel/stipe: Small stipe
Carpels: 5
Number of wings: 5
Margins: Entire
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: Densely hairy, hairs unbranched
Venation: Downward arching subparrallel

Loranthaceae

Nuyitsia. Loranthaceae are a family known for being parasitic on tree branches. Fruits of this genus are usually fleshy. *Nuytsia* is a tree or shrub and has three-winged wind dispersed fruits. Lamont (1985) studied the dispersal of these fruits and found a maximum dispersal capability of 50 meters. Nevertheless, he concluded that this supports evidence that this genus reproduces mainly by suckering.

Species examined: N*uytsia sp.* (USNSH)
Type of fruit: Indehiscent
Length: 1 cm
Width: 0.8cm
Shape in outline: Elliptical
Ovary condition: Inferior.
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Carpels: 3-4
Number of wings: 3
Margins: Entire
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Transverse veins occasionally dichotomizing, arising from midline of fruit

Malvaceae

Cavanillesia (Figure 2-5A). The fruits of *Cavanillesia* are the largest fin-winged fruits at over 12 cm. long. Garwood (1985) studied the role of mucilage in seedling development of *Cavanillesia*. This genus produces large amounts of mucilage in the fruits, and the mucilage is present during dispersal.

Species examined: C*avanillesia platanifolia* H.B. & K (R. Foster 2247, GH)
Type of fruit: Indehiscent capsule
Length: 12 cm
Width: 14 cm
Shape in outline: Widely elliptical
Apex: Cordate
Base: Cordate
Ovary condition: Superior
Persistence of styles/perianth: Apical protuberance
Persistence of pedicel/stipe: No
Carpels: 5 (one or two seeded fruits)
Number of wings: 4
Margins: Tattered
Wing derivation: Ovary
Wing thickness: Membranous
Trichomes: No
Venation: At first glance, veins appear to be subparrallel and of a single order, but closer examination reveals a reticulum of lower order veins between the primaries which form areoles of 1mm or less, the veins are very fibrous and remain as a skeleton after the wing surface is lost.

Abroma (Figure 2-5 B)
Species examined: A*broma augusta* L.f. (C.Wang 41264, A) (A.D.E Elmer 21446, A)
Type of fruit: Loculicidal capsule
Length: 4-5cm.
Width 5-6 cm
Shape in outline: Obovate
Apex: Truncate
Base: Rounded
Ovary condition: Superior
Persistence of styles/perianth: Calyx
Persistence of pedicel/stipe: No
Locules: 5
Number of wings: 5
Margins: Thick suture
Wing derivation: Ovary
Wing thickness: Chartaceous

Trichomes: Tri-branched hairs.
Venation: Veins thick, ascending to tips, dichotomising and anastomosing occasionally forming transversely long areoles.

Kleinhovia (Figure 2-5C). *Kleinhovia* is a vine or a tree and grows in Asia and Australia. Hjerpe and Hedenas (2001) found that *Kleinhovia hospita* is a species that thrives in the disturbed habitat after a cyclone.

Species examined: K*leinhovia hospita* L. (Huang et al. 16132, A)
Type of fruit: Inflated capsule
Length: 1.4 cm
Width: 2.3 cm
Shape in outline: Obcordate
Ovary condition: Superior
Persistence of styles/perianth: Remnants at base
Persistence of pedicel/stipe: Pedicel and stipe
Carpels: 5
Number of wings: 5
Margins: Sutured
Wing derivation: Perianth
Wing thickness: Chartaceous
Trichomes: No
Venation: Veins coursing apically forming large transversely elongate areoles. Veinlets ending within areoules with a small hook.

Maxwellia (Figure 2-5D). *Maxwellia* is a New Caledonia endemic with the unusual condition of having many small seeds in an indehiscent fruit (Wilkins and Chappell 2002, Robyns et al. 1977).

Species examined: M*axwellia lepidota* Baill. (Hürliman 13129, A)
Type of fruit: Indehiscent
Length: 3 cm
Width: 2.3 cm.
Shape in outline: Elliptical
Apex: Obcordate
Base: Cordate
Ovary condition: Superior
Persistence of styles/perianth: Perianth at base
Persistence of pedicel/stipe: Pedicel on specimen examined
Carpels: 3-4
Number of wings: 3-4(-5)
Margins: Entire and wavy
Wing derivation: Ovary
Wing thickness: Coriaceous

Trichomes: No
Venation: Wing too thick to observe

Craigia (Figure 2-5J). Modern *Craigia* is found in Eastern China and Taiwan; but there are also fruit fossils from the Tertiary of North America, Europe and Asia (Kvaĉek et al. 1991).

Species examined: C*raigia yunnanensis* (UF 1124)
Type of fruit: Capsule
Length: 3.1 cm
Length: 2.3 cm
Shape in outline: Elliptical
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: No
Carpels: 3-4
Number of wings: 5
Margins: Entire; marginal vein
Wing derivation: Ovary?
Wing thickness: Papery/membranous
Trichomes: No
Venation: Primaries radiating dichotomizing and anastomosing to form elongate areoles, secondaries interconnecting and also forming freely ending veinlets which are sometimes branched.

Pentace (Figure 2-8 K)
Species examined: P*entace laxiflora* Merr. (Leopold 78602, A)
Type of fruit: Indehiscent samara
Length: 1.7 cm
Width: 1 cm
Shape in outline: Elliptical
Ovary condition: Superior
Persistence of styles/perianth: Perianth at base
Persistence of pedicel/stipe: Pedicel
Carpels: 2-10
Number of wings: 5
Margins: Slightly tattered
Wing derivation: Ovary?
Wing thickness: Papery
Trichomes: No
Venation: Sinuous, radiating, some dichotomizing and anastomosing near the margin

Malpighiaceae

Aspidopterys. *Aspidopterys* is a liana which grows in tropical Asia.
Species examined: A*spidopterys roxburghiana* A.Juss. (Griffith 924, A) (Narayanaswami 18, A)

Type of fruit: Samara
Length: 3 cm/ 4.3 cm
Width: 2.3 cm/ 1.5 cm
Shape in outline: Ovate/ oblong
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: No
Carpels: 3
Number of wings: 3
Margins: Entire with veins looping along margin
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Primaries forming loops with the secondaries interconnecting and looping at the margin, tertiaries interconnect

Nyctaginaceae

This family has many species and genera with fin-winged fruits formed from accrescent tepals (Spjut 1994). Seed have a curved embryo. Only one genus is detailed here, a survey within the family needs to undertaken to document the diversity within the family.

Abronia. *Abronia* has been thoroughly studied for anatomy (Wilson 1974, Wilson, 1975), dispersability (Wilson 1976) and compared to the similar genus *Tripterocalyx* (Galloway 1975).

Phaeoptilum (Figure 2-1C)
Species examined*: P. spinosum* Radlk. (R. Srydel "≥ 199", USNSH)
Type of fruit: Indehiscent anthocarp
Length: 2.1 cm
Width: 1.8 cm
Shape in outline: Elliptical with lobate base
Ovary condition: Superior
Persistence of styles/perianth: Yes wings are derived from accrescent tepals
Persistence of pedicel/stipe: No
Carpels: 1
Number of wings: 4
Margins: Entire
Wing derivation: Accrescent tepals
Wing thickness: Chartaceous
Trichomes: No
Venation: Radiating slightly sinuous

Onagraceae

Megapterium (Figure 2-1G)
Species examined: M*egapterium missouriense* Spach. (L.E Wham s.n., USNSH)
Type of fruit: Apically opening capsule (dispersing via anemoballisty)
Length: 6.8 cm
Width: 6.8 cm
Shape in outline: Transversly elliptical/ round
Apex: Rounded
Base: Rounded
Ovary condition: Inferior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: No
Number of wings: 4
Margins: Entire and sutured?
Wing derivation: Ovary.
Wing thickness: Chartaceous.
Trichomes: No.
Venation: Striations radiating.

Oenothera (Figure 2-1F)
Species examined: O*enothera missouriensis* Sims (Stevens 561, Harvard Seed Collection), *Oenothera macrocarpa* (Hitchcock 165, Harvard Seed Collection) (Wagner s.n., Seed Herbarium)
Type of fruit: Loculicidal capsule dispersing via anemoballisty
Length: 3.5/ 4 cm
Width: 1.8/ 4 cm
Shape in outline: Slightly ovate/ slightly obovate/ longitudinally elliptical/ round
Ovary condition: Inferior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: No/ sometimes small pedicel?
Locules: 4
Number of wings: 4
Margins: Entire and sutured
Wing derivation: Ovary?
Wing thickness: Chartaceous
Trichomes: Sometimes small hairs
Venation: Radiating striations

Pedaliaceae

Holubia (Figure 2-8F). Holubia is an herb native to Madagascar
Species examined: H*olubia saccata* Oliver (Anonymous 301, USNSH)
Type of fruit: Indehiscent
Length: 5.4 cm
Width: 5.3 cm

Shape in outline: Round
Apex: Rounded slightly cordate
Base: Rounded slightly cordate.
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Carpels: 2 locules
Number of wings: 4
Margins: Entire sinuous with marginal vein
Wing derivation:
Wing thickness: Chartaceous
Trichomes: No
Venation: One order, radiating outward; dichotomizing and anastomosing to form transverse longitudinal to polygonal areoles; marginal vein present

Pterodiscus (Figure 2-8G)
Species examined: P*terodiscus aurantiacus* Welw. (Werdermann 2290, GH) (Dister 4635, GH)
Type of fruit: Indehiscent
Length: 3.1 cm/ 3.3 cm
Width: 3.1cm/ 3.4 cm
Shape in outline: Round
Apex: Rounded
Base: Lobate
Ovary condition: Superior
Persistence of styles/perianth: Perianth at base, small apical protrusion
Persistence of pedicel/stipe: Pedicle
Carpels: 2-4 reported for the family
Number of wings: 4
Margins: Entire with marginal vein
Wing derivation:
Wing thickness: Chartaceous
Trichomes: No
Venation: Radiating outward with some dichotomizing and anastomosing particularly towards the margin. Marginal vein is present

Phyllanthaceae

Hymenocardia. Hymenocardia is the only wind dispersed member or the Phyllaanthaceae and has previously been put into its own family (Hymenocardiaceae) (Wurdak et al. 2004).

Species examined*: Hymenocardia ulmoides* Oliver (Robyns 799, USNSH)
Type of fruit: Schizocarp
Length: 2.3 cm

Width: 1.9 cm
Shape in outline: Round-Elliptical
Apex: Obsaggitate
Base: Rounded
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Both
Carpels: Bilocular
Number of wings: 2
Margins: Entire with marginal vein
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Central vein running apically through the basal portion of the wing and over the apically placed seed cavity. Secondary veins radiating transversely and dichotomizing and anastomosing irregularly, marginal vein present.

Polygalaceae

Polygala
Species examined: P*olygala sp.* (Britton 10129, USNSH)
Type of fruit: Dehiscent or indehiscent
Length: 4 cm
Width: 3 cm
Shape in outline: Obovate-round or asymmetrical elliptical
Ovary condition: Superior
Persistence of styles/perianth: Apical protrusion may be present and small disk at base
Persistence of pedicel/stipe: Pedicel
Carpels: 2
Number of wings: 2-3
Margins: Entire
Wing derivation: Ovary
Wing thickness: Papery
Trichomes: Yes, unbranched
Venation: Radiating, dichotomizing and anastomosing infrequently

Polygonaceae

Polygonaceae are a family with many genera with fin-winged fruit. The fruit type in this family is an achene, and the wings, in these fruits are formed from perianth parts. The fruits may be biwinged or triwinged and the shape is quite variable. Laubengayer (1937) detailed the anatomy of the flower. Genera with fin-winged fruits include *Antigonon, Atraphaxis*

Calligonium, Polygonum, Rheum, Rumex, and *Triplaris*. Three of these genera are described below.

Antigonon
Species: A*ntigonon guatemalense* Meisn. (PI 146197, USNSH).
Type of fruit: Achene with perianth forming wings
Length: 3 cm
Width: 3 cm
Shape in outline: Round with lobate base
Ovary condition: Superior
Persistence of styles/perianth: Perianth forming wings
Persistence of pedicel/stipe: Pedicel
Carpels: 2-3
Number of wings: 3
Margins: Entire
Wing derivation: Perianth
Wing thickness: Papery
Trichomes: No
Venation: Primaries form reticulum with polygonal areoles, a few secondaries interconnect or end freely.

Atraphaxis
Species examined: *Atraphaxis spinosa* Eichw. (Viedumnu 1927-2, A)
Type of fruit: Indehiscent
Length: 0.8 cm
Width: 0.85 cm
Shape in outline: Ovate, apex rounded, base cordate
Ovary condition: Superior
Persistence of styles/perianth: Wings and perianth at base
Persistence of pedicel/stipe: Pedicel
Carpels: 2-3
Number of wings: 3
Margins: Entire
Wing derivation: Perianth
Wing thickness: Papery
Trichomes: No
Venation: Single primary running from base to apex over central body, secondaries dichotomizing and anastomosing occasionally across the wing.

Rumex
Species examined: *Rumex obtusifolius* Herb.Buch.-Ham. Ex Wall. (HARVARD SEED COLLECTION); *Rumex venosus* Pursh (77, USNSH).
Type of fruit: Indehiscent
Length: .8 cm/ 2.3 cm
Width: .45 cm/ 3 cm
Shape in outline: Obovate/ wide elliptical
Ovary condition: Superior

Persistence of styles/perianth: Perianth forming wings
Persistence of pedicel/stipe: Stipe on obtusifolius
Carpels: 3
Number of wings: 3
Margins: Entire
Wing derivation: Tepals
Wing thickness: Papery
Trichomes: No
Venation: Single order forming reticulum with polygonal areoles or primaries forming reticulum with secondaries running laterally forming interconnections.

Rhamnaceae

Anatomy and dispersability of the winged fruits of one subfamily, the Gouaniaeae, has been studied in detail (Medan 1988).

Gouania (Figure 2-7A)
Species examined: *Gouania domingensis* Aubl. (Rodriguez 2566, GH) *Gouania lupuloides* Urb. (Brumbach 9537, GH) (Brass 21138, GH)
Type of fruit: Capsule
Length: 1 cm/ 1.1 cm
Width: 1.4 cm/ 0.9 cm
Shape in outline: Wide elliptical
Ovary condition: Superior
Persistence of styles/perianth: Apical disk
Persistence of pedicel/stipe: Stipe
Carpels: 3
Number of wings: 3
Margins: Entire often with an intramarginal vein
Wing derivation: Ovary
Wing thickness: Coriaceous
Trichomes: No
Venation: Irregular meshwork of irregularly spaced asymmetrical veins forming large irregular areoles marginal vein sometimes present.

Chaydaia (Figure 2-7B)
Species examined: *Chaydaia berchemiaefolia* Koidz. (Horder 601, USNSH)
Type of fruit: Septicidal capsule
Length: 1.4 cm
Width: 1.1 cm
Shape in outline: Circular
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Stipe
Carpels: 3
Number of wings: 3
Margins: Undulating

Wing derivation: Ovary/hypanthium
Wing thickness: Papery
Trichomes: No
Venation: Single order of irregularly looping veins forming large polyhedral areoles sometimes looping to form an intramarginal vein.

Reissekia (Figure 2-7C)
Species examined: *Reissekia smilacina* Endl. (L.O Williams 6834, USNSH)
Type of fruit: Inflated schizocarp
Length: 1 cm
Width: 1.6 cm
Shape in outline: Butterfly shaped
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: No
Carpels: 3
Number of wings: 3
Margins: Entire with marginal vein
Wing derivation:
Wing thickness: Papery
Trichomes: No
Venation: Marginal vein and one order of veins radiating outwards dichotomizing and anastomosing rarely in wing but frequently over the central body.

Rutaceae

The subfamily Pteleinae has three genera with winged fruits (*Ptelea*, *Helietta*, and *Balfourodendron)*, and one genus (*Taravalia*) with a nut like capsule. Of these*, Ptelea* and *Balfouodendron* are fin winged *while Helietta* is similar to *Acer* in having two asymmetrical mericarps (Pirani 1998). Spathelia is another genus in the family with fin-winged fruits, but is not described here.

Balfourodendron (Figure 2-8A). *Balfourodendron* is found in both Central and South America. Pirani (1998) describes the samara as typically having four one-seeded locules in which most of the seeds are aborted. The epicarp, which forms the wings, is described as thin and coriaceous, the mesocarp thicker, soft and dotted glandular dotted, the endocarp forms a hard lignified stone (Pirani 1998).

Species examined: B*alfourodendron riedelianum* Engl. (Vanni et al. 385, GH)
Type of fruit: Indehiscent samara

Length: 1.7 cm
Width: 2.3 cm
Shape in outline: Widely elliptical
Ovary condition: Superior
Persistence of styles/perianth: Remnants only
Persistence of pedicel/stipe: Stipe present
Carpels: 4-5
Number of wings: 4
Margins: Entire
Wing derivation: Ovary
Wing thickness: Papery
Trichomes: No
Venation: Three orders of venation, the first order arcing downwards, the second interconnecting, and third forming a reticulum. Venation is sinuous. Areoles polygonal and small (2/10 mm).

Ptelea (Figure 2-8BC). Fossilized *Ptelea* samaras from North America were critically examined by Call and Dilcher (1995). They found three features to be particularly important in identifying the fruits of this genus 1) Superior. ovary demonstrated by floral disk at the base of the fruit where it joins the pedicel, 2) wings fused above and below the seed cavity, 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. I agree with these characters, although *P. crenulata* venation does not loop, but rather dichotomizes.

Species examined: P*telea crenulata* Greene (HARVARD SEED COLLECTION), *Ptelea polyadenia* Greene (HARVARD SEED COLLECTION), *Ptelea trifolata* L. (HARVARD SEED COLLECTION)
Type of fruit: Samara
Length: 2.3 cm/ 1.5 cm
Width: 2.5 cm/ 1.2 cm
Shape in outline: Rounded
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel and stipe
Carpels: 2-3 locules
Number of wings: 2 or 3
Margins: Entire somewhat wavy; tattered in *P. crenulata*
Wing derivation: Ovary
Wing thickness: Papery
Trichomes: No

Venation: In *P. crenulata* veins dichotomizing and anastomosing irregularly forming elongate areoles; in *P. trifolata* forming loops to create a reticulum of polygonal areoles.

Sapindaceae

The Sapindaceae have many genera with fruits that are dispersed by air. Some of these fruits are fin-winged and others are not. All of the fin-winged fruits have a marginal vein. Detailed comparisons of the fruits of the Paullineae have been made (Weckerle and Rutishauser, 2005). The fruits in this section may have internal hairs that are either unicellular or multicellular and all are three carpellate. Genera with fin-winged fruits include *Dodonaea, Guioa, Majidea, Serjania Thouindium Toulicia Stocksia* and *Urvillea*. Five of these genera are described below.

Guioa
Species examined: G*uioa comesperma* Radlk. (Talucuchi 8673, GH)
Type of fruit: Capsule
Length: 2 cm
Width: 2.3cm
Shape in outline: Obcordate
Ovary condition: Superior
Persistence of styles/perianth: Disk at base
Persistence of pedicel/stipe: No
Carpels: 1 (3 locular)
Number of wings: 3
Margins: Entire
Wing derivation: Ovary
Wing thickness: Woody
Trichomes: No
Venation: Unavailable because the wing was too woody

Stocksia
Species examined: *Stocksia brauhica* image from Steven Manchester only
Shape in outline: Ovate
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Margins: Entire with marginal vein
Wing derivation: Ovary
Venation: Reticulum reaching to margin with secondaries interconnecting or freeling ending in branched or unbranched veinlets.

Thouindium
Species examined: T*houindium* image from Steven Manchester only.
Type of fruit: Capsule.
Shape in outline: Elongate, base slightly cordate, apex opening.
Ovary condition: Superior.
Persistence of styles/perianth: Basal disk.
Persistence of pedicel/stipe: Small pedicel.
Number of wings: 3.
Margins: Entire with marginal vein.
Wing derivation: Ovary.
Venation: Single order coursing downwards dichotomizing and anastomosing to form polygonal to elongate areoles; veins entering the marginal vein.

Toulicia
Species examined: *Toulicia* image from Steven Manchester only.
Shape in outline: Rounded obovate.
Ovary condition: Superior.
Persistence of styles/perianth: No.
Persistence of pedicel/stipe: No.
Number of wings: 3.
Margins: Entire with marginal vein.
Wing derivation: Ovary.
Trichomes: No.
Venation: Primaries radiating, dichotomizing and anastomosing entering marginal vein; secondaries interconnecting and forming reticulum of polygonal areoles or freely ending.

Urvillea (Figure 2-8D)
Species examined: U*rvillea andersonii* Ferrucci (Anderson 9150, NY)
Type of fruit: Septifragal capsule
Length: 3.6 cm
Width: 1.7 cm
Shape in outline: Elongate
Ovary condition: Superior
Persistence of styles/perianth: Styles at apex
Persistence of pedicel/stipe: Pedicel present, stipe present
Carpels: 3
Number of wings: 2
Margins: Entire with marginal vein
Wing derivation: Ovary
Wing thickness: Chartaceous
Trichomes: No
Venation: Marginal vein and radiating sub parallel with some dichotomizing

Styracaceae

Halesia (Figure 2-5F). *Halesia* fruit fossils are found in Europe and reports have been made of fruits in North America. Fritsch et al. (2001) used these reports, and molecular phylogenies to suggest a North American origin for the genus. They admit that the fossils do not show the intramarginal vein found in *Halesia* species, but they still consider it to be this genus.

Species examined: H*alesia carolina* L. (Hill 17001, GH), *Halesia diptera* L. (Harbison 1129, GH)
Type of fruit: Indehiscent drupe
Length: 3.7cm
Width: 1.7 cm
Shape in outline: Spatulate
Apex: Cordate-sagittate
Base: Obtuse
Ovary condition: Inferior
Persistence of styles/perianth: Calyx at apex
Persistence of pedicel/stipe: Pedicel
Carpels: 2
Number of wings: 2, 4
Margins: Entire wavy
Wing derivation: Ovary
Wing thickness: Thick semi-opaque
Trichomes: No
Venation: Intramarginal veins present
Other: Fruits may persist on branches even after leaves seasonally fall, prominent apical beak present.

Trigonaceae

Humbertiodendron (Figure 2-7F)
Species examined: H*umbertiodendron soboundani* Leandri (Anonymous, 244, USNSH)
Type of fruit: Indehiscent samara
Length: 2.5 cm
Width: 2.3 cm
Shape in outline: Round
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: None dispersed, pedicle present on branch
Carpels: 3
Number of wings: 3
Margins: Entire.
Wing derivation: Ovary
Wing thickness: Chartaceous

Trichomes: Yes (long-pilose)
Venation: Marginal vein; primary veins transverse to radiating upwards at approximately 45 degrees; occasionally dichotomizing in wing but dichotomizing more frequently near margin.

Tropaeolaceae

Tropaeolum (Figure 2-7H)
Species examined: *Tropaeolum porifolium* (Cav.) L.Andersson & S.Andersson (A. Donat 51, USNSH)
Type of fruit: Schizocarp
Length: 1.6 cm
Width: 1.3 cm.
Shape in outline: Longitudinally elliptical
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: No
Carpels: 3
Number of wings: 3
Margins: Entire not smooth with a marginal vein
Wing derivation:
Wing thickness: Papery
Trichomes: No
Venation: Marginal vein; radiating outwards occasionally dichotomizing near the margin

Zygophyllaceae

Fruits of Zygophyllaceae may be capsular or Schizocarp.ic (Beier 2003). Some of these fruits develop wings in the fin-winged fashion. Four genera are described below.

Bulnesia (Figure 2-6AB)
Species examined: B*ulnesia chilensis* Gay. (Werdermann 429, GH); *Bulnesia foliosa* Griseb. (Schreiter 2849, GH); *Bulnesia retamo* Griseb. (Hutchinson & Wright 7115, GH)
Type of fruit: Schizocarp
Length: 1.6cm/ 4cm
Width: 1.3/ 4 cm
Shape in outline: Elliptical to round/elliptical
Ovary condition: Superior
Persistence of styles/perianth: Perianth at base in *B. foliosa* and *B. chiliensis*; stylar protrusion in *B. foliosa*
Persistence of pedicel/stipe: Stipe, sometimes pedicle
Carpels: 5.
Number of wings: 5.
Margins: Entire.
Wing derivation: Ovary.
Wing thickness: Chartaceous.

Trichomes: Yes unbranched on *B. foliosa* and *B. rivas-martinezii* (see Navarro, 1994).
Venation: Radiating, dichotomizing, looping at margin with some interconnections particularly towards the margin.

Morkillia
Species examined: M*orkillia mexicana* Rose & Painter (Sousa 4601, GH) (Chase 7332, GH)
Type of fruit: Capsule
Length: 3.5 cm/ 3.75 cm
Width: 2.5 cm/ 2 cm
Shape in outline: Elliptical-ovate with truncate apex or apex with rounded invagination creating a saggitate appearance
Ovary condition: Superior
Persistence of styles/perianth: No
Persistence of pedicel/stipe: Pedicel
Carpels: 4
Number of wings: 4
Margins: Entire
Wing derivation: Ovary
Wing thickness: Coriaceous
Trichomes: Yes, densely hairy
Venation: Unknown

Porleria (Figure 2-6D)
Species examined: *Porlieria angustifolia* A.Gray (Moore 3288, Harvard)
Type of fruit: Schizocarp
Length: 1.7 cm
Width: 1.7 cm
Shape in outline: Widely ovate
Ovary condition: Superior
Persistence of styles/perianth: Stylar protrusion and basal disk
Persistence of pedicel/stipe: Yes, both
Carpels: 4
Number of wings: 3
Margins: Entire
Wing derivation: Ovary
Wing thickness: Coriaceous
Trichomes: Yes unbranched
Venation: Not visible by transmitted or reflected light

Zygophyllum (Figure 2-6C)
Species examined: (*Zygophyllum morgsana* L. (Marloth 12275, A); *Zygophyllum retrofractum* Thunb. (Marloth 650, A)
Type of fruit: Schizocarp
Length: 2 cm (+1cm. pedicel)/ 3 cm (+several centimeter pedicel)
Width: 2.5cm/ 3cm
Shape in outline: Elliptical
Persistence of styles/perianth: Style at apex
Persistence of pedicel/stipe: Pedicel
Carpels: 4
Number of wings: 4
Margins: Entire
Wing derivation: Ovary
Wing thickness: Chataceous
Trichomes: No
Venation: Dichotomizing anastomosing and looping
Ovary condition: Superior. to form a reticulum of areoles, that are transversely elongate towards the central body and increasingly polygonal toward the margin.

CHAPTER 4
RESULTS

Fossil Fin-Winged Fruits of North America With Possible Affinities to Combretaceae

The fossil history of the Combretaceae has been reported to include fossilized leaves and fruits (ex. Berry 1916), wood (ex. Sakala 2002), a possible flower (Takahashi et al. 1999) and pollen (ex. Salzman 2000). Three winged-fruit fossils from North America will be treated here (*Terminalia vera, Terminalia estamina* and *Terminalia oregona*). These fruits were not assigned to the genus *Terminalia* because it was the best fit based on careful comparisons, but simply because it is a genus in the Combretaceae. Additionally, these fruits were not compared to all of the genera that have fin-winged fruits, and it may be that there is a better match among the modern fin-winged fruits than any of the genera of Combretaceae.

Carpolithes prangosoides Berry

Basionym: *Carpolithes prangosoides* Berry 1916, USGS Prof. Paper 91, p. 351, pl. 104, Figure 2-9.

Terminalia vera. Berry 1926. Torrey Botanical Club Bulletin. Vol. 53, p. 61, figs. 1-5.

Carpolithus henryensis. Berry 1916, USGS Prof. Paper 91, p. 352, pl. 112, fig. 16.

Emended Description

Fruit fin-winged, usually radially symmetrical, appearing bisymmetric in face view, elliptical, 1.2 —3.3 cm long, 1—1.5cm wide; composed of a central body with 5 fin-like, radiating wings, pedicel not dispersed with fruit. Style not persistent.

Fruit body elongate, appearing smooth or longitudinally striated. Each wing lies in a radial plane intersecting with the longitudinal axis of the fruit, auriform to half-elliptic in shape. Near the distal end of the fruit, apical flaps persist in some specimens and it is unclear from what tissue these flaps arise. The wing venation is uniformly oriented towards the apex at about 30

degrees from the fruit's central axis. Venation consists of numerous fine veins, frequently dichotomizing, forming loops along the way toward the margin, with secondary veins interconnecting and forming areoles of the reticulum 0.7-1.5 mm. Marginal or intramarginal vein absent.

Comments. This species is common in claypits of the Middle Eocene Claiborne Fm in Tennessee and Kentucky. Although the original specimen figured as *Carpolithus prangosoides* (Berry 1916) does not clearly show the wing venation, it does show a pair of elongate lateral wings that can be matched with specimens found later and described as *Terminalia vera* Berry (1930). An elongate central bulge in this specimen, representing the fruit body shows a median longitudinal groove that we interpret as a third wing, while the counterpart of this specimen (broken) shows at least one additional groove, which we interpret as another wing. *Carpolithes henryensis* is represented by only a single specimen, which lacks a counterpart. This specimen also shows a central body with elongate lateral wings with a groove, which is interpreted as a third wing. Based on the observed features, these specimens can be matched to those Berry (1930) illustrated later under the name *Terminalia vera*, and we place all of these in synonymy under the earlier name *Carpolithes prangosoides*.

Most of the *C. prangosoides* specimens are exposed in longitudinal fractures that show only two visible wings, positioned laterally on either side of the fusiform central body and lying in a common plane (Figures 2-10 & 2-11). This configuration is an artifact of the horizontal orientation of the fruit within the sediment in which it was buried, and of the lengthwise plane through the sediment that intercepted and exposed the fossil. In describing *Terminalia vera*, Berry considered that the fruits possessed only two wings. (Berry 1930). Careful microscopy of some specimens shows a stairstep fracture pattern in which multiple levels on which different

wings are exposed. In order to determine the full number of wings, two specimens were deliberately fractured transversely in the laboratory and show unequivocally that there are five wings (Figure 2-10).

None of the specimens show the pedicel, styles or the locule condition. Because pedicels have not been found attached to the fruits, it may be inferred that the fruits were sessile or that they were shed by abscising from the top of the pedicel. Because the fruit is always found with a full complement of wings it is inferred that it was not schizocarpic. But the available characters, including the number and position of wings and their venation allows for detailed comparison with extant fruits of similar form.

Although this species was assigned to the Combretaceae based on its lateral wings, detailed comparison of wing venation distinguishes the fossil from most of the genera within this family. The complex system with primary veins forming loops and secondaries interconnecting is similar to the venation in the wings of *Calycopteris* and *Macropteranthes*. *Calycopteris* does not have a fin-winged fruit; its wings are arranged like a propeller around the apex, and are derived from accrescent perianth. *Macropteranthes*, which is a member of a separate tribe, Laguncularíaeae (Excell and Stace 1965) is fin-winged with four wings derived from two bracteoles, such that a pair of wings extends from each bracteole. The venation is strikingly similar to that of the fossil. The geometry of a five-winged fruit would be difficult to reconcile with formation of two wings per bracteole.

Other families with five winged fruits include Apiaceae, Lophopyxidaceae, Malvaceae and Zygophyllaceae (Table 2-1). The fruits of Zygophyllaceae are mericarps and those of Malvaceae are usually capsular so those two families can be eliminated. Apiaceae do not have prominent venation and can be eliminated and Lophopyxidaceae lack the looping pattern of

venation on the fruits. Although no genus fits closely; the family, Combretaceae seems to be morphologically most similar to these fossils. The fruit lacks the distinguishing characteristics of the family such as combretaceous hairs, and because these fruits may be those of an in an extinct genus, there is not enough evidence to place this fossil in the family.

***"Terminalia stamina"* MacGinitie**

MacGinitie (1941) described *Terminalia estamina* based on three unattached leaf specimens and a winged fruit from the Middle Eocene Chalk bluffs flora of California. He called the cited specimens "cotypes," but did not designate a holotype. Subsequently (MacGinitie 1969, p. 129), he made a formal new combination, transferring the species to *Mastixia estamina* (MacGinitie) MacGinitie, based on two of the leaf specimens that had been figured earlier. In this transfer, he cited the two of the leaf specimens but specifically excluded the remaining leaf and fruit specimens, stating that "only Figure 2-2, plate 42 represents a leaf of *Terminalia*" and "The fruit, Figure 2-4, plate 43, is correctly assigned to *Terminalia*." This created the awkward situation that the two specimens that MacGinitie (1969) still considered to represent *Terminalia* were left without an epithet. To resolve this situation, a new epithet will have to be given to this fossil.

Description. Fruit elliptical in outline, symmetrical, rounded over the apex, length is 3-3.5 cm, width 2.5 cm. The fossil fruit has a fusiform central body, 13 mm long, 4 mm wide, from which at least five longitudinal wings radiate. Fruit is indehiscent. An axial vein extends about 7 mm from the base of the fruit to the base of the central body. Venation of the wings radiates from the central body toward the margin. Veins of the wing fine, dichotomizing and anastomosing, spaced from 0.5-1 mm apart without prominent looping or cross-veins. No marginal vein present. Features of style and perianth are unknown.

Comments. I have seen only two fruit specimens of this species, both of which are broken and incomplete. One of the specimens has been fractured obliquely across the fruit, such that impression surfaces of five wings can be counted (Figure 2-11). Both specimens seem to have the wings intact and because no dispersed mericarps of this type have been found in the fossil flora, we believe it to be non-schizocarpic, indehiscent fruit.

In his treatment, MacGinitie compared the Eocene fossil fruits that he called *Terminalia estamina* to the modern species *Terminalia hainanensis* and *Terminalia triflora,* which I have not observed in fruit. The other species of the genus that I examined also showed some similarity of form and venation.

Important features of this fossil fruit include apparent indehiscence, a fusiform central body, and presence of five wings with fine venation which dichotomizes. Other genera of angiosperms with a similar pattern of venation include *Ptelea*, *Wimmeria*, *Tripterigium*, *Bulnesia*, *Tropaelum*, and *Pterodiscus*. None of these genera have five wings as does the fossil and as do members of the Combretaceae (Table 2-1). *Pentace* is a genus with similar venation and five wings, but the wing edges in this genus are reinforced by many dichotomizations near the margin, which is not consistent with the fossil because the dichotomizations lie within the wing rather than along the margin. If we exclude those modern genera with fewer than five wings and those with dehiscent fruits, the only remaining candidates for comparison with this fossil are in the Lophopyxidaceae and Combretaceae (Table 2-1). The vein density of *Lophopyxis* is much greater with at least five veins per millimeter rather than 1-2 veins per millimeter of the fossil. Fruits of *Combretum* and *Terminalia* (Combretaceae) can show similar form to the fossil, including the presence of a fusiform central body that is positioned above the

base of the fruit. They also tend to have higher vein density than the fossil and their margins tend to be ragged due to lack of reinforcing venation.

Of the modern fin-winged fruits, fruits of genera within the Combretaceae seem to be most similar to these fossils. Some diagnostic features of the family could not be observed in these fossils including the inferior ovary, the number and positioning of seeds, presence of combretaceous hairs. Additionally, the venation is quite different in *Macropteranthes*. *Meiostemon* and *Thiloa* have only four wings and *Pteleopsis* has only two. Within the Combretaceae, the fruit fits best as either the genus *Terminalia* or the genus *Combretum*. This does not mean that this necessarily belongs to this family because the similarity lies partly in the absence of any distinguishing characters, and the fossils may represent an extinct species in another family.

Indeed, the fossil seems to differ from both *Combretum* and *Terminalia* in some aspects. The genus *Combretum* tends to have edges which fray because the veins so rarely dichotomize and the venation is very fine so that there is nothing to stop a small tear from becoming a large one. The fossil in contrast has smooth edges and there are clearly spaces between the veins. *Terminalia* may also have these very fine veins and tattered edges, but it can also have more widely spaced veins and smoother edges (e.g. *Terminalia)*. The assignment of this fossil to the genus Combretaceae is not certain without confirming characters such as combretaceous hairs or apical placentation, and the assignment to the genus *Terminalia* is certainly not justified.

Terminalia oregona (Lakhanpal) Meyer and Manchester

Basionym: *Halesia oregona* Lakhanpal, 1958, pro parte, University of California Publications in Geological Sciences 35, p. 36, pl. 9, fig. 1, Pl. 10, Figure 2-4 only.

Terminalia sp. Brown 1959, pro parte, Journal of Paleontology 33, p. 128; Pl. 24, Figure 2-16 only.

Terminalia oregona (Lakhanpal) Meyer and Manchester, 1997, University of California Publications in Geological Sciences 141, p. 128, pl. 51, Figures 2-1 through 2-4.

Description. This fruit is elliptical to obovate, pedicellate, symmetrical, base ranging from cuneate and acute to rounded and cordate, apex obcordate and rounded, length (20 mm, 25 mm, 45 mm, 33 mm, 40 mm, 55 mm, 33 mm), width (18 mm, 20 mm, 31 mm, 30 mm, 20 mm, 27 mm, 25 mm). Pedicel is 1 mm wide and up to 14 mm long. The fruit is nonschizocarpic. The fossil fruit has a fusiform central body mainly confined to the upper 1/3 of the fruit, 17-21 mm long, and 5-6.5mm wide with several prominent longitudinal ribs. A single vein leads from the pedicel to the central body. Fruits have up to at least three wings. Fruits with at least two wings, and in one specimen (Figure 2-13 5,6) at least three were observed. Veins of moderate thickness, radiating outward from the central axis and occasionally dichotomizing, spaced 0.5 mm apart, without prominent looping or cross veins, no marginal vein present. Stylar protrusion with a thickened disk like structure at its junction with the central body.

Comments. Important features include apparently three wings, inferior ovary with persistent stylar protrusion and apical disk, central body ridged and situated in the upper 1/3 of the fruit. Modern fin-winged fruits with an inferior ovary include Apiaceae, Begoniaceae, Burmanniaceae, Combretaceae, Dioscoreaceae, Hernandiaceae, Loranthaceae, Onagraceae, and Styracaceae. We are uncertain if they were variable in wing number from 2-3 or whether those specimens showing two wings are incompletely preserved.

Dioscoreaceae and Begoniaceae are eliminated because they have a marginal vein which is not found on the fossil. Lakhanpal (1958) believed it might be *Halesia* (Styracaceae). *Halesia* is distinguished by prominent intramarginal veins on the wings distinctive of this genus and not seen in the fossil. *Halesia* has perianth remaining at the apex where the fossil does not (Figure

2-7F). Apiaceae fruits are typically smaller without obvious venation. Hernandiaceae venation was sinuous without dichotomizations. Onagraceae venation tends to be obscure or arching upward. Loranthaceae venation tends to be more closely spaced. Each character in this fossil can be found in some species of the Combretaceae, but not in combination.

Terminalia oregona is a fossil with characters not inconsistent with the Combretaceae. This fruit has three wings with radiating venation that only rarely dichotomizes. This venation pattern is consistent with some species in both *Terminalia* and *Combretum*. The apical protrusion is similar to that found in *Meiostemon* and the apical position of the seed cavity can be found in *Pteleopsis*.

None of these fossils shows characters that would clearly place it into the Combretaceae, but none are wholly inconsistent. *Terminalia vera* has venation strikingly similar to *Macropteranthus*, but the difference in wing number is difficult to reconcile. *Terminalia estamina* and *Terminalia oregona* are both most similar to either *Combretum* or *Terminalia*. *Terminalia estamina* has five wings and radiating venation, but the veins are not closely spaced as is the common condition. *Terminalia oregona*, also has venation which is more widely spaced than usual for the family.

Overall, the lack of any diagnostic character placing these fruits in this family, the lack of critical examination of the leaves formerly placed in Combretaceae leaves me unwilling to state that there was a record of the family in the United States during the Eocene-Oligocene.

CHAPTER 5
CONCLUSIONS

Based on the previous chapters I have been able to compare the various modern fin-winged fruits and determine the status of the fossils. These results are presented below.

Modern Winged Fruits

Based on the survey presented in chapter three, fin-winged fruits occur in at least 19 orders of Angiosperms, occurring in magnoliids, monocots, and eudicots. Within eudicots, such fruits are particularly well represented among the rosids, with 18 of the 30 families that include genera with fin-winged fruits. These fruits are also represented in basal eudicots and asterids (Figure 2-8). Anemoballistic fruits were found convergently in three families.

Of the 87 genera known, only 34 had an inferior ovary, less than half had a marginal vein, suture, or intermarginal vein. Many of those that lack the marginal vein did have reinforcement towards the edge, either dichotomizing more frequently or forming loops distally. Presumably this helps prevent the wings from becoming tattered. Fruits of *Combretum*, which lack marginal veins and looping, are often frayed along the margin (Figure 2-2).

Wings can be formed from ovary tissue, from perianth parts and/or bracts. Those formed from perianth or bracts may take the form of lamina appressed to the ovary. In these cases, the wings may be formed from the fusion or partial fusion of two adjacent lamina (*Reisseika*) or each lamina may form two wings freely (*Macropteranthus*).

The fin-winged fruit type is found on every continent except Antarctica, and in habitats ranging from desert (*Macropteranthus*) to rainforest (*Cavanellesia*). These fruits occur on trees (*Cavanellisia, Craigia,Balfourodendron*), shrubs (*Phaeoptilum, Maxwellia, Wimmeria*) vines (*Dioscorea, Triptergium, Kleinhovia*) and herbs (*Polygonum, Stackhousia, Abronia*).

Fin-winged fruits have enough distinguishing characters to separate them by family. A dichotomous key to the fin-winged fruits (by family) is given below.

1a. Fruit from an inferior ovary
  2a. Fruit dispersing via anemoballisty with many seeds
    3a. Fruit with two or four wings.....Onagraceae
    3b. Fruit with three wings
      4a. Fruit opening apically, wings equal in size, seeds may be winged..... Dioscoreaceae/Burmanniaceae
      4b. Fruit splitting along sutures, wings equal or unequal in size, seeds not winged..... Begoniaceae
  2b. Fruit dispersing otherwise, capsule, mericarp, samara etc.
    5a. Fruits wing with intramarginal vein ..... Styracaceae
    5b. Fruits without intramarginal vein
      6a. Fruit a schizocarp.....Apiaceae
      6b. Fruit non-schizocarpic
        7a. Unicarpellate fruit with sinuous venation .....Hernandiaceae
        7b. Three-five carpellate, venation otherwise
          8a. Fruit small (1cm), wings 3, carpels 3-4 ..... Loranthaceae
          8b. Fruits usually greater than 1cm, carpels 4-5, wings 2, (3), 4, 5 .....Combretaceae
1b. Fruit from a superior ovary
  9a. Number of wings five or greater
    10a. Venation arching downwards..... Lophopyxidaceae
    10b. Venation otherwise (radiating, transverse, ascending)
      11a. Wings six-many, may be incomplete, fruit indehiscent.....Achariaceae
      11b. Wings five (or fewer in *Maxwellia*), wings complete, membranous-chartaceous (coriaceous in *Maxwellia*), fruit a capsule..... Malvaceae
  9b. Number of wings less than five (2, 3, or 4)
    12a. Marginal vein present
      13a. Four wings, fruit nearly round in outline.....Pedaliaceae
      13b. Two-three wings, fruit not round in outline
        14a. Fruits indehiscent
          15a. Marginal vein only, style persistent, long (1cm) and thick (2mm). ..... Cardiopteridaceae
          15b. Venation more than just marginal vein, style if persistent less than 1cm and less than 2mm thick.
            16a. Calyx persisting at the base of fruit..... Celastraceae
            16b. Calyx not persisting..... Cunonaceae
        14b. Fruits dehiscent, capsular or schizocarpic
          17a. Two winged
            18a. Fruit schizocarpic, bilocular ovary ..... Phyllanthaceae
            18b. Fruit capsular, ovary with three carpels ...Sapindaceae (Urvillea)
          17b. Three winged

19a. Fruit schizocarpic
20a. Calyx persistent at base, venation radiating from central body with no interconnections, joining the marginal vein ..... Stackhousiaceae
20b. Calyx not persistent, venation otherwise
21a. Fruit elliptical, longer than wide ..... Tropaelaceae
21b. Fruit butterfly shaped, wider than long..... Rhamnaceae (*Reisseika*)
19b. Fruit capsular
22a. Venation irregular, asymmetrical, forming variably sized polygonal areoles ..... Rhamnaceae
22b. Venation radiating, dichotomizing and anastomosing.....Sapindaceae
12b. Marginal vein absent
23a. Fruit schizocarpic, four wings.....Zygophyllaceae
23b. Fruit non-schizocarpic, wings 2,3, or 5
24a. Fruit coriaceous with many small seeds/fruit..... Malvaceae (Maxwellia)
24b. Fruit not coriaceous, fewer seeds/fruit
25a. Fruit formed from persistent perianth
26a. Fruit an achene ..... Polygonaceae
26b. Fruit otherwise.....Nytaginaceae
25b. Fruit formed from ovary
27a. Sepals or disk persistent at base
28a. Sepals persistent, no persistent disk..... Cyrillaceae
28b. Sepals not persistent, disk persistent..... Polygalaceae
27b. Sepals/disk not persistent
29a. Three-winged
30a. Veins forming loops, trichomes absent .. Malpighiaceae
30b. Veins dichotomizing but not looping, trichomes present.....Trigonaceae
29b. Two or four winged
31a. Fruit longer than wide .....Fabaceae
31b. Fruit wider than long or nearly equal .....Rutaceae

Fossil Winged Fruits

As presented in Chapter 4, three different occurrences of fossil fin-winged fruits have been attributed previously to Combretaceae in North America. Two are from the Eocene, one from the Oligocene, and all have been assigned to the genus *Terminalia*. Each of these was reexamined with attention to the original fossil specimens and closely compared with extant fruits of Combretaceae and other extant families. The features preserved in these fossils are insufficient to confirm identification to that family. Although similar in many respects to

Combretum and *Terminalia*, these fossils may represent convergence in fruit form and could represent another family.

In order to confidently assign a fossil fin-winged fruit to the Combretaceae, characters such as cross sectional anatomy, seed condition, or presence of "combretaceous hairs"(long, straight, sharply pointed, unicellular, very thick walled, with conical internal component at base), should be present. Tattered wing margins are common in *Combretum* and could be a contributing character when analyzing a fossil.

It is hoped that the survey of extant fin-winged fruits presented here will provide an improved basis for evaluating similar types of fruits from the fossil record. Such winged fruits are known as early as the late Albian of Kansas (Dilcher, pers. comm. 2006) and are well represented in Tertiary floras. 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 provides a basis for recognizing extinct taxa.

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BIOGRAPHICAL SKETCH

Elizabeth O'Leary was born in Pittsfield, Massachusetts, in 1981. She attended elementary school through high school in the public school system of Natick, Massachusetts and graduated at age 17 in the year 1999. She entered College of the Atlantic in the same year, majoring in human ecology. She graduated from College of the Atlantic in 2003; her final project was an easy to read book about plant reproduction. In 2004 and 2005, she took several courses through Harvard Extension School and then applied for graduate school at the University of Florida. She began graduate school in the spring of 2005 with a focus in paleobotany, working under the supervision of Steven Manchester. She graduated with a Master of Science degree in 2007.