American Journal of Botany 91(7): 1126–1139. 2004.

DUABANGA-LIKE LEAVES FROM THE MIDDLE EOCENE PRINCETON CHERT AND COMPARATIVE LEAF HISTOLOGY OF LYTHRACEAE SENSU LATO[1]

STEFAN A. LITTLE,[2] RUTH A. STOCKEY,[2,4] AND RICHARD C. KEATING[3]

[2]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada; and [3]Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299 USA

A permineralized lythraceous leaf type found in close association with fruits, stems, and roots of *Decodon allenbyensis* Cevallos-Ferriz et Stockey in the Middle Eocene Princeton chert of British Columbia, Canada, is described. Midribs have a prominent C-shaped midvein surrounded by sclerenchyma, with an adaxial epidermis of rectangular to rounded cells lacking enlarged mucilage cells. Leaves are dorsiventral, 180–270 μm thick at the lamina, with a double palisade layer. Abaxial epidermal cells have prominent papillae, and these epidermal cells can be infected by fungi, forming dark sterile stromata. Fossil leaves are similar to those of Myrtales and are compared to those of Lythraceae sensu lato. Although these leaves are thought to belong to the previously described *Decodon allenbyensis* found in the same chert layer, they lack the diagnostic features of extant *Decodon* leaves. Instead they share most anatomical similarities with *Duabanga grandiflora* Roxburgh ex DC Walpers (Lythraceae, subfamily Duabangoideae) including vascular tissues, palisade and spongy mesophyll, bundle fibers, and abaxial epidermal papillae. *Duabanga grandiflora* differs from the fossil in having mucilaginous cells and a consistently V-shaped abaxial midrib. Although anatomically similar to *Duabanga*, the fossil leaves are considered those of *D. allenbyensis*, based on association and the depositional environment prior to preservation. Recent phylogenetic analyses place *Duabanga* and *Decodon* in separate clades within Lythraceae, but relationships between these clades are not well supported, indicating that fossil leaves should provide useful anatomical characters for elucidating relationships within Lythraceae.

Key words: *Decodon*; *Duabanga*; Eocene; leaf histology; Lythraceae; Punicaceae; Sonneratiaceae.

Lythraceae is a large family in the order Myrtales, containing about 600 species that are mainly distributed in tropical to subtropical regions (Graham, 1964; Graham et al., 1993). Punicaceae (*Punica* L.) and Sonneratiaceae (*Sonneratia* L.f. and *Duabanga* Buchanan-Hamilton) have been included in Lythraceae by several authors, sometimes with Trapaceae (*Trapa* L.) (Dahlgren and Thorne, 1984; Thorne, 1992a, b; Graham et al., 1993; Graham, 1999; Judd et al., 1999). Phylogenetic analyses using morphological (Johnson and Briggs, 1984; Graham et al., 1993) and molecular characters (Conti et al., 1996, 1997; Shi et al., 2000; Huang and Shi, 2002) have resulted in the recognition of a lythraceous clade that also includes *Sonneratia*, *Duabanga*, and *Punica*. Lythraceae sensu lato includes five subfamilies: Lythroideae with 28 genera, and Punicoideae, Sonneratioideae, Duabangoideae, and Trapoideae (Graham et al., 1998), each with a single genus.

The oldest fossil records of Lythraceae are of seeds from the Campanian (Cretaceous) of Mexico (Rodríguez-de la Rosa et al., 1998) and from the Paleocene of southern England (Reid and Chandler, 1933; Chandler, 1961). Fossils of Lythraceae include fruits, seeds, leaves, and pollen (Graham and Graham, 1971; Muller, 1981; Tiffney, 1981; Friis, 1985). Leaves assignable to the genus *Decodon* J. F. Gmelin have been reported from compression/impression fossils from North America (Wolfe and Tanai, 1980; Wehr and Hopkins, 1994; Stockey and Wehr, 1996) and western Europe (Kvaček and Sakala, 1999). However, detailed anatomical data are not known for these leaves, and we cannot be certain that they represent this genus. Manchester et al. (1998) point out that assigning isolated leaves of the order Myrtales to extant taxa in the absence of fruit and flower data is not advised because of the similarities in venation pattern in the order. The mosaic of characters seen in fossil myrtalean taxa such as *Syzygioides* Manchester Dilcher et Wing (1998) illustrate that with isolated organs, fossils of Myrtales may be difficult to assess and that whole-plant reconstructions are necessary.

In this paper, we describe a lythraceous leaf type from the Middle Eocene Princeton chert of British Columbia, Canada. These leaves are closely associated in the same chert layers with fruits, seeds, and recently described vegetative axes with lacunate phellem, of *Decodon allenbyensis* Cevallos-Ferriz et Stockey (Cevallos-Ferriz and Stockey, 1988; Little and Stockey, 2003). We histologically compare the fossil leaves to those of Myrtales and in particular to those of Lythraceae sensu lato, using characters of the lythraceous leaves described by Keating (1984), and using new characters, to assess their affinities. This comparison, along with original observations of *Decodon verticillatus* (L.) Ell. leaves, demonstrates newly recognized diversity in Lythraceae of the Middle Eocene of western North America.

MATERIALS AND METHODS

Permineralized leaf specimens studied here come from the Princeton chert locality on the east bank of the Similkameen River, 8.4 km southwest of Princeton, British Columbia (UTM 10U FK 786725; 49°22′33″ N, 120°32′18″ W). The chert is part of the Allenby Formation, Princeton Group and is dated at 48.7 million years bp (Hills and Baadsgaard, 1967; H. Baadsgaard, University of Alberta, personal communication 1999). Leaves come from layer #43 of the chert and are most often associated with the fruits, seeds, and vegetative axes of *Decodon allenbyensis* (Little and Stockey, 2003) as well

[1] Manuscript received 2 October 2003; revision accepted 6 March 2004.

The authors thank Kathleen Pigg for helpful review of the manuscript; we thank Randy Mandryk, George Braybrook, and Heidi Schwab at the University of Alberta for their help with histology, SEM, and imaging, respectively. Shirley A. Graham (Kent State University) provided leaves of extant *Decodon verticillatus*. This research was supported in part by NSERC grant A6908 to R. A. Stockey, an NSERC postgraduate scholarship to S. A. Little, and the Department of Biological Sciences, University of Alberta.

[4] E-mail: ruth.stockey@ualberta.ca.

as the fruits and seeds of *Paleomyrtinaea princetonensis* Pigg, Stockey et Maxwell (1993).

Fossil specimens were prepared with the cellulose acetate peel technique (Joy et al., 1956) modified for hydrofluoric acid (Basinger and Rothwell, 1977; Basinger, 1981). Peel sections were mounted with Eukitt rapid mounting medium (O. Kindler, Freiburg, Germany) for microscopic examination. All fossil specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Slides of extant Myrtales were examined from the material sectioned by Keating (1984). The sample of species of Lythraceae sensu lato were originally illustrated by camera lucida, but are photographed for the first time here, and additional data are provided based on these microscopic sections. Leaves were preserved in FAA or FPA, embedded in paraffin, sectioned at 10 μm and stained with safranin-O/fast green (Keating, 1984). All leaves were sectioned at midlevel in transverse section (Keating, 1984). The sections of extant leaves used in this study are currently housed at the University of Alberta.

Leaves of extant *Decodon verticillatus*, examined here for the first time, were studied using paraffin-embedded sections stained with safranin-O/fast green (Johansen, 1940). In addition, leaves of extant *D. verticillatus* were examined by Cryo-SEM (scanning electron microscopy) using an EMITECK (K1250) cryosystem, and the chromium trioxide technique (Alvin and Boulter, 1974). Samples were coated with 15 nm Au with a Nanotek sputter coater, and viewed with a Japan Electronics Optics (JEOLUSA) scanning electron microscope (JSM 6301) at 5 kV. Images were taken with a Leaf Microlumina System version 1.2 (Leaf Systems, Westborough, Massachusetts, USA) and a Phase One digital studio camera (Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe Photoshop (Adobe Systems, Inc., San Jose, California, USA).

RESULTS

Fossil leaves—Leaves are often found as islolated fragments and in small groups that are associated with roots and stems of *Decodon allenbyensis*; however they have not been found in attachment (Fig. 1). The longest leaf found (ca. 26 mm long) is also the most intact in transverse section (Fig. 2). Leaves were degraded prior to preservation, and midribs are not complete for all tissues in a given specimen (Figs. 3, 4). Fine venation observed in paradermal section shows polygonal areolation with freely ending veinlets (Fig. 6).

The lamina is dorsiventral and 180–270 μm thick (Figs. 7, 8). The epidermis is often missing in the fossil leaves (Fig. 5). Adaxial epidermal cells are rectangular to rounded; enlarged epidermal cells with contents have not been observed (Figs. 7, 8). The abaxial epidermis is papillate (Figs. 7, 8), but is non-papillate over the midribs and ribs of major veins (Fig. 3). Cells of the adaxial epidermis are larger than those of the abaxial epidermis. Prominent overarching papillae are observed in the abaxial epidermis, and these areas probably represent the positions of stomata (Figs. 7, 8, arrows). Multicellular trichomes and cuticle were not observed.

The mesophyll is well differentiated into a double-layered palisade that makes up 50% of the lamina thickness; spongy layers are 5–7 cells thick at the lamina. Midribs are flat to convex adaxially and prominently rounded/convex to V-shaped abaxially (Figs. 2, 3, 4). Midvein xylem and phloem are rarely well preserved, possibly degraded by fungi (Figs. 3, 4). Although preservation makes observation of midvein and surrounding tissues difficult, midveins appear to be C-shaped, incurved adaxially, surrounded by periphloic fibers except for an adaxial gap, and surrounded by ground tissue (Figs. 3, 4). Secondary vein ribs are flat adaxially and abaxially convex or slightly biconvex, with C-shaped secondary veins that are surrounded by fibers (Table 1). Minor veins are also surrounded by fibers (Fig. 5). Crystals were not observed in the leaves.

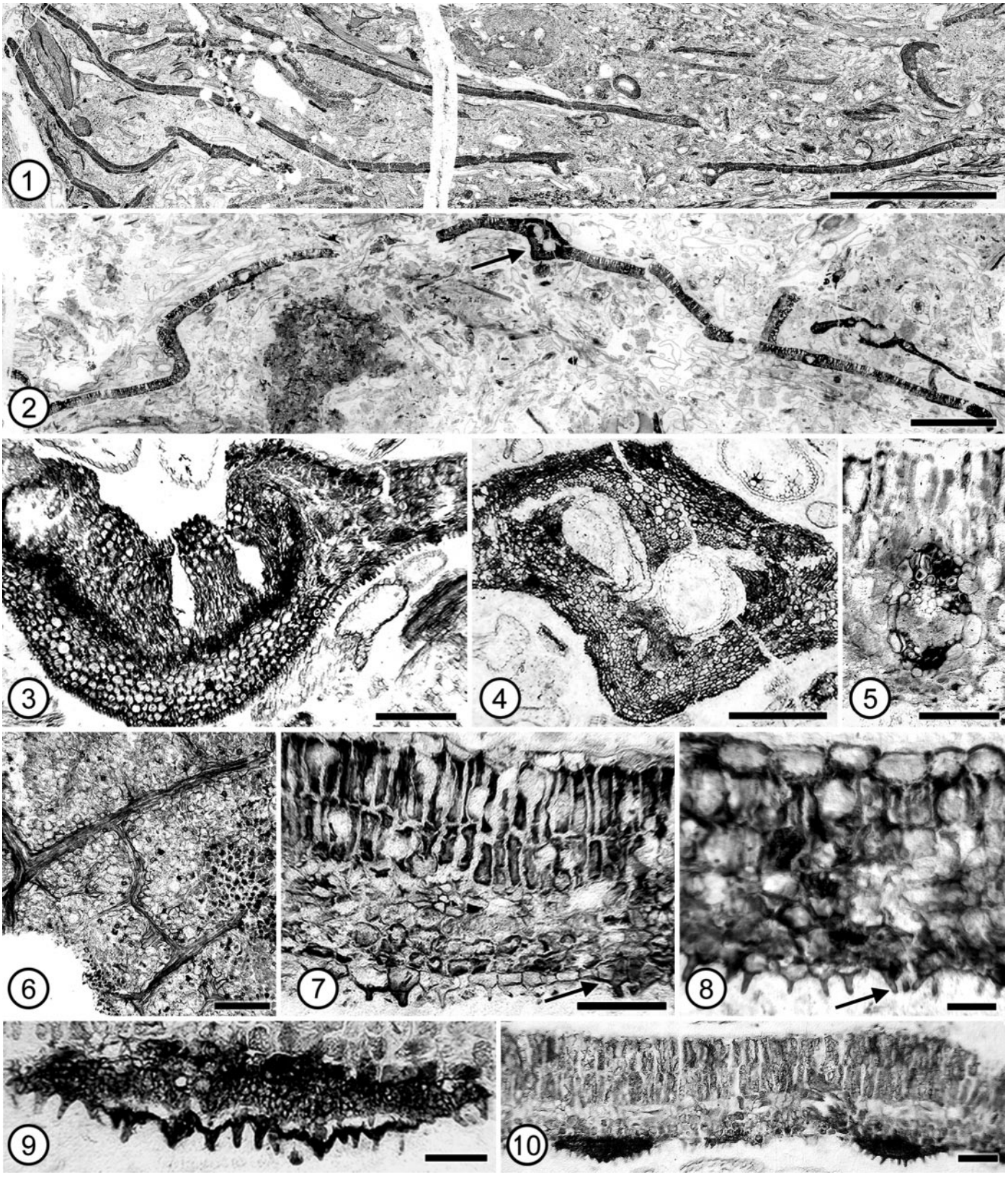
Many of the fossil leaves have tissues invaded by septate fungal hyphae. Dark-colored hyphal masses, almost exclusively on the abaxial side of the lamina, invade and replace the papillate epidermal cells and mesophyll tissue (Figs. 9, 10). Spores and/or conidia from these dark sterile stromata were not observed.

Leaves of Decodon verticillatus (L.) Ell.—In surface view, anomocytic stomata are level with the epidermis and occur on both leaf surfaces (Figs. 11–14). Epidermal cells appear polygonal when observed with cryo-SEM, with a clear outline and smooth surface (Figs. 13, 14). Isolated, dried cuticle observed with SEM appears striated/wrinkled, and the outline of the epidermal cells is often less clear (Figs. 11, 12). Multicellular, branched trichomes occur on both leaf surfaces (Fig. 14) and are more dense on or near veins. Fine ornamentation is visible on the trichomes (Fig. 14).

In transverse section, leaves are up to 20 mm wide (Fig. 15). The lamina is dorsiventral and 110–125 μm thick. The adaxial and abaxial epidermis is similar in thickness and made up of rectangular to rounded cells, with some enlarged, mucilage-filled cells (Fig. 16). Some epidermal cells contain spherical clusters of birefringent crystals (Table 1). Trichome ornamentation in sections is not as clear as when viewed with SEM (Fig. 15). The mesophyll is well differentiated into a single palisade that makes up 50% of the lamina thickness and spongy layers three cells thick. Midribs are prominently ridged adaxially and convex/trapezoidal abaxially (Fig. 15). Midveins are C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are ridged adaxially and convex/trapezoidal abaxially, similar to midribs (Table 1), with weakly C-shaped secondary veins. Druses are observed in the midrib ground tissue and the mesophyll.

Leaves of other extant Lythraceae—*Duabanga grandiflora (Roxb. ex DC) Walpers*—The two specimens examined had some differences. The lamina is dorsiventral and 180–225 μm (Figs. 17, 18) or 285–335 μm thick (Figs. 30, 31). Epidermal cells are rectangular to rounded with some cells enlarged and mucilaginous. Cells of the adaxial epidermis are about twice as large as abaxial epidermal cells. Abaxial epidermal cells are papillate (Figs. 18, 20) over the lamina, but non-papillate on midribs and secondary vein ribs. The cuticle is thin to thick and smooth or ornamented on the abaxial papillae. Stomata are only found on the abaxial surface, with the guard cells level with the epidermis, and the surrounding papillate cells overarching the guard cells (Figs. 19, 20). Trichomes are not present. The well-differentiated mesophyll is a palisade layer, two or 2–3 cells thick that makes up 40–50% of the lamina thickness and spongy layers 4–9 cells thick (Fig. 18). Midribs are slightly grooved to flat adaxially and V-shaped abaxially (Fig. 17) or convex/round to flat adaxially and V-shaped abaxially (Fig. 19). Midveins are C-shaped, incurved adaxially, bicollateral, and surrounded by periphloic fibers except for an adaxial gap. Midveins are surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially convex or slightly biconvex (Table 1), with C-shaped secondary veins that are surrounded by fibers (Figs. 17, 19). Druses are observed in midrib and mesophyll tissues.

Duabanga moluccana Bl.—The two specimens examined had some differences. The lamina is dorsiventral and 140–190 μm or 260–310 μm thick (Figs. 21, 22). Epidermal cells are


1
2
3
4
5
6
7
8
9
10

rectangular to rounded, with some enlarged mucilaginous cells. Cells of the adaxial epidermis are about twice as large as those of the abaxial epidermis. The cuticle is thick and ornamented. One specimen has stomata only on the abaxial surface, the other specimen is amphistomatic. Guard cells are level with the epidermis or slightly sunken into the epidermal cells in adaxial stomata. Trichomes were not observed. The mesophyll is well differentiated into a palisade, two or 2–3 cells thick that makes up 40–50% of the lamina thickness and spongy layers 4–6 cells thick (Fig. 22). Midribs are flat adaxially and convex/rounded abaxially in one specimen (Fig. 21). The other specimen has a midrib that is convex adaxially and convex/square abaxially. The bicollateral midveins form a cylinder surrounded by periphloic fibers and ground tissue. Secondary vein ribs are flat adaxially and abaxially convex, with C-shaped secondary veins that are surrounded by periphloic fibers, abaxial ground tissue, and a parenchymatous adaxial extension (Table 1). Druses are observed in midrib and mesophyll tissues.

Lythrum alatum var. lanceolatum (Ell.) Rothrock—The lamina is dorsiventral and 120–130 μm thick (Fig. 23). The adaxial and abaxial epidermis is similar in thickness with rectangular to rounded cells and with some enlarged and mucilaginous cells. Some epidermal cells contain spherical clusters of birefringent crystals. The cuticle is thin and appears striated. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes were not observed. The mesophyll has one distinct palisade layer, occasionally with a less well-differentiated layer below, and together the layer(s) make up 30% of the lamina thickness. Spongy mesophyll is three cells thick. Midribs are sunken, grooved adaxially, and slightly V-shaped abaxially (Fig. 23). Midveins are short arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are slightly biconvex with small and circular secondary veins (Table 1). Druses are observed in the midrib ground tissue and the mesophyll.

Nesaea longipes A. Gray—The lamina is dorsiventral and 180–260 μm thick (Fig. 24). The adaxial and abaxial epidermis is similar in thickness, with rectangular to rounded cells and with some enlarged mucilaginous cells. The cuticle is thin and appears striated. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated with a single palisade layer, that makes up 30% of the lamina thickness. Spongy mesophyll is five cells thick. Midribs are flat, level adaxially, and slightly convex abaxially (Fig. 24). Midveins are weak arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are slightly biconvex with circular secondary veins (Table 1). Druses are observed in the midrib ground tissue and mesophyll.

Ammannia coccinea Rottb.—The lamina is dorsiventral and 130–160 μm thick (Fig. 25). Adaxial epidermal cells are larger than cells of the abaxial epidermis. Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Some epidermal cells contain spherical clusters of birefringent crytstals. Cuticle is very thin and smooth. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated with a single palisade layer that makes up 50% of the lamina thickness. Spongy mesophyll is 3–5 cells thick at the lamina. Midribs are concave/grooved adaxially and rounded/convex abaxially (Fig. 25). Midveins are weak arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially, with circular secondary veins (Table 1). Druses are observed in the midrib ground tissue and mesophyll.

Cuphea spectabilis S. Graham—The lamina is dorsiventral and 120–160 μm thick (Fig. 26). Adaxial epidermal cells are slightly larger than cells of the abaxial epidermis. Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Cuticle is very thin and smooth. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes are uniseriate, 1–4 celled, and thin walled. The mesophyll is well differentiated with a single palisade layer that makes up 30% of the lamina thickness. Spongy mesophyll is five cells thick. Midribs are concave/grooved adaxially and convex/square abaxially (Fig. 26). Midveins are weak arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are adaxially grooved and abaxially convex, similar to midribs, with weakly C-shaped secondary veins surrounded by ground tissue (Table 1). Druses are observed in the midrib ground tissue and mesophyll.

Heimia salicifolia (H.B.K.) Link.—The lamina is dorsiventral, 100–125 μm thick (Fig. 27). Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells. Adaxial epidermal cells are slightly larger than those of the abaxial epidermis. The cuticle is thin, striated, and ornamented. Stomata are found only on the abaxial surface with guard cells level with the epidermis. Trichomes are not present. The well-differentiated mesophyll is a single palisade layer that makes up 30% of the lamina thickness and a spongy layer 3–5 cells thick. Midribs are concave/grooved adaxially and V-shaped abaxially (Fig. 27). Midveins are weakly C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are adaxially and abaxially convex with weakly C-shaped secondary veins surrounded by ground tissue (Table 1). Druses are observed in the midrib ground tissue and mesophyll.

Lagerstroemia speciosa (L.) Pers.—The lamina is dorsiventral and 180–210 μm thick (Fig. 28). Epidermal cells are rect-

←

Figs. 1–10. Light micrographs of sections of fossil lythraceous leaves. **1.** Transverse sections of several leaves in chert matrix. P5104 C top #2. Bar = 5 mm. **2.** Transverse section of leaf with midrib (arrow) and lamina. P5999 D #4. Bar = 2 mm. **3.** Transverse section of leaf midrib showing vascular tissues, presence of papillate abaxial epidermis over lamina, and absence of papillae over midrib. P5139 D bot #2a. Bar = 0.2 mm. **4.** Transverse section of leaf midrib showing continuity of tissues on adaxial surface P5999 D #4. Bar = 0.3 mm. **5.** Transverse section of leaf showing vascular bundle with bundle sheath. P4947 B bot #9a. Bar = 0.06 mm. **6.** Paradermal section through mesophyll, showing veins. P4947 B bot #3a. Bar = 0.2 mm. **7.** Transverse section of leaf showing abaxial epidermis, double palisade, spongy mesophyll, and abaxial epidermal papillae surrounding possible stoma (arrow). P5997 D top #2. Bar = 0.05 mm. **8.** Abaxial epidermis showing papillae surrounding possible stoma (arrow). P5139 D bot #2a. Bar = 0.04 mm. **9.** Leaf abaxial surface showing fungal stroma beneath and invading epidermal papillae. P5997 D top #11. Bar = 0.04 mm. **10.** Leaf with abaxial fungal infection. P5981 C #1. Bar = 0.1 mm.

TABLE 1. Selected anatomical features for leaves of Lythraceae. Characters in boldface type match or overlap with those of the fossil leaf.

	Midvein				Secondary veins					Mesophyll	
	Rib[a]		Vein		Rib[a]		Vein				
Species	External adaxial shape	External abaxial shape	Shape x.s.[b]	Fibers[d]	External adaxial shape	External abaxial shape	Shape x.s.[c]	Fibers[d]	Adaxial extension	Structure[e]	No. palisade layers
Fossil leaf	Co	Co-V	si	SX	Co-Fl	Co	c	S	−	D	2(−3)
Decodon verticillatus	**Co**	Tr	s	—	**Co**	Tr	a	—	−	**D**	1
Duabanga grandiflora	Ca-Fl-**Co**	**V**	**si**	**SX**	**Co**-Fl	**Co**	**c**	**S**	−	**D**	**2(−3)**
Duabanga moluccana	**Co**-Fl	**Co**-Sq	cy	AdI	**Fl**	**Co**	**c**	**S**	+	**D**	**2(−3)**
Lythrum alatum	**Co**	**V**	a	—	**Co**	**Co**	ci	—	−	**D**	1**(−2)**
Nesaea longipes	**Co**-Fl	**Co**	a	—	**Co**	**Co**	ci	—	−	**D**	1
Ammannia coccinea	Ca	**Co**	a	—	**Fl**	Fl	ci	—	−	**D**	1
Cuphea spectabilis	Ca	**Co**-Sq	a	—	Ca	**Co**	a	—	−	**D**	1
Heimia salicifolia	Ca	**V**	a	—	**Co**	**Co**	a	—	−	**D**	1
Lagerstoemia speciosa	**Co**	Sq	cy	S	**Fl**	**Co**	a	AbB	+	**D**	**2**
Lafoensia speciosa	**Co**	Sq	s	AbB	**Fl**	**Co**	a	AbB	+	**D**	1
Lawsonia inermis	**Co**	**Co**	a	—	**Fl**	Fl	ci	—	−	**D**	1**(−2)**
Punica protopunica	**Co**-Fl	**Co**	a	—	**Co-Fl**	**Co**	a	—	+	**D**-I	**2(−3)**
Punica granatum	Ca-Fl	**Co**	a	—	**Fl**	**Co**	a-ci	—	−	**D**	1
Sonneratia sp.	Ca-Fl	**Co**	s	—	**Fl**	Fl	**c**	—	−	**D**-I	**3(−4)**
Sonneratia apetala	**Co**	**Co**	cy	—	**Fl**	Fl	**c**	—	−	I	3 + 3

[a] Rib shape: Co = convex; Ca = concave; Fl = flat; Sq = square; Tr = trapezoidal; V = V-shaped.
[b] Midvein shape: s = C-shaped; si = C-shaped with incurved abaxial ends; cy = cylinder.
[c] Secondary vein shape: c = C-shaped; a = weak arc; ci = circular.
[d] Vein fibers: SX = surround midvein except for adaxial gap; S = surround midvein; AdI = adaxial and lateral islands of fibers; AbB = abaxial band.
[e] Structure: D = dorsiventral; I = isobilateral.
[f] Crystals: D = druses; P = prismatics.
[g] Size: ad > ab = adaxial epidermal cells larger than abaxial; ad = ab = adaxial epidermal cells similar in size to abaxial.
[h] Mucilage cells: E = mucilage cells are epidermal; M = mucilage cells in mesophyll/below epidermis.
* Trichomes: presence or absence scored here, but Lythraceae trichome types are diverse and taxonomically important (Koehne, 1881; Amarasinghe et al., 1991).
[i] Stomatal location: Ab = Abaxial stomata only; Am = Amphistomatic/stomata adaxial and abaxial.
[j] Stomata level: l = guard cells level with epidermis, s = guard cells sunken into epidermis.

angular to rounded, with periclinally divided cells occurring regularly. Some epidermal cells contain spherical clusters of birefringent crystals, and some cells are enlarged and mucilaginous. The mucilage cells tend to protrude into the mesophyll and sometimes appear to be below the epidermis. Cells of the adaxial epidermis are about twice as large as those of the abaxial epidermis. The cuticle is thin, smooth, and slightly ornamented. Stomata are found only on the abaxial surface with guard cells level with the epidermis. Trichomes are uniseriate, 1–4 celled, and thin walled. The mesophyll is well differentiated, composed of a double palisade layer that makes up 40% of the lamina thickness and spongy layers 4–6 cells thick. Midribs are convex/rounded adaxially and convex/square abaxially (Fig. 28). Bicollateral midveins form a cylinder surrounded by periphloic fibers and ground tissue. Secondary vein ribs are flat adaxially and abaxially convex, with weakly C-shaped secondary veins that have an abaxial band of periphloic fibers, abaxial ground tissue, and a parenchymatous adaxial extension (Table 1). Prismatic crystals and druses are abundant in midrib and mesophyll tissues.

Lafoensia speciosa (H.B.K.) DC—The lamina is dorsiventral and 130–185 μm thick (Fig. 29). Adaxial and abaxial epidermis is similar in thickness, with rectangular to rounded cells and with some enlarged mucilaginous cells. Some epidermal cells contain spherical clusters of birefringent crystals. Cuticle is thin and smooth. Stomata are found only on the abaxial surface with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated, with a single palisade layer that makes up 25% of the lamina thickness and spongy layers 6–8 cells thick. Midribs are grooved adaxially and convex/rounded abaxially (Fig. 29). Midveins are C-shaped, bicollateral with an abaxial band of periphloic fibers, and surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially convex, with weakly C-shaped secondary veins that have an abaxial band of periphloic fibers, abaxial ground tissue, and a parenchymatous adaxial extension (Table 1). Prismatic crystals and druses are abundant in midrib and mesophyll tissues.

Lawsonia inermis L.—The lamina is dorsiventral and 180–210 μm thick (Fig. 30). Adaxial and abaxial epidermis is similar in thickness, with rectangular to rounded cells, with some enlarged mucilaginous cells. The cuticle is thin, smooth, or slightly ornamented. Leaves are amphistomatic with guard cells level with the epidermis. Trichomes are not present. The mesophyll cells are dense, with a single palisade layer, occasionally double, that makes up 30–40% of the lamina thickness; spongy layers are 4–6 cells thick. Midribs are convex/rounded adaxially and convex/rounded abaxially (Fig. 30). Bicollateral midveins are C-shaped and surrounded by ground tissue. Secondary vein ribs are flat adaxially and abaxially, with circular secondary veins (Table 1). Druses are observed in midrib and mesophyll tissues.

Punica protopunica Balf. f.—The lamina is dorsiventral, tending to isobilateral, and 230–290 μm thick (Fig. 31). Epidermal cells are rectangular to rounded, with some enlarged

TABLE 1. Extended.

Mesophyll				Epidermis						
				Cells					Stomata	
Lamina palisade (%)	No. spongy layers	Sclereids	Crystals[f]	Size[g]	Papillate abaxial cells	Mucilage cells[h]	Birefringent crystals	Trichomes*	Stomatal location[i]	Stomata level[j]
50	5–7	−	?	ad > ab	+	?	?	−	Ab	l
50	3	−	D	=	−	**E**	+	+	Am	**l**
40–50	**4–9**	−	D	**ad > ab**	**+**	**E**	−	−	**Ab**	**l**
40–50	**4–6**	−	D	**ad > ab**	−	**E**	−	−	Am, **Ab**	**l**&s
30	3	−	D	=	−	**E**	+	−	Am	**l**
30	**5**	−	D	=	−	**E**	−	−	Am	**l**
50	3–**5**	−	D	**ad > ab**	−	**E**	+	−	Am	**l**
30	**5**	−	D	**ad > ab**	−	**E**	−	+	Am	**l**
30	**3–5**	−	D	=	−	**E**	−	−	**Ab**	**l**
40	**4–6**	−	D, P	**ad > ab**	−	**E**	+	−	**Ab**	**l**
25	**6–8**	−	D, P	=	−	**E**	+	−	**Ab**	**l**
30–40	**4–6**	−	D	**ad > ab**	−	**E**	−	−	Am	**l**
30–40	**5–8**	−	D, P	**ad > ab**	−	—	−	−	**Ab**	**l**
40–50	3–4	−	D, P	**ad > ab**	−	—	−	−	**Ab**	**l**
25–30	10–12	+	D	=	−	M	−	−	Am	s
50–60	**5–8**	+	D	=	−	M	−	−	Am	s

mucilagious cells. Adaxial epidermal cells are about twice as large as abaxial epidermal cells. The cuticle is thick and ornamented. Stomata are only found on the abaxial surface with guard cells level with the epidermis. Trichomes were not observed. The mesophyll is well differentiated into a palisade that is two or three cells thick that makes up 30–40% of the lamina thickness and spongy mesophyll 5–8 cells thick. The three most abaxial spongy mesophyll layers are densely packed and rectangular, imparting a partially isobilateral appearance to the lamina. Midribs are slightly convex to flat adaxially and convex/round abaxially (Fig. 31). Midveins are weak arcs, bicollateral, and surrounded by ground tissue. Secondary vein ribs are slightly convex adaxially and abaxially, similar to midribs, with weakly C-shaped secondary veins that have a parenchymatous adaxial extension (Table 1). Prismatics are observed in mesophyll tissues.

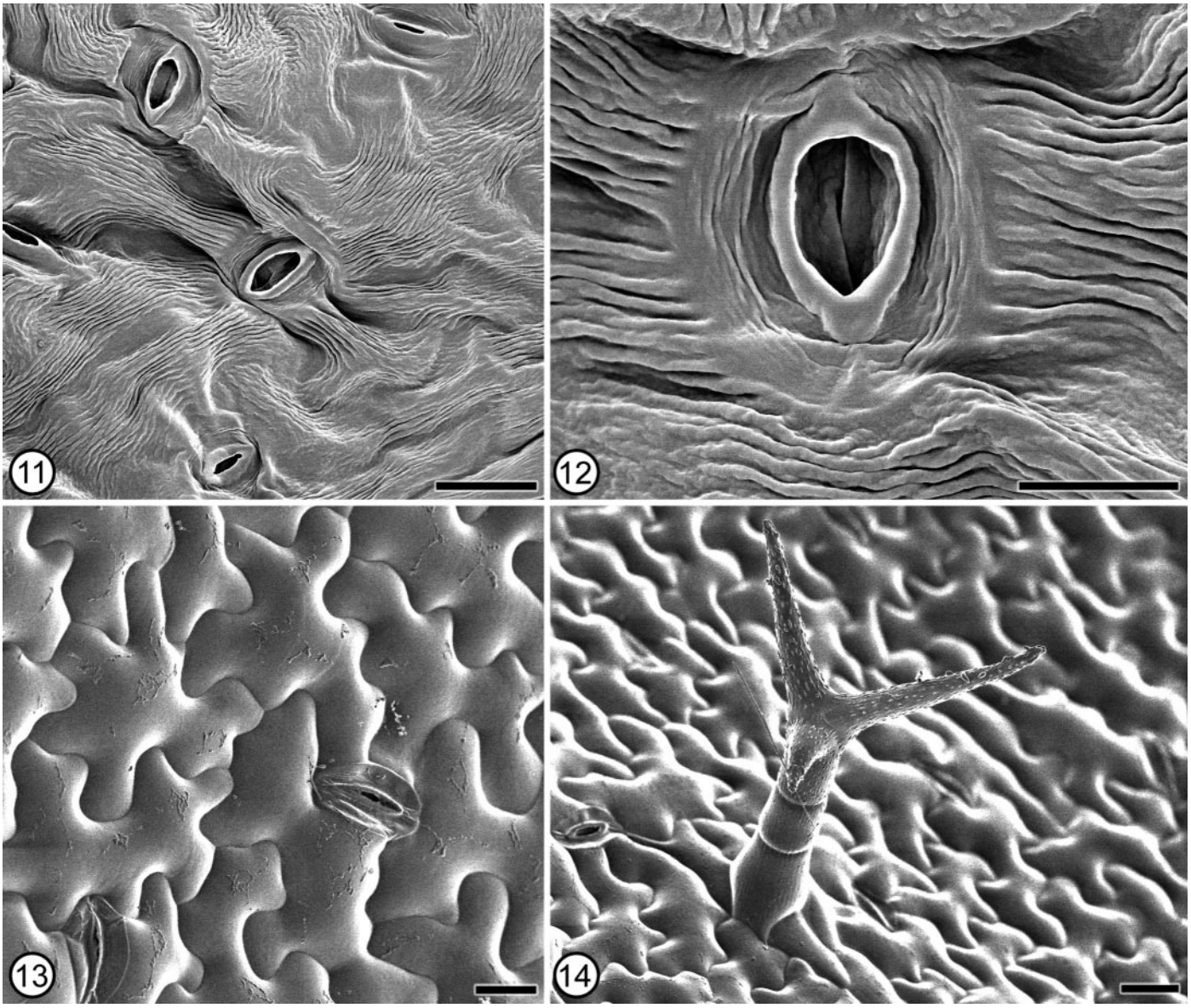
Punica granatum L.—The lamina is dorsiventral and 345–380 μm thick (Fig. 32). Epidermal cells are rectangular to rounded, and no enlarged mucilaginous cells were observed. Cells of the adaxial epidermis are larger than those of the abaxial epidermis. Cuticle is thin, smooth to slightly ornamented. Stomata are found only on the abaxial surface, with guard cells level with the epidermis. Trichomes were not observed. The well-differentiated mesophyll is a single palisade layer, about 40–50% of the lamina thickness, and spongy layers 3–4 cells thick. Midribs are slightly concave to flat adaxially and convex/round abaxially (Fig. 32). Midveins are C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are flat adaxially and slightly convex/rounded abaxially with weakly C-shaped to circular secondary veins (Table 1). Prismatics and druses are observed in midrib and mesophyll tissues.

Sonneratia sp.—The lamina is dorsiventral, tends toward isobilateral, and is 325–415 μm thick (Fig. 33). Epidermal cells are rectangular to rounded, with some enlarged mucilaginous cells that intrude into the mesophyll appearing to be just internal to the epidermis. Adaxial and abaxial epidermal cells are similar in size. The cuticle is thick and ornamented. Leaves are amphistomatic, and guard cells are slightly sunken with slightly overarching subsidiary cells. Trichomes were not observed. Mesophyll is well differentiated into a palisade 3–4 cells thick, that makes up 25–30% of the lamina thickness, and spongy layers 10–12 cells thick. The lowest 3–4 mesophyll layers are densely packed and rectangular, imparting a partially isobilateral appearance to the lamina. Midribs are slightly flat to concave adaxially and convex/round to V-shaped abaxially (Fig. 33). Midveins are C-shaped, bicollateral, and surrounded by ground tissue. Secondary vein ribs are not apparent with the C-shaped secondary veins embedded in the mesophyll (Table 1). Sclereids are observed in the mesophyll, and druses in the midrib and mesophyll tissues.

Sonneratia apetala Buch.-Ham.—The lamina is isobilateral and 244–510 μm thick (Fig. 34). Epidermal cells are rectangular to rounded, with enlarged mucilaginous cells intruding into the mesophyll appearing just internal to the epidermis. Abaxial and adaxial epidermal cells are similar in size. Cuticle is thick and ornamented. Leaves are amphistomatic, and guard cells are slighly sunken, with slightly overarched subsidiary cells. Trichomes are not present. Well-developed adaxial and abaxial palisade, both three cells thick, together make up 50–60% of the lamina thickness. Spongy mesophyll layers are 5–8 cells thick. Midribs are convex/round adaxially and abaxially (Fig. 34). Bicollateral midveins form a cylinder, surrounded by ground tissue. Secondary vein ribs are not apparent with the C-shaped secondary veins embedded in the mesophyll (Table 1). Sclereids are observed in the mesophyll and druses in the midrib and mesophyll tissues.

DISCUSSION

Permineralized plant remains from layer #43, the most extensively surveyed of the outcrop, include the following taxa: monocots, Araceae, and Alismatales (Currah and Stockey, 1991; Smith and Stockey, 2003); *Allenbya*, Nymphaeaceae (Cevallos-Ferriz and Stockey, 1989); *Eorhiza arnoldii*, incertae sedis (Robinson and Person, 1973; Stockey and Pigg, 1994); *Paleomyrtinaea*, Myrtaceae (Pigg et al., 1993); and *Decodon allenbyensis* (Cevallos-Ferriz and Stockey, 1988; Little and Stockey, 2003). Of these taxa, the leaves are hypothesized

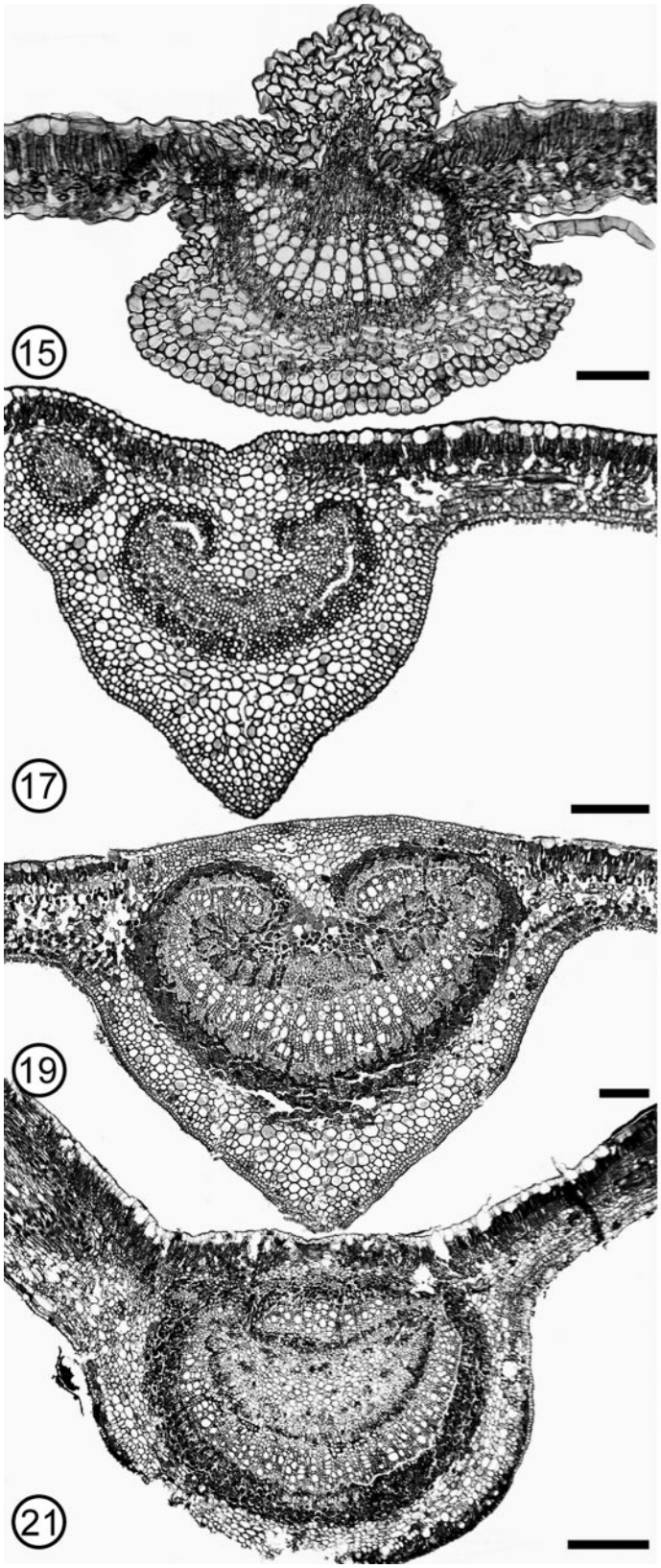


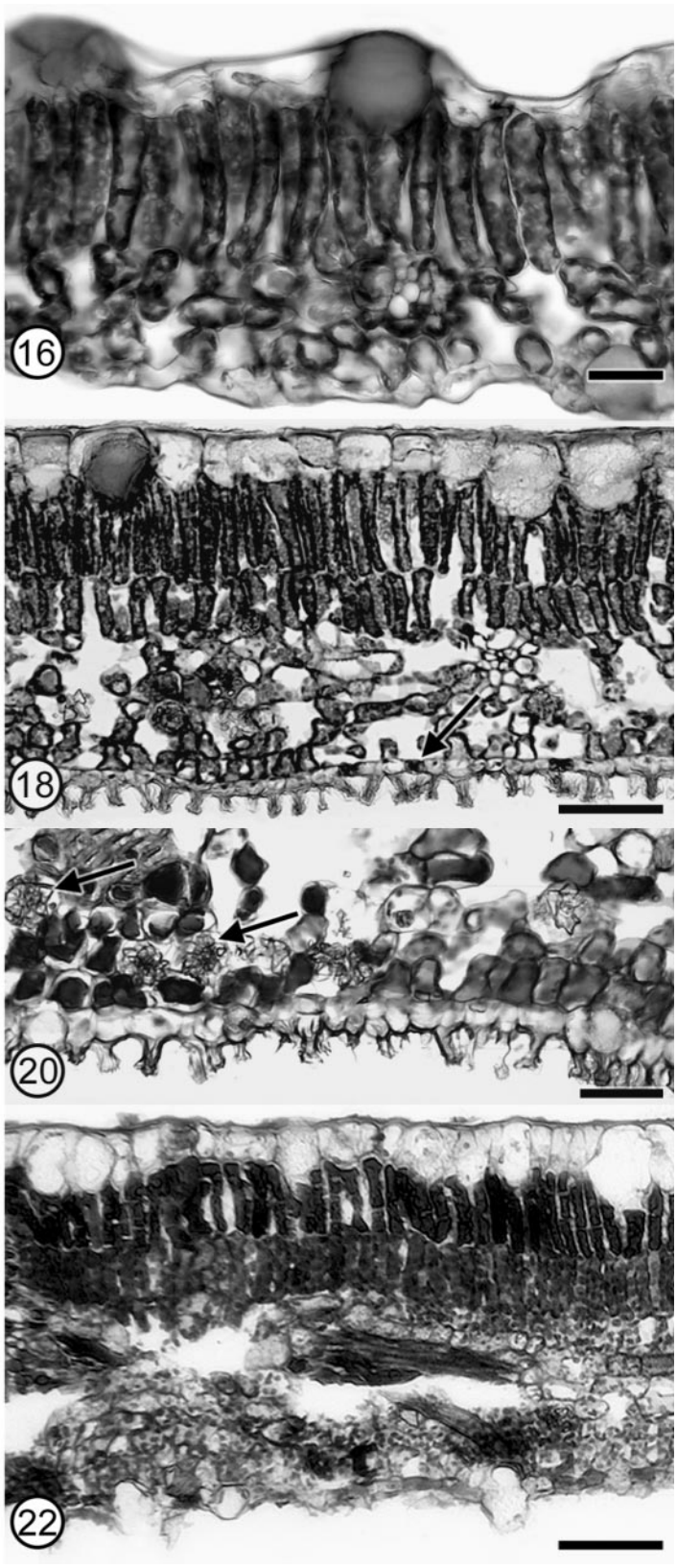
Figs. 11–14. Scanning electron microscopy of *Decodon verticillatus* leaves. **11.** Adaxial cuticle showing stomata after chromium trioxide technique and air drying. Decolf13. Bar = 0.02 mm. **12.** Adaxial cuticle on stomatal apparatus after chromium trioxide technique, showing striations. Decolf13. Bar = 0.01 mm. **13.** External abaxial leaf surface under Cryo-SEM showing anomocytic stomata. Decryl02. Bar = 0.02 mm. **14.** External abaxial leaf surface under Cryo-SEM showing trichome. Decryl03. Bar = 0.10 mm.

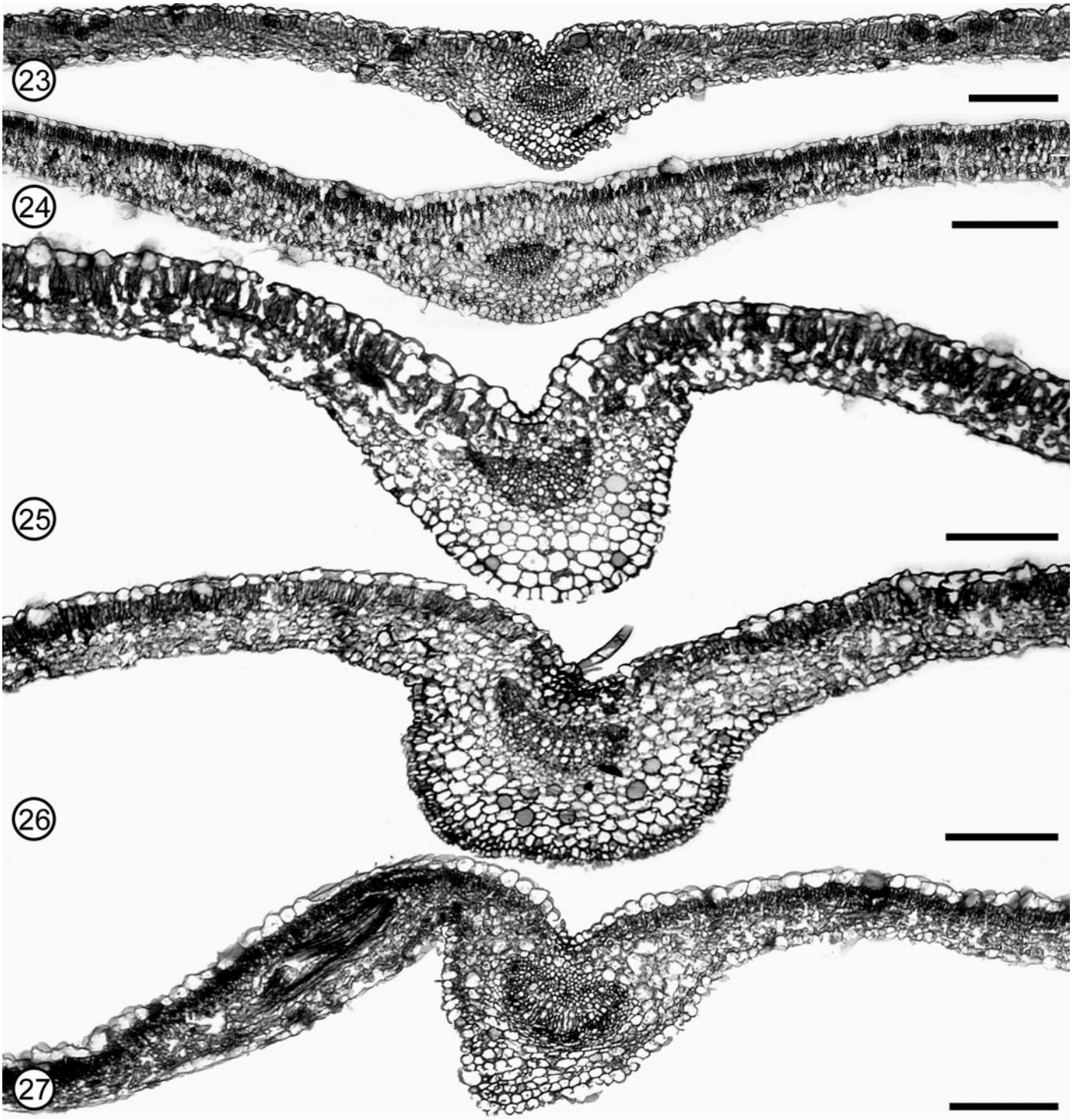
to belong to *Decodon* on the basis of their lythraceous features and close association to abundant fruits, seeds, stems, and aquatic stems and roots of this taxon (Little and Stockey, 2003). Other plants of layer #43 either have leaves that are already known (i.e., *Eorhiza arnoldii*) or would likely have dissimilar leaves (i.e., Nymphaeaceae and monocots) to the fossil leaves described here. Finally, the most closely related taxon to *Decodon*, *Paleomyrtinaea* (Myrtales), a guava-like

→

Figs. 15–22. Light micrographs of transverse sections of leaves of Lythraceae (Lythroideae and Duabangoideae). **15.** *Decodon verticillatus* (L.) Ell. showing adaxial midrib bulge, C-shaped xylem strand, double palisade, and multicellular trichome, at right. SL12902. Bar = 0.1 mm. **16.** *Decodon verticillatus* lamina showing double palisade and enlarged mucilage cells in epidermis. SL12902. Bar = 0.03 mm. **17.** *Duabanga grandiflora* (Roxb. ex DC) Walpers showing C-shaped midvein and trace to secondary vein with flat to slightly grooved adaxial surface and prominent ridged abaxial surface. 2062 #1. Bar = 0.3 mm. **18.** *Duabanga grandiflora* lamina showing double palisade, adaxial epidermis with mucilage cell, and abaxial epidermal papillae overarching stoma (arrow). 1859 #1. Bar = 0.1 mm. **19.** *Duabanga grandiflora* showing strongly curved midvein, nearly flattened adaxial surface, and prominent ridge on abaxial surface. 1859 #1. Bar = 0.3 mm. **20.** *Duabanga grandiflora* lamina showing spongy mesophyll with druses (arrows) and finely ornamented, abaxial, epidermal papillae. 1859 #1. Bar = 0.05 mm. **21.** *Duabanga moluccana* Bl. Showing broad flat zone of adaxial midrib, circular midvein, and prominent rounded abaxial midrib. 1935 #4. Bar = 0.3 mm. **22.** *Duabanga moluccana* lamina showing double palisade, epidermal mucilage cells, and lack of abaxial papillae. 1935 #4. Bar = 0.1 mm.


15
17
19
21

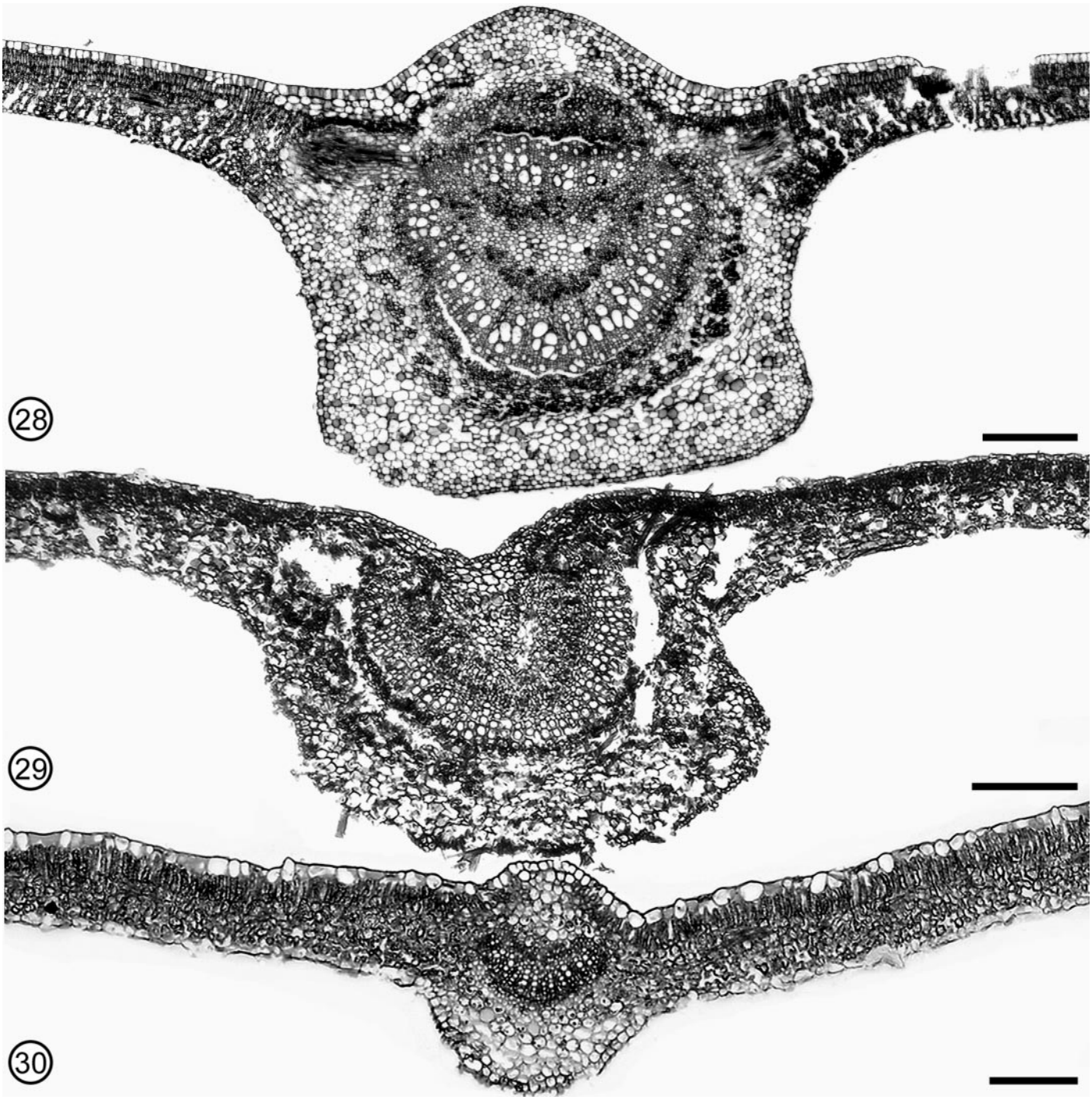

16
18
20
22



Figs. 23–27. Light micrographs of transverse sections of leaves of Lythraceae (Lythroideae). **23.** *Lythrum alatum* var. *lanceolatum* (Ell.) Rothrock showing adaxial groove and epidermal mucilage cells. 1729 #1. Bar = 0.2 mm. **24.** *Nesaea longipes* A. Gray showing smooth adaxial surface and epidermal mucilage cells. 1727 #4. Bar = 0.3 mm. **25.** *Ammannia coccinea* Rottb. showing grooves adaxial surface and mucilage cells in adaxial epidermis. 2126 #1. Bar = 0.2 mm. **26.** *Cuphea spectabilis* S. Graham showing adaxial groove, mucilage cells, and multicellular trichome. 1726 #1. Bar = 0.2 mm. **27.** *Heimia salicifolia* (H.B.K.) Link. showing adaxial groove and mucilage cells. 1728 #2. Bar = 0.2 mm.

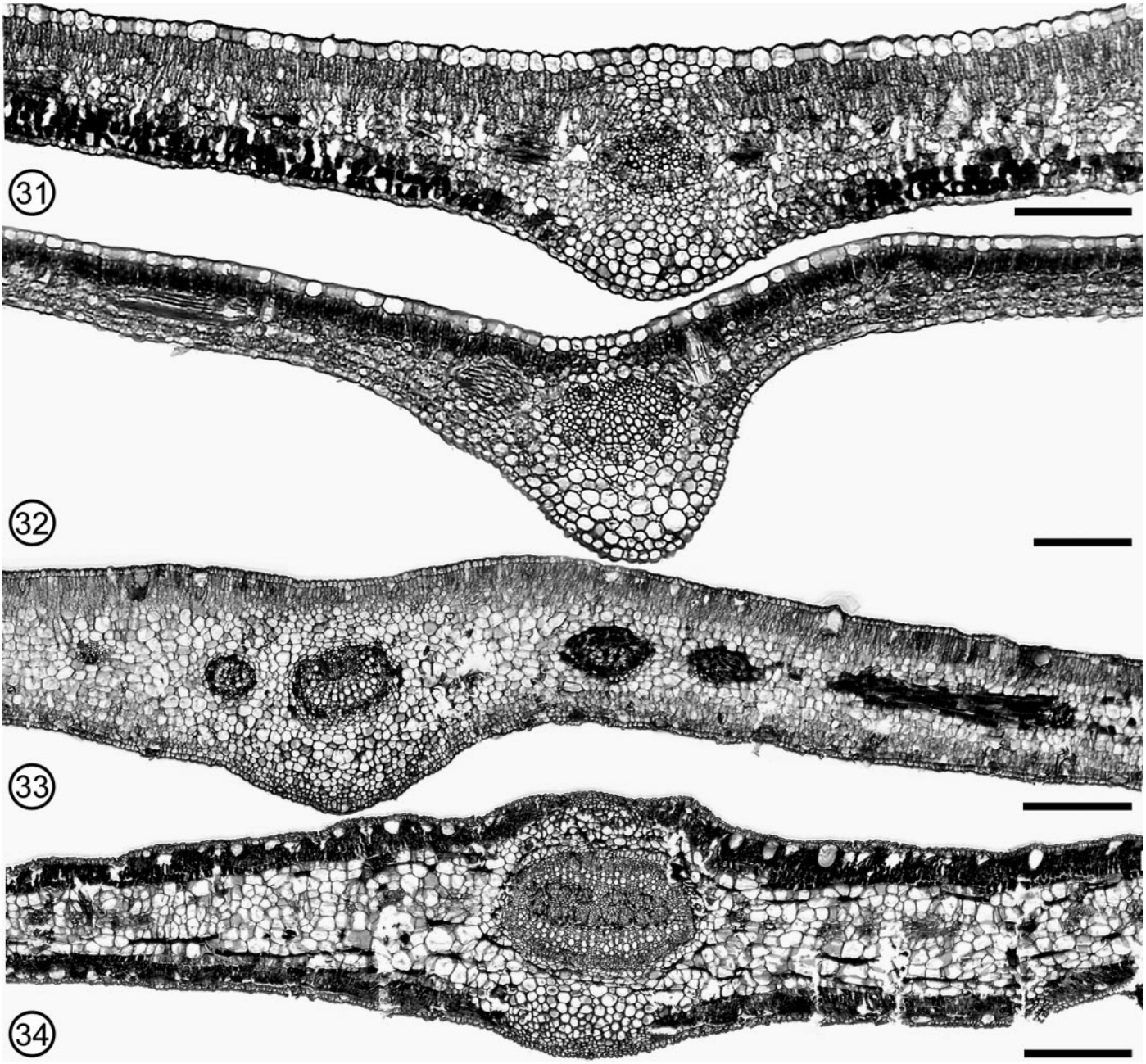
plant, is unlikely to have this leaf type because the fossil leaves lack secretory canals and hypodermis, features that are typically found in the mesophyll of many Myrtaceae (Keating, 1984). For these reasons we believe the leaves most likely belong to *Decodon allenbyensis*, if not some other unknown taxon.

The fossil *Decodon allenbyensis* has wood and periderm anatomy in its stems and roots that is very similar to that seen



Figs. 28–30. Light micrographs of transverse sections of leaves of Lythraceae (Lythroideae). **28.** *Lagerstroemia speciosa* (L.) Pers. showing nearly cylindrical midvein with adaxial ridge prominent abaxial bulge with angular outline. 1794 #2. Bar = 0.3 mm. **29.** *Lafoensia speciosa* (H.B.K.) DC showing C-shaped midvein and grooved adaxial surface. 1784 #1. × 57. Bar = 0.2 mm. **30.** *Lawsonia inermis* L. showing nearly circular midrib with C-shaped vein and epidermal mucilage cells. 1808 #2. Bar = 0.2 mm.

in extant *D. verticillatus* (Little and Stockey, 2003). We, therefore, investigated leaf anatomy of *D. verticillatus*, the only living species in the genus, to assess if there are any diagnostic characters of the leaves that may serve to link the fossil leaves with the *D. allenbyensis* axes. However, leaves of *D. verticillatus* have distinctive leaf anatomy in Lythraceae and differ from the fossil leaves (Table 1). The fossils have adaxially convex/round midribs and adaxially flat secondary vein ribs. The adaxially ridged midribs and secondary vein ribs of *D. verticillatus* are distinctive in shape and prominence, unlike those found in other Lythraceae. The trapezoidal abaxial midrib in *D. verticillatus* is most similar to the square shaped midrib of *Cuphea spectabilis* or *Lafoensia speciosa* and is unlike midribs of the fossil leaves that are abaxially convex/



Figs. 31–34. Light micrographs of transverse sections of leaves of Lythraceae (Punicoideae and Sonneratioideae). **31.** *Punica protopunica* Balf. f. showing small C-shaped midvein, level adaxial surface, and slightly convex abaxial surface of midrib. C2180 #2. Bar = 0.2 mm. **32.** *Punica granatum* L. showing slightly grooved adaxial surface, C-shaped midvein, and rounded, convex abaxial surface. 1810 #1. Bar = 0.1 mm. **33.** *Sonneratia* sp. showing nearly flat adaxial midrib, C-shaped midvein, slightly ridged abaxial midrib, and epidermal mucilage cells. 1892 #2. Bar = 0.3 mm. **34.** *Sonneratia apetala* Buch.-Ham. showing isobilateral leaf with two zones of palisade, oval-shaped midvein with gently sloping midrib. 1926 #4. Bar = 0.3 mm.

round to V-shaped (Table 1). Secondary vein ribs with a trapezoidal abaxial shape also appear to be diagnostic for *D. verticillatus*. *Decodon verticillatus* has a single palisade layer and no extraxylary fibers around its veins, traits common in Lythraceae (Table 1), and the large multicellular hairs are similar to those seen in *Lagerstroemia* (Solereder, 1908; Gin, 1909; Metcalfe and Chalk, 1950). However, the fossil leaves have fibers around veins, a double palisade, and no multicellular trichomes have been observed.

Isolated *Decodon verticillatus* cuticle viewed with SEM has striations, but fresh leaf surfaces with cryo-SEM have no striations. These striations, an artifact of dessication due to the thin and delicate cuticle, may be misinterpreted as cuticle ornamentation in Lythraceae, where true ornamentation also occurs. Kvaček and Sakala (1999) observed striated cuticle from preparations of Miocene *Decodon* from Northern Bohemia. These leaves were borne on axes bearing fruits the striations were used to identify other isolated foliage with similar venation to *Decodon gibbosus* (Reid) Reid in Nitikin. One cannot debate that the leaves attached to fruits with seeds, from

the Miocene of Northern Bohemia, are those of *Decodon*. However, many leaves in order Myrtales tend to have similar venation (Manchester et al., 1998), and cuticle thickness may vary depending on environmental conditions. Therefore, striations alone cannot distinguish *Decodon* from other Myrtales in the fossil record. We have avoided using striations as a taxonomic character, and we suggest that using them to identify and link isolated fossil leaves of Myrtales may prove spurious without further evidence such as anatomy or attachments of leaves to reproductive structures.

The fossil leaves fit well into the general range of characters seen in Myrtales (Keating, 1984) and appear to be most similar to those of Lythraceae. Lythraceae typically have adaxially grooved to convex and abaxially convex/rounded midribs, with C-shaped midveins, rounded to rectangular epidermal cells, and 1–3 palisade layers (typically one or two in a given leaf) (Solereder, 1908; Gin, 1909; Metcalfe and Chalk, 1950; Keating, 1984). Within this family several anatomical features, such as extraxylary fiber distribution, presence of leaf sclereids, and trichomes are diagnostic (Table 1). Enlarged mucilage-filled cells, often in the epidermis, are considered diagnostic for Lythraceae within order Myrtales (Keating, 1984). These have not been observed in the fossil leaves; however, well-preserved epidermis is rare.

The combination of characters seen in the fossils is most similar to *Duabanga grandiflora*, sharing 16 of 22 characters (Table 1). Leaves of *D. grandiflora* and the fossils have the same number of palisade layers, type of midrib and midvein shape, midvein fibers, and the same secondary vein and secondary vein rib shape. Fossil leaves and leaves of *D. grandiflora* have overlapping ranges in midrib shape and in the number of spongy mesophyll layers (Table 1). Variability of observed fossil midrib shapes may be due, in part, to the placement of the section, as the midrib shape may change from the petiole to the apex, and the exact level of sectioning is unknown for the fossil leaves. *Punica protopunica* shares 10 characters and *Duabanga moluccana* shares 13 characters with the fossil leaves. If one includes overlapping ranges of features such as number of mesophyll layers and midrib shape, along with shared qualitative features, such as presence or absence of druses, the fossils share 6–8 characters with most of the extant taxa surveyed here (Table 1).

Fossil leaves and leaves of *Duabanga grandiflora* share a distinctive papillate abaxial epidermis among all the leaves described. These unique papillae were called ''long mamilliform papillae'' by Solereder (1908) and ''mamilliforme'' by Gin (1909). Solereder (1908) stated that this type of epidermis is diagnostic for *Duabanga*. In this study, we observed it only in one species, *D. grandiflora*, but not in *D. moluccana* (Table 1). Abaxial epidermal papillae are also reported in other Myrtales, including species of *Olinia* (Oliniaceae) (Mujica and Cutler, 1974) and in *Crypteronia paniculata* (Crypteroniaceae) (Gin, 1909). However, when present in *Olinia*, they are more irregular and less elongate than in the fossil leaves. *Olinia* leaves further differ from the fossils in having a hypodermis over the veins and at the laminar margins, sclereids in the mesophyll, distinct angular epidermal cells, and thick cuticles (Mujica and Cutler, 1974). *Crypteronia paniculata* abaxial papillae resemble small, uniseriate trichomes with attenuate tips and occur occasionally (Gin, 1909), in contrast to the distinctive ''mamilliform'' papillate abaxial epidermal cells present throughout the lamina of the fossil leaves. This taxon also differs from the fossil in having a circular midvein and regular rectangular epidermal cells (our observation from Myrtales leaf slide collection).

Diffuse mesophyll sclereids are mentioned as characters for Sonneratiaceae (Rao and Das, 1979) (comprised by *Duabanga* and *Sonneratia*). In contrast, we observed diffuse sclereids only in *Sonneratia* in the current study (Table 1).

Types of crystals are taxonomically important for families of Myrtales (Mujica and Cutler, 1974; Keating, 1984). For example, raphides in Myrtales are found only in Onagraceae (Keating, 1982). Druses occur in all lythraceous taxa, but prismatic crystals were restricted to a few taxa (Table 1). Epidermal cells containing birefringent crystals were also observed for certain lythraceous taxa (Table 1). Unfortunately, the silicification that formed the chert, as well as the HF etching in the cellulose acetate peel technique, makes observation of crystals in Princeton chert fossils unlikely.

Trichomes are diverse in Lythraceae and are used to identify and describe taxa (Koehne, 1903). Amarasinghe et al. (1991) systematically surveyed trichome types in the genus *Cuphea* and found them to be valuable taxonomic characters. Although our data does not at first indicate the importance of trichomes (Table 1), certain types of trichomes such as globose multicellular trichomes in *Woodfordia*, *Lourtella*, *Adenaria*, *Koehneria*, *Pehria*, and possibly *Cuphea* are likely a synapomorphy for the clade containing these taxa (Graham et al., 1993; S. A. Graham, Missouri Botanical Garden, personal communication, 2003). Therefore, further systematic studies of leaf and floral indument may yield more taxonomically useful characters, as well as characters for phylogenetic analyses.

The large number of anatomical similarities between the fossil leaves and those of *Duabanga grandiflora*, especially the diagnostic papillate abaxial epidermis, may indicate that a *Duabanga*-like plant was present at the Princeton chert locality during the Middle Eocene. Because extant species of *Duabanga* range from the rainforest region of southeastern Himalaya to New Guinea (Jayaweera, 1967), the presence of these fossil leaves supports the interpretation that Princeton was more tropical in the Middle Eocene (Pigg and Stockey, 1996). If our fossil leaves are *Duabanga* then this is, to our knowledge, the only macrofossil record for the genus. However, we believe that these leaves are those of *Decodon allenbyensis*. This idea is supported by the mutual abundance and close association of these leaves and in situ roots, isolated stems, and fruits of *Decodon* in layer #43 (Little and Stockey, 2003). Because the chert represents a near-shore lacustrine environment (Cevallos-Ferriz et al., 1991), we would expect the leaves to have been deposited parautochthonously and preserved along with the other aboveground organs (Little and Stockey, 2003). If this hypothesis is supported by future work, then *Decodon allenbyensis* possesses a combination of characters not known for any living Lythraceae: it is similar in growth habit and wood, fruit, and seed anatomy to *Decodon*, but has *Duabanga*-like leaves.

The reconstruction of *Decodon allenbyensis* will become increasingly valuable for cladistic analyses. As demonstrated by Huelsenbeck (1991), a fossil taxon, complete in its character set and near the common ancestor, can improve resolution of a phylogeny. This is caused by improved knowledge of ancestral characters, constraining the possible inferred states at internal nodes of the cladogram, thereby reducing the number of most parsimonious trees in phylogenetic analysis. A fully reconstructed 48 million-year-old fossil *Decodon* is clearly closer to the common ancestor of the clade than any living

species, thereby fulfilling both of Huelsenbeck's criteria for when fossils are more valuable than extant taxa in phylogenetic analysis. As not all intrafamilial relationships in Lythraceae are well supported in both morphological and molecular cladistic analyses (Graham et al., 1993; Conti et al., 1997; Shi et al., 2000; Huang and Shi, 2002), the importance of a complete character set for a fully reconstructed and anatomically preserved fossil plant is highlighted. Therefore, the Princeton chert has great value, not only providing in depth knowledge of an ancient biota (Cevallos-Ferriz et al., 1991; Pigg and Stockey, 1996), but also towards elucidating uncertain phylogenetic hypotheses through detailed anatomical character sets, including those from reconstructed fossil plants.

LITERATURE CITED

ALVIN, K. L., AND M. C. BOULTER. 1974. A controlled method of comparative study of taxodiaceous leaf cuticles. *Botanical Journal of the Linnean Society* 69: 277–286.

AMARASINGHE, V., S. A. GRAHAM, AND A. GRAHAM. 1991. Trichome morphology in the genus *Cuphea* (Lythraceae). *Botanical Gazette* 152: 77–90.

BASINGER, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany* 59: 2379–2410.

BASINGER, J. F., AND G. W. ROTHWELL. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany* 55: 1984–1990.

CEVALLOS-FERRIZ, S. R. S., AND R. A. STOCKEY. 1988. Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Lythraceae. *Canadian Journal of Botany* 66: 303–312.

CEVALLOS-FERRIZ, S. R. S., AND R. A. STOCKEY. 1989. Permineralized fruits and seeds from the Princeton Chert (Middle Eocene) of British Columbia—Nymphacaeceae. *Botanical Gazette* 150: 207–217.

CEVALLOS-FERRIZ, S. R. S., R. A. STOCKEY, AND K. B. PIGG. 1991. The Princeton chert: evidence for in situ aquatic plants. *Review of Palaeobotany and Palynology* 70: 173–185.

CHANDLER, M. E. J. 1961. Flora of the Lower Headon Beds of Hampshire and the Isle of Wight. *Bulletin of the British Museum (Natural History) Geology* 5: 93–157.

CONTI, E., A. LITT, AND K. J. SYTSMA. 1996. Circumscription of Myrtales and their relationships to other rosids: evidence from *rbcL* sequence data. *American Journal of Botany* 83: 221–233.

CONTI, E., A. LITT, P. G. WILSON, S. A. GRAHAM, B. G. BRIGGS, L. A. S. JOHNSON, AND K. J. SYTSMA. 1997. Interfamilial relationships in Myrtales: molecular phylogeny and patterns of morphological evolution. *Systematic Botany* 22: 629–647.

CURRAH, R. S., AND R. A. STOCKEY. 1991. A fossil smut fungus from the anthers of an Eocene angiosperm. *Nature* 350: 698–699.

DAHLGREN, R., AND R. F. THORNE. 1984. The order Myrtales: circumscription, variation, and relationships. *Annals of the Missouri Botanical Garden* 71: 633–699.

FRIIS, E. M. 1985. Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark). *Biologiske Skrifter, Det Kongelige Danske Videnskabernes Selskab* 24: 1–165.

GIN, A. 1909. Recherches sur les Lythracées. *Travaux du Laboratoire de Matière Médicale de l'Ecole Superieure de Pharmacie de Paris* 6(3): 1–168.

GRAHAM, S. A. 1964. The genera of Lythraceae in the southeastern United States. *Journal of the Arnold Arboretum* 45: 235–251.

GRAHAM, S. A. 1999. The emerging picture of Lythraceae: cladistic analysis of morphological and cpDNA characters. *XVI International Botanical Congress Abstracts* 250.

GRAHAM, S. A., J. V. CRISCI, AND P. C. HOCH. 1993. Cladistic analysis of the Lythraceae sensu lato based on morphological characters. *Botanical Journal of the Linnean Society* 113: 1–33.

GRAHAM, S. A., AND A. GRAHAM. 1971. The geologic history of the Lythraceae. *Brittonia* 23: 335–346.

GRAHAM, S. A., R. F. THORNE, AND J. L. REVEAL. 1998. Validation of subfamily names in Lythraceae. *Taxon* 47: 435–436.

HILLS, L. V., AND H. BAADSGAARD. 1967. Potassium-argon dating of some lower Tertiary strata in British Columbia. *Canadian Petroleum Geology* 15: 138–149.

HUANG, Y., AND S. SHI. 2002. Phylogenetics of Lythraceae sensu lato: a preliminary analysis based on chloroplast *rbcL* gene, *psaA-ycf3* spacer, and nuclear rDNA internal transcribed spacer (ITS) sequences. *International Journal of Plant Sciences* 163: 215–225.

HUELSENBECK, J. P. 1991. When are fossils better than extant taxa in phylogenetic analysis? *Systematic Zoology* 40: 45–469.

JAYAWEERA, M. A. 1967. The genus *Duabanga*. *Journal of the Arnold Arboretum* 48: 89–100.

JOHANSEN, D. A. 1940. Plant microtechnique. McGraw–Hill, New York, New York, USA.

JOHNSON, L. A. S., AND B. G. BRIGGS. 1984. Myrtales and Myrtaceae a phylogenetic analysis. *Annals of the Missouri Botanical Garden* 71: 700–756.

JOY, K. W., A. J. WILLIS, AND W. S. LACEY. 1956. A rapid cellulose peel technique in paleobotany. *Annals of Botany (London), new series* 20: 635–637.

JUDD, W. S., C. S. CAMPBELL, E. A. KELLOGG, AND P. F. STEVENS. 1999. Plant systematics: a phylogenetic approach. Sinauer, Sunderland, Massachusetts, USA.

KEATING, R. C. 1982. The evolution and systematics of Onagraceae: leaf anatomy. *Annals of the Missouri Botanical Garden* 69: 770–803.

KEATING, R. C. 1984. Leaf histology and its contribution to relationships in the Myrtales. *Annals of the Missouri Botanical Garden* 71: 801–823.

KOEHNE, E. 1903. Lythraceae. *In* A. Engler [ed.], Das Pflanzenreich, Heft 17. IV 216: 1–326. Englemann, Leipzig, Germany.

KVAČEK, Z., AND J. SAKALA. 1999. Twig with attached leaves, fruits and seeds of *Decodon* (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds. *Review of Palaeobotany and Palynology* 107: 201–222.

LITTLE, S. A., AND R. A. STOCKEY. 2003. Vegetative growth of *Decodon allenbyensis* (Lythraceae) from the Middle Eocene Princeton chert with anatomical comparisons to *D. verticillatus*. *International Journal of Plant Sciences* 164: 453–469.

MANCHESTER, S. R., D. L. DILCHER, AND S. L. WING. 1998. Attached leaves and fruits of myrtaceous affinity from the Middle Eocene of Colorado. *Review of Palaeobotany Palynology* 102: 153–163.

METCALFE, C. R., AND L. CHALK. 1950. Anatomy of the Dicotyledons, vols. I and II. Oxford University Press, Oxford, UK.

MUJICA, M. B., AND D. F. CUTLER. 1974. Taxonomic implications of anatomical studies on the Oliniaceae. *Kew Bulletin.* 29: 93–123.

MULLER, J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1–142.

PIGG, K. B., AND R. A. STOCKEY. 1996. The significance of the Princeton chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. *Washington Geology* 24: 32–36.

PIGG, K. B., R. A. STOCKEY, AND S. L. MAXWELL. 1993. *Paleomyrtinaea* a new genus of permineralized myrtaceous fruits and seeds from the Eocene of British Columbia and Paleocene of North Dakota. *Canadian Journal of Botany* 71: 1–9.

RAO, T. A., AND S. DAS. 1979. Leaf sclereids—occurrence and distribution in the angiosperms. *Botaniska Notiser* 132: 319–324.

REID, E. M., AND M. E. J. CHANDLER. 1933. The London Clay flora. British Museum (Natural History), London, UK.

ROBINSON, C. R., AND C. P. PERSON. 1973. A silicified semiaquatic dicotyledon from the Eocene Allenby Formation of British Columbia. *Canadian Journal of Botany* 51: 1373–1377.

RODRÍGUEZ-DE LA ROSA, R. A., S. R. S. CEVALLOS-FERRIZ, AND A. SILVA-PINEDA. 1998. Paleobiological implications of Campanian coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 142: 231–254.

SHI, S., Y. HUANG, F. TAN, X. HE, AND D. E. BOUFFORD. 2000. Phylogenetic analysis of the Sonneratiaceae and its relationship to Lythraceae based on ITS sequences of nrDNA. *Journal of Plant Research* 113: 253–258.

SMITH, S. Y., AND R. A. STOCKEY. 2003. Aroid seeds from the Middle Eocene Princeton chert (*Keratosperma allenbyense*, Araceae): comparisons with extant Lasioideae. *International Journal of Plant Sciences* 164: 239–250.

SOLEREDER, H. 1908. Systematic anatomy of the Dicotyledons, vols. I and II. Clarendon Press, Oxford, UK.

STOCKEY, R. A., AND K. B. PIGG. 1994. Vegetative growth of *Eorhiza arnoldii* Robison and Person from the Middle Eocene Princeton chert lo-

cality of British Columbia. *International Journal of Plant Sciences* 155: 606–616.

STOCKEY, R. A., AND W. C. WEHR. 1996. Flowering plants in and around Eocene lakes of the interior. *In* Rolf Ludvigsen [ed.], Life in stone: a natural history of British Columbia's fossils, 234–247. University of British Columbia Press, Vancouver, British Columbia, Canada.

THORNE, R. F. 1992a. Classification and geography of the flowering plants. *Botanical Review* 58: 225–348.

THORNE, R. F. 1992b. An updated phylogenetic classification of the flowering plants. *Aliso* 13: 365–389.

TIFFNEY, B. H. 1981. Fruits and seeds of the Brandon Lignite, VI. *Microdiptera* (Lythraceae). *Journal of the Arnold Arboretum* 62: 487–513.

WEHR, W. C., AND D. Q. HOPKINS. 1994. The Eocene orchards and gardens of Republic, Washington. *Washington Geology* 22: 27–34.

WOLFE, J. A., AND T. TANAI. 1980. The Miocene Seldovia Point flora of the Kenai Group, Alaska. *United States Geological Survey Professional Paper* 1105: 1–52.

APPENDIX

Index of specimens shown in the plates

Decodon verticillatus (L.) Ell. SL12902 = S.A.Graham 578; Portage Co., Wingfoot Lake, Ohio, USA.

Duabanga grandiflora (Roxb. ex DC) Walpers 2062#1 = C1613 (as *D. sonneratiodes*, a synonym).

Duabanga grandiflora 1859#1 = C1501; B.C.Stone 12837; U. Malaya; Perak, Malaya.

Duabanga moluccana Bl. 1935#4 = C1540; L.Madani; SAN 81066; Sepilok Forest Reserve; Sandakan, Sabah.

Lythrum alatum var lanceolatum (Ell.) Rothrock 1729 #1 = C1300; S.A.Graham 460 (MICH); Rankin Co., Mississippi, USA.

Nesaea longipes A Gray 1727#4 = C1298; B.L.Turner 6163 (TEX) (progeny), Mexico: Coahuila.

Ammannia coccinea Rottb. 2126#1 = C1669; S. Graham 489 (MICH) (progeny); Grayson Co., Texas, USA.

Cuphea spectabilis S. Graham 1726#1 = C1297; J. Reveal, et al. 4339 (MARY); (progeny) Mexico: Guerrero.

Heimia salicifolia (H.B.K.) Link. 1728#2 = C1299; S.A.Graham 141 (MICH); (progeny); Mexico: Jalisco.

Lagerstroemia speciosa (L.) Pers. 1794#2 = C1445; (obtained by P.H.Raven; cult FTG (Fairchild Tropical Garden), 57–119).

Lafoensia speciosa (H.B.K.) DC 1784#1 = C1433; (obtained by P.H.Raven; cult FTG, X-5–20).

Lawsonia inermis L. 1808#2 = C1461; P.H.Raven 26570; cult MO 751624–4; seed progeny; Hong Kong herbarium.

Punica protopunica Balf. f. C2180#2; P. Rudall, Jodrell Laboratory, cult K [also described as genus *Socotrea*, the second genus of Punicaceae, endemic to Socotra].

Punica granatum L. 1810#1 = C1463; P.H.Raven 26569; cult MO, source unknown.

Sonneratia sp. 1892#2 = C1563; B.C.Stone & E.F.Anderson BCS13165; = SAN86792; Sabah, Malaya.

Sonneratia apetala Buch.-Ham. 1926#4 = C1530; Thanikaimoni, s.n. 15mar77; Pichaveram mangrove; Pondicherry, India.