

## EARLY EOCENE MACROFLORA FROM THE RED HOT TRUCK STOP LOCALITY (MERIDIAN, MISSISSIPPI, USA)

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### ABSTRACT

The U.S. Gulf Coast has an extensive but poorly dated paleobotanical record. A fossil locality behind the former Red Hot Truck Stop in Meridian, Mississippi, is well-known for its unusually rich biota of late Paleocene and early Eocene mammals, fish, snakes, mollusks, and plants. The latter include palynomorphs, fruits, and leaves, which are found in the basal Bashi Formation and are studied here for the first time. Though generally not well-preserved, the Red Hot leaf flora is significant because it is reliably dated to the first ~1.6 million years of the Eocene and possibly lies within the Paleocene-Eocene Thermal Maximum; in contrast, nearly all other Eocene Gulf Coast macrofloras are middle Eocene or uncertain in age.

We recognize 18 leaf species and morphotypes, including *Lygodium kaulfussi* (a climbing fern), and representatives of Lauraceae (laurel family), Myrtaceae (guava family), Fabaceae (legumes), *Platycarya* (Juglandaceae, walnut family), *Rhus* (Anacardiaceae, sumac family), and a new genus and species of Ochnaceae (ochna family), all consistent with a tropical to subtropical climate. Additionally, two dispersed cuticle morphotypes are described that probably represent a monocot and a liverwort. The occurrence of *Platycarya* is the first macrofossil record of this Eocene index taxon from the eastern USA and corroborates pollen occurrences from the same strata. The Ochnaceae specimens are currently the only reliable leaf fossils of this distinctly tropical group with ~30 genera and ~500 species today; due to their significance, we assign them to a new taxon, *Rhabdophyllites diapyros* gen. et sp. nov. Most of the recognizable plant taxa are present at, or near, this time in the well-dated sequences of the Rocky Mountain region, indicating their wide North American distribution. The Red Hot

flora shows the potential to build a well-dated record of Paleogene floras on the Gulf Coast, improving understanding of plant migration and evolution.

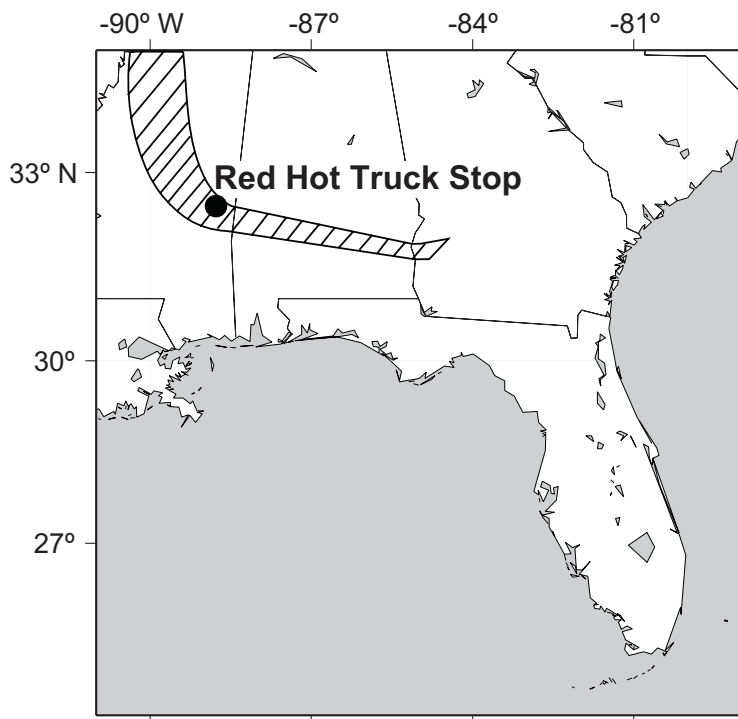
**KEY WORDS:** Bashi Formation; Gulf Coast; new species; Ochnaceae; *Rhabdophyllum*; *Rhabdophyllites diapyros*; *Platycarya*; cuticle; Wasatchian; Eocene; PETM

## INTRODUCTION

Numerous Eocene macrofloras from the North American Gulf Coast, found in strata known historically as the Wilcox and Claiborne Groups, have produced a classic suite of botanical discoveries (e.g., Berry 1914, 1916, 1923, 1924, 1930, 1937; Dilcher 1963, 1969, 1973a, 1973b; Dilcher and McQuade 1967; Dilcher and Mehrotra 1969; Dilcher and Dolph 1970; Dilcher et al. 1976; Dilcher and Daghlian 1977; Crepet et al. 1974, 1975; Crepet and Dilcher 1977; Roth and Dilcher 1979; Jones and Dilcher 1980; Kovach and Dilcher 1984; Dilcher and Manchester 1986, 1988; Grote and Dilcher 1989, 1992; Herendeen and Dilcher 1990a, 1990b, 1990c; Call and Dilcher 1992, 1995; Herendeen 1992; Dilcher and Lott 2005). These studies have provided fundamental information about the origins and early diversity of living and extinct

plant groups, as well as Eocene paleoclimates of the Gulf Coast. However, the floras mostly come from stratigraphically isolated and poorly dated clay pits (e.g., Dilcher 1973a; Dilcher and Lott 2005), and thus the considerable record cannot be well placed into a chronological framework. Little progress has been made since Berry's investigations to correlate megafloral deposits, although Wolfe and Dilcher (2000) made preliminary efforts in Texas. The Claiborne floras, the target of nearly all systematic investigations, are now considered middle Eocene (Dilcher 1973a; Dilcher and Lott 2005).

A highly fossiliferous Wilcox section from Meridian, Mississippi, known as the Red Hot Truck Stop locality (Figure 1) after a former business nearby, is unusually well constrained stratigraphically. The Red Hot Truck Stop section contains the



**Figure 1.** Location of the Red Hot Truck Stop fossil site. The crosshatched area approximates surface exposure of late Paleocene and early Eocene strata. Redrawn from Harrington (2003a).

latest Paleocene and earliest Eocene upper Tuscaloosa Formation and the early Eocene Bashi and Hatchetigbee Formations, dated locally from mammals, pollen, dinoflagellates, and sequence stratigraphy, and from calcareous nannoplankton and foraminifera in correlative deposits elsewhere (Siesser 1983; Beard and Tabrum 1991; Ingram 1991; Gibson and Bybell 1994; Frederiksen 1998; Beard and Dawson 2001; Harrington 2003a). The Red Hot Truck Stop locality is particularly notable for being the only site east of the Rocky Mountain region that contains an extensive and diverse suite of Wasatchian mammals. The Red Hot local fauna, first discovered by G.R. Case in 1979 (see Beard and Dawson 2001) now includes 11 mammalian orders and more than 24 species to date, primarily from the uppermost Tuscaloosa Formation (Beard and Tabrum 1991; Beard and Dawson 2001; Dawson and Beard 2007). Among these are marsupials, primates, rodents, condylarths, perissodactyls, artiodactyls, pantolestids, pantodonts, and carnivores (Beard and Dawson 2001; Dawson and Beard 2007). The Tuscaloosa Formation at the Red Hot Truck Stop locality also contains more than 30 fossil species of bony and cartilaginous fish as well as remains of snakes, birds, lizards, and crocodylians (Case 1986, 1994a, 1994b; Holman et al. 1991; Ingram 1991; Holman and Case 1992; Beard and Dawson 2001), and the Bashi Formation contains mammals, bivalves, gastropods, and trace fossils (Beard and Tabrum 1991; Ingram 1991).

Call et al. (1993) described a macrofloral assemblage from the Bashi Formation at the Red Hot Truck Stop locality with degraded wood, fern rhizomes (also found in the uppermost Tuscaloosa), and angiosperm fruits permineralized in pyrite. These authors interpreted the fruits of *Wetherellia* (an extinct genus of unknown affinity) as water-dispersed from mangrove or other warm coastal habitats. Harrington (2003a; see also Harrington and Kemp 2001; Harrington 2001, 2003b; Harrington and Jaramillo 2007; Harrington et al. 2004) found 113 palynomorphs from the Tuscaloosa and Bashi formations at the Red Hot Truck Stop locality, some representing characteristically thermophilic families such as Annonaceae, Arecaceae, Burseraceae, Fabaceae, and Sapindaceae. Ingram (1991) first noted the presence of compression/impression fossil leaves in the lower Bashi Formation, which are described here for the first time from a new collection. Although the here-designated Red Hot leaf flora is generally not well-preserved, it holds importance as the only Gulf

Coast macroflora to date that can be placed confidently in the very early Eocene, less than ~1.6 m.y. after, or possibly within, the Paleocene-Eocene Thermal Maximum (PETM), as discussed below.

The onset of the PETM at 55.8 Ma coincides with the Paleocene-Eocene boundary and the base of the Wasatchian North American land-mammal age (Gradstein et al., 2004). The PETM and the broader late Paleocene-early Eocene time interval are well-known for both rapid and long-term warming events that affected organisms in marine and terrestrial environments (e.g., Gingerich 1989, 2006; Kennett and Stott 1991; Koch et al. 1992; Wing 1998; Wilf 2000; Zachos et al. 2001; Gibbs et al. 2006). However, previous studies have not yielded much stratigraphically controlled information about early Eocene vegetation in subtropical latitudes. The early Eocene age of the Red Hot leaf flora allows comparisons to the more heavily studied, coeval Western Interior floras. Most of the well-dated early and middle Eocene floras from North America were collected at middle to high latitudes in the Rocky Mountain region and the Pacific Northwest (e.g., Wing 1987; Wolfe and Wehr 1987; Manchester 1994; Wolfe et al. 1998). The highest temporal resolution for early Eocene floras comes from the densely sampled Bighorn and greater Green River basins of northwestern and southwestern Wyoming, respectively (Wing 1998; Wilf 2000; Wing et al. 2000, 2005; Wing and Harrington 2001). The Bighorn Basin holds the only well-constrained PETM macrofloras (Wing et al. 2005; Wing and Lovelock 2007).

In this paper, we describe 18 leaf morphotypes and two dispersed cuticle morphotypes from the Red Hot leaf flora, provide identifications when possible, and make comparisons to floras of equivalent age from the better understood Rocky Mountain region.

## GEOLOGIC SETTING AND AGE

The Red Hot Truck Stop section exposes the latest Paleocene and earliest Eocene upper Tuscaloosa, and the early Eocene Bashi and Hatchetigbee formations; detailed stratigraphic sections were published previously (Ingram 1991; Harrington 2003a). The T4 sand unit of the uppermost Tuscaloosa contains a vertebrate lag deposit with one of only two Wasatchian mammal faunas from the eastern USA (Beard and Dawson 2001; Dawson and Beard 2007; the other is less extensive and is from Virginia: Rose 1999). The Tuscaloosa-Bashi contact is marked by a regional unconformity extending from western Alabama through eastern-

most Mississippi. The Bashi Formation locally has both a lower lowstand unit and an upper transgressive marine unit; the lowstand deposits, only known from the Red Hot Truck Stop section, are considered the oldest Bashi deposits on the Gulf Coast (Ingram 1991). The lowstand unit, 3 m thick, is composed of interbedded, white, fine to medium sands and brown to gray shales, containing the plant fossils in this study within the lower half of the unit. The transgressive marine unit of sand and glauconite, about 1.2 m thick, is unconformable upon the lowstand unit and contains a fossiliferous boulder layer that is easily recognized in outcrop to western Alabama (Ingram 1991). Abundant *Ophiomorpha* burrows extend downwards into the lowstand unit. The Bashi sediments are interpreted as remains of a range of coastal environments from near-shore marine to tidal channels and estuaries (Ingram 1991), the latter two being the most probable paleoenvironments for the leaf fossils due to small grain size and relatively dark color indicating organic content.

An unusual wealth of evidence constrains the Red Hot leaf flora to the early part of the early Eocene. Significantly, the mammalian fauna from the T4 sand immediately underlying the Red Hot leaf flora, contains species restricted to earliest Wasatchian zone Wa0 (Gingerich 1989) in the Bighorn Basin of Wyoming (Beard and Dawson 2001). Zone Wa0 coincides with the PETM and associated carbon isotope excursion in Wyoming (e.g., Koch et al. 1992; Gingerich 2006), and ongoing work confirms an earliest Wasatchian age for the Red Hot local fauna (K.C. Beard, personal commun. 2007). The T4 sand locally contains a dinoflagellate assemblage that correlates to calcareous nannoplankton zone NP9 (discussed in Beard and Dawson 2001), which straddles the PETM (e.g., Gradstein et al. 2004).

Additional local chronostratigraphic data come from diagnostic early Eocene pollen, of *Platycarya* (Juglandaceae, genus currently endemic to East Asia) from the leaf-bearing layers of the basal Bashi at the Red Hot Truck Stop locality (Frederiksen 1998; Harrington 2003a), and from an omomyid primate, found in the Bashi above the leaf remains, that further constrains the flora to the Wasatchian (Beard and Tabrum 1991).

The marine portion of the Bashi Formation, overlying the lowstand unit that bears the flora, has not produced calcareous nannoplankton locally, but these have been recovered from Bashi sections in Alabama that represent the same transgression. Siesser (1983) reported *Discoaster*

*mohleri* from the type Bashi section in Clarke County, Alabama, whose last appearance is within NP9. However, Gibson and Bybell (1994) reported *Tribrachiatos bramletti* from the marine Bashi in Coffee County, Alabama, an indicator species for the lower half of NP10, and they disputed Siesser's identification of *D. mohleri*. Also in the Bashi of Alabama, foraminifera occur that are assigned to foraminiferal zone P6b (Oliver and Mancini 1980; Mancini 1981), which is consistent with NP10 but not with NP9 (e.g., Gradstein 2004).

One line of evidence suggests that the flora is basal Eocene in age, within the PETM. As discussed by Beard and Dawson (2001), Ingram's (1991) sequence stratigraphic assignment of the Bashi lowstand unit (lowstand systems tract of sequence TE1.1) is the same that Steurbaut (1998) assigned to the Belgian Tienen Formation strata that contain the well-studied, basal Eocene Dormaal fauna and which also contain the base of the carbon isotope excursion marking the onset of the PETM (Smith et al. 2006).

In summary, the maximum age of the Red Hot leaf flora is set by the underlying mammal fauna as earliest Eocene, or 55.8 Ma, and the minimum age is constrained by nannoplankton from the younger, marine Bashi that represent the first half of zone NP10, or 54.2 to 54.8 Ma (ages from Gradstein et al. 2004). If the sequence stratigraphic correlation discussed by Beard and Dawson (2001) is correct, the Red Hot leaf flora belongs to the early phase of the PETM.

## METHODS

Compressed plant fossils were collected by PW, accompanying a Carnegie Museum of Natural History vertebrate paleontological expedition led by K.C. Beard in November 2000. Approximately 113 specimens were collected from two sites within the Bashi lowstand unit, field numbers PW0001 and PW0002. These are designated as USNM (National Museum of Natural History, where all specimens are deposited in the Division of Paleobotany) localities 43409 and 41312, respectively, and referred hereafter as "site 1" and "site 2" for simplicity. Site 1 (N32.35643°, W88.68343°, GPS ±4 m, NAD27 CONUS datum), within a temporary outcrop excavated for a bridge support pylon related to the construction of a Wal-Mart, produced 58 specimens. The lithology at site 1 is fine-medium, burrowed white sands; leaf fossils with relatively good preservation of venation detail occur in interbedded shale and siltstone units. These specimens were more prone to desiccation



and fragmentation than at nearby site 2 (N32.35600°, W88.68430°). This locality produced 55 specimens immediately above the T4 sand, from "overburden" generated by vertebrate collecting in that unit. At site 2, the lithology was finer grained (clay rich) and darker (more organic material); the plant specimens were less fragmented than those from site 1, but fine venation details were generally not preserved (i.e., the opposite attributes to site 1).

At both sites, the fossiliferous matrix was extremely friable and moist. To prevent immediate desiccation cracking after exposure to air, fossil plant specimens were brushed lightly with a 1:1:1 solution of ethanol, glycerin, and water (after Call et al. 1993). Specimens were then immediately wrapped in paper, labeled, wrapped again in aluminum foil, and allowed to dry slowly in storage. Unwrapping of specimens occurred in June 2005. Some damage occurred as expected, but the procedure conserved the majority of specimens.

Plant remains were prepared using air scribes; detailed preparation was done using fine-tipped, hand-held carbide rods. Fine-haired paint brushes and compressed air were used to remove debris from leaf surfaces. Prepared leaves were examined under a Nikon SMZ-1500 stereomicroscope. Up to fifth order venation was preserved, but vein detail was often absent due to coalification or poor preservation. Photographs (excepting most cuticle images, see below) were taken using a Nikon Coolpix 8800 digital camera (Nikon, Melville, New York, USA) and a Nikon DXM-1200F camera mounted on the stereomicroscope.

Cuticle, where present, was first examined on the stereomicroscope with normal light and using an X-Cite 120 epifluorescence illumination unit (EXFO Electro-Optical Engineering Inc., Quebec, Quebec, Canada). Unprepared, uncoated cuticle was observed using an FEI Quanta 2000 ESEM. Cuticle was further examined by directly mounting unprepared cuticle with Cytoseal 60 mounting medium (Richard-Allan Scientific, Kalamazoo, Michigan, USA) for microscopic observation. An Olympus BX61 Epi-Fluorescence Microscope, and an Olympus FV1000 Laser Scanning Confocal Microscope (Olympus America Inc., Melville, New York, USA) were used for digital microscopy and fluorescence imaging of cuticle. The confocal excitation wavelength was 633 nm, and the emitted wavelength captured for the images was 647 nm. Microscopy images were deconvolved, and image stacks were merged using Autoquant 9.3 (Media Cybernetics, Bethesda, Maryland, USA). All

images were further processed and composed using Adobe Photoshop (Adobe Systems Incorporated, Seattle, Washington, USA).

Fossil plants were organized into 18 full-leaf morphotypes (RH- prefix), based on shared suites of venation and leaf form characteristics sufficient to distinguish them (Ash et al. 1999), and two distinct cuticle morphotypes, all described below. Exemplary specimens of each morphotype are illustrated and assigned USNM repository numbers. The quantity is noted of any additionally referred, deposited specimens that are not illustrated or individually catalogued. Some morphotypes were assignable to taxonomic groups, and one of these merited full typification as a new taxon. Otherwise, we did not develop new nomenclature or formally designate type specimens because the preservation quality was not sufficient to make comparisons to pre-existing type collections. Margin preservation and number of morphotypes were not adequate for paleoclimate estimation from leaf physiognomy (e.g., Wilf 2000). Descriptions below begin with the distinguishing features that best delineate the morphotype within the assemblage. Classifications of angiosperms follow the Angiosperm Phylogeny Working Group (2003).

## THE RED HOT LEAF FLORA

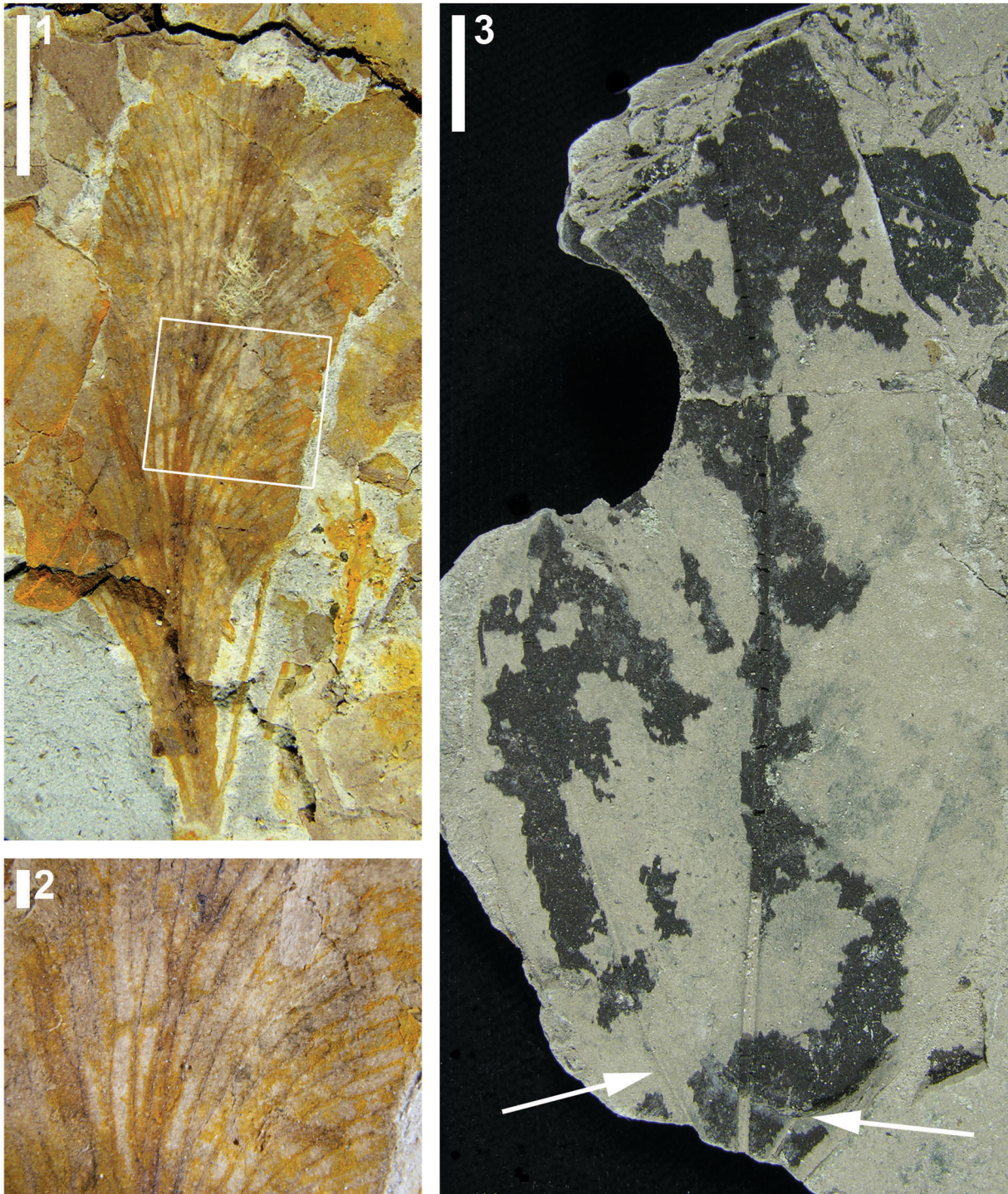
### Ferns

Order SCHIZAEALES Frank, 1877  
Family LYGODIACEAE Roemer, 1840  
Genus *LYGODIUM* Swartz, 1801  
*Lygodium kaulfussi* Heer, 1861

**Specimen.** USNM 535047 (Figure 2.1, 2.2; site 1). Morphotype RH06.

**Distinguishing features and description.** Width mostly uniform. Numerous, closely spaced secondary veins strongly decurrent on primary vein, diverging at low angles and dichotomizing multiple times. A lobe fragment with preserved length 3.8 cm, preserved width 1.6 cm.

**Comments.** The specimen clearly matches the distinctive venation of *Lygodium* (Manchester and Zavada, 1987). *Lygodium* leaves are typically digitate-lobed, and this specimen is most likely a fragment of a single lobe. Berry (1914, 1916, 1924, 1930) reported several *Lygodium* species from various localities of the Gulf Coast Eocene, including *L. kaulfussi* which was widespread in the Eocene of North America, Europe, and Asia (Manchester and Zavada 1987). Manchester and Zavada (1987)



**Figure 2.** (1, 2) Leaf fragment of *Lygodium kaulfussi*, USNM 535047, showing low-angle, dichotomizing venation from primary vein of presumed lobe. (1) Whole specimen; scale bar equals 1 cm. (2) Venation close-up along right margin corresponding to inset box in (1); scale bar equals 1 mm. (3) Leaf of Lauraceae, USNM 535048. Arrows indicate acute basal secondary veins. Scale bar equals 1 cm.



concluded that all of Berry's species are indistinguishable from *L. kauffussi*, which they considered the sole recognizable species of *Lygodium* in the Northern Hemisphere Eocene. The *Lygodium* considered here is also not distinguishable from *L. kauffussi* and is accordingly placed in that species. Harrington (2003a) reported two schizaeaceous spore types from the Red Hot Truck Stop locality that could have been produced by *Lygodium*.

### Angiosperms

Order LAURALES Perleb, 1826  
Family LAURACEAE Durande, 1782  
Genus *incertae sedis*

**Specimen.** USNM 535048 (Figure 2.3; site 2). Morphotype RH12.

**Distinguishing features.** Entire margin, acute basal pair of secondaries, and opposite percurrent tertiary veins that are approximately perpendicular to the primary vein.

**Description.** Lamina elliptic, symmetrical, preserved length 8.3 cm, preserved width 4 cm; estimated l:w ratio 2.25:1; base convex, base angle acute, apex straight, apex angle acute; margin entire. Venation pinnate, primary vein straight. Secondary veins eucamptodromous, straight to slightly curved, angle from midvein 28°–65°, basal pair strongly acute, spacing irregular. Tertiary veins opposite percurrent, approximately perpendicular to the primary vein, or random reticulate. Fourth order veins random reticulate (photograph poorly).

**Comments.** The combination of entire margin, acute basal secondaries, and tertiary veins oriented perpendicular to the midvein is widely prevalent among Lauraceae, to which we tentatively assign this single, poorly preserved fossil.

MONOCOTYLEDONS de Candolle, 1819  
*Incertae sedis*, morphotype RH03

**Specimens.** USNM 535050 (Figure 3.1; site 2). Morphotype RH03.

**Distinguishing features and description.** Two orders of parallel venation (*A* and *B* veins) with straight, curved, or sigmoidal oblique cross veins intersecting the parallel veins, both *A* and *B*. There are approximately 2–3 *B* veins between each pair of *A* veins. The cross veins run obliquely to the *A* and *B* veins and can be straight, curved, or sigmoidal.

**Comments.** The parallel venation pattern and sigmoidal, oblique cross veins are characteristic of several monocot groups. Due to the lack of preser-

vation details in these fragmented compression fossils, lower order taxonomic assignments cannot be made.

Order MYRTALES Reichenbach, 1828  
Family MYRTACEAE Adanson, 1763  
Genus *incertae sedis*

**Specimens.** USNM 535051 (Figure 3.2, 3.3; site 1). Additional deposited specimens: four from site 1 and one from site 2. Morphotype RH02.

**Distinguishing features.** Numerous thin, decurrent secondaries and intersecondaries that join a prominent intramarginal vein, and an entire margin. This distinctive architecture can be found in many genera of Myrtaceae (Carr et al. 1986).

**Description.** Lamina oblong, symmetrical, narrow; preserved l:w ratio (l:w) ~5:1; precise l:w unknown; preserved length 4.7–7.0 cm, estimated to 8 cm; width 1.3–2.0 cm; base angle acute, apex not preserved; margin entire, fimbrial vein present. Venation pinnate; primary vein straight, thick basally. Secondary veins numerous (6–9 per cm), irregularly spaced, arising decurrently from primary vein at consistent 65° angles curving near intramarginal vein. Intersecondary veins strong, ~1 intersecondary per secondary with most intersecondaries reaching the intramarginal vein. Tertiaries not visible.

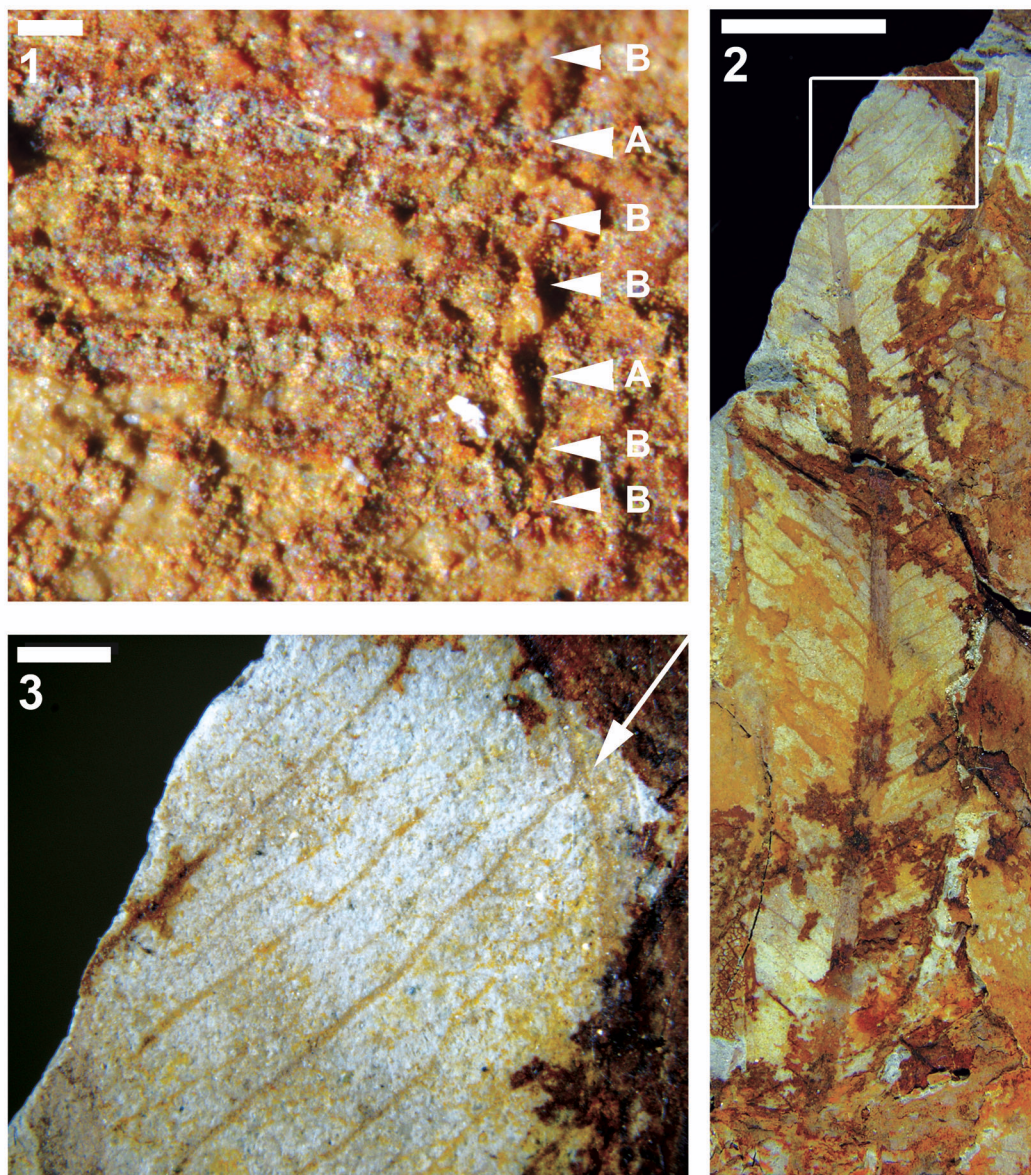
**Comments.** Berry (e.g., Berry 1930) assigned various Eocene Gulf Coast leaves to myrtaceous genera such as *Calyptanthes* Swartz (1788), *Eugenia* Linnaeus (1753), and *Myrcia* de Candolle (1827), although these assignments are doubtful at the generic level (Manchester et al. 1998) and have never been revised. More recently, Dilcher and Lott (2005) tentatively assigned myrtaceous leaves from the middle Eocene Powers Clay Pit to *Myrcia*.

Order FABALES Bromhead, 1838  
Family FABACEAE Lindley, 1836a  
Genus *incertae sedis*

**Specimens.** USNM 535052 (Figure 4; site 1). Additional deposited specimens: 24 from site 1. Morphotype RH07.

**Distinguishing features.** Conspicuously pulvinate, marginally inserted petiolule; entire margin. Secondary veins diverge at low angle, extend distally without branching.

**Description.** Lamina ovate to elliptical, symmetrical, usually narrow (preserved l:w 2:1 to 4:1; estimated l:w ~3:1; preserved length 1.0–4.5 cm, estimated 1.4–6 cm; width 0.7 cm to estimated 2.0

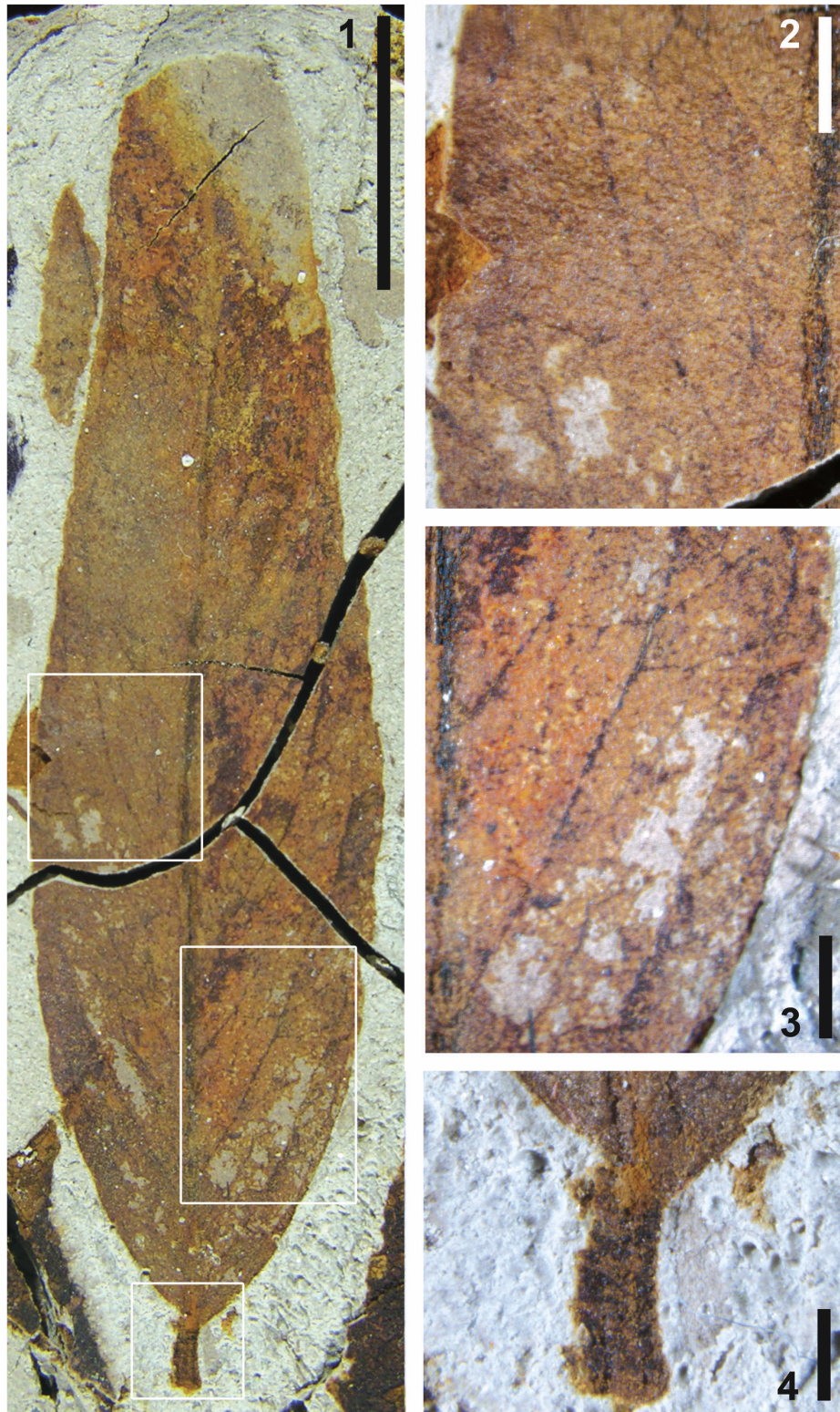


**Figure 3.** (1) Leaf morphotype RH3 (monocot fragment), USNM 535050. Close-up, showing large A veins (off-white in photo). Between each set of A veins are 1 to 2 smaller-width B veins. Sigmoidal, oblique cross veins are visible between the A-B veins. Scale bar equals 0.2 mm. (2) Leaf of Myrtaceae, USNM 535051. Scale bar equals 1 cm. (3) Close-up corresponding to inset box in (2). Arrow indicates the prominent intramarginal vein receiving numerous fine secondaries and intersecondaries. Scale bar equals 1 mm.

cm), base convex, base angle acute; apex generally straight, apex angle acute; margin entire, fimbrial vein present. Petiolule pulvinulate. Venation pinnate, primary vein straight. Secondary veins weak brochidodromous to eucamptodromous, extending distally, straight to slightly curved; ~3-4 secondaries/cm, arising from the midvein ~25°, spacing irregular, vein angles gradually decreasing and becoming more uniformly spaced proximally. Secondary veins closely spaced near the margin,

becoming nearly parallel with margin, then joining superjacent secondary or diminishing. Intersecondaries weak to strong, not consistently present between each pair of secondaries. Tertiary veins opposite percurrent, perpendicular to the midvein between the closely spaced secondary veins near margin. Fourth order veins random reticulate; fifth order veins random reticulate to regular polygonal reticulate; freely ending veinlets (FEVs) unbranched.





**Figure 4.** Fabaceae, USNM 535052. (1) Whole specimen. The specimen has an entire margin with a fimbrial vein; the apparent incisions that resemble teeth are from breaks in the margin and areas where the margin was not completely prepared due to the delicacy of the specimen. Scale bar equals 1 cm, with insets for close-ups of (2) and (3) secondary and tertiary venation, scale bar equals 1 mm, and (4) the pulvinulate petiolule, scale bar equals 1 mm.

**Comments.** Legumes have been recognized in the Gulf Coast floras since Berry's time, and middle Eocene representatives have been extensively revised (Herendeen and Dilcher, 1990a, 1990b, 1990c; Herendeen, 1992). This morphotype is similar to *Ormosia* sp. reported by Herendeen (1992). Harrington (2003a) reported two pollen types from the Red Hot Truck Stop locality assignable to Fabaceae or Sapotaceae Durande (1782).

Order FAGALES Engler 1898

Family JUGLANDACEAE de Candolle, ex Perleb  
1818

Genus *PLATYCARYA* de Siebold et Zuccarini 1843  
*Platycarya* sp.

**Specimen.** USNM 535053 (Figure 5; site 2). Morphotype RH13.

**Distinguishing features.** Base acute; margin irregularly serrate, tooth apices rounded, tooth apices weakly glandular. Secondary divergence angle ~65°; secondaries curve steeply distally near margin; intersecondaries weakly developed. Tertiary veins percurrent, sinuous, junctions with subjacent secondaries perpendicular to obtuse.

**Description.** Lamina elliptic to ovate, symmetrical, narrow (preserved and estimated l:w ~3:1; preserved length 9.3 cm, estimated 12 cm; preserved width 3.6 cm, estimated 4 cm). Base angle acute, base shape unknown; apex angle and shape unknown; margin serrate, fimbrial vein present. Venation pinnate, primary vein straight. Secondary veins craspedodromous, straight near midvein, then steeply curving near the margin, 10–12 pairs, angle 60–75°, spacing irregular, angles smoothly decreasing proximally. Intersecondary veins weak; agrophic veins absent. Tertiary veins opposite percurrent, straight to sinuous; angle to primary obtuse, decreasing exmedially, junctions with subjacent secondaries perpendicular to obtuse. Fourth order veins random reticulate. Teeth small and in one order, weakly glandular, sinuses rounded, spacing irregular, about three teeth per centimeter.

**Comments.** The venation of the single specimen is preserved only as faint impressions in the matrix and photographs poorly (Figure 5); nevertheless, it is surprisingly complete. In particular, the opposite percurrent, straight to sinuous tertiaries and their perpendicular to obtuse junctions with subjacent secondaries are clearly but faintly visible (Figure 5.2, 5.3). Despite the preservation, this fossil demonstrates the defining characteristics of *Platycarya* foliage (Wing and Hickey 1984; extant *Platycarya* may have simple or compound leaves depending

on species). Pollen of this genus is also found in the same sediments (Frederiksen 1998; Harrington, 2003a). The specimen corresponds best to the Eocene Western Interior taxa *P. americana* (Hickey 1977) and *P. castaneopsis* (Lesquereux) Wing and Hickey (1984), whose leaves have many differences with living *Platycarya* but whose fruits and seeds are generically diagnostic (Wing and Hickey 1984). Due to preservation, one character found in *Platycarya* leaves, the ascending vein from sinus to superjacent tooth (Wing and Hickey 1984), was not observed.

Order MALPIGHIALES von Martius, 1835

Family OCHNACEAE de Candolle, 1811a  
*Rhabdophyllites* gen. nov.

**Description.** This morphogenus is erected for leaves having certain characteristics found in the extant genus *Rhabdophyllum* van Tieghem (1902a). The diagnostic characters of *Rhabdophyllites*, in combination, are: a toothed margin; closely spaced, thin, and numerous secondary veins of the “*Clusia*” type discussed by Gentry (1993) and Keller (2004); and distinct intersecondary veins.

**Discussion.** This morphogenus is assigned to Ochnaceae, which is the sole extant family having the distinctive combination of toothed margin and “*Clusia*” venation. The morphogenus designation and *-ites* suffix (Greek, “having the nature of”: Brown 1956) conservatively allow placement in the family and highlight the general similarity to extant *Rhabdophyllum* (tropical Africa) without categorization to any extant genus.

**Type species.** *Rhabdophyllites diapyros*

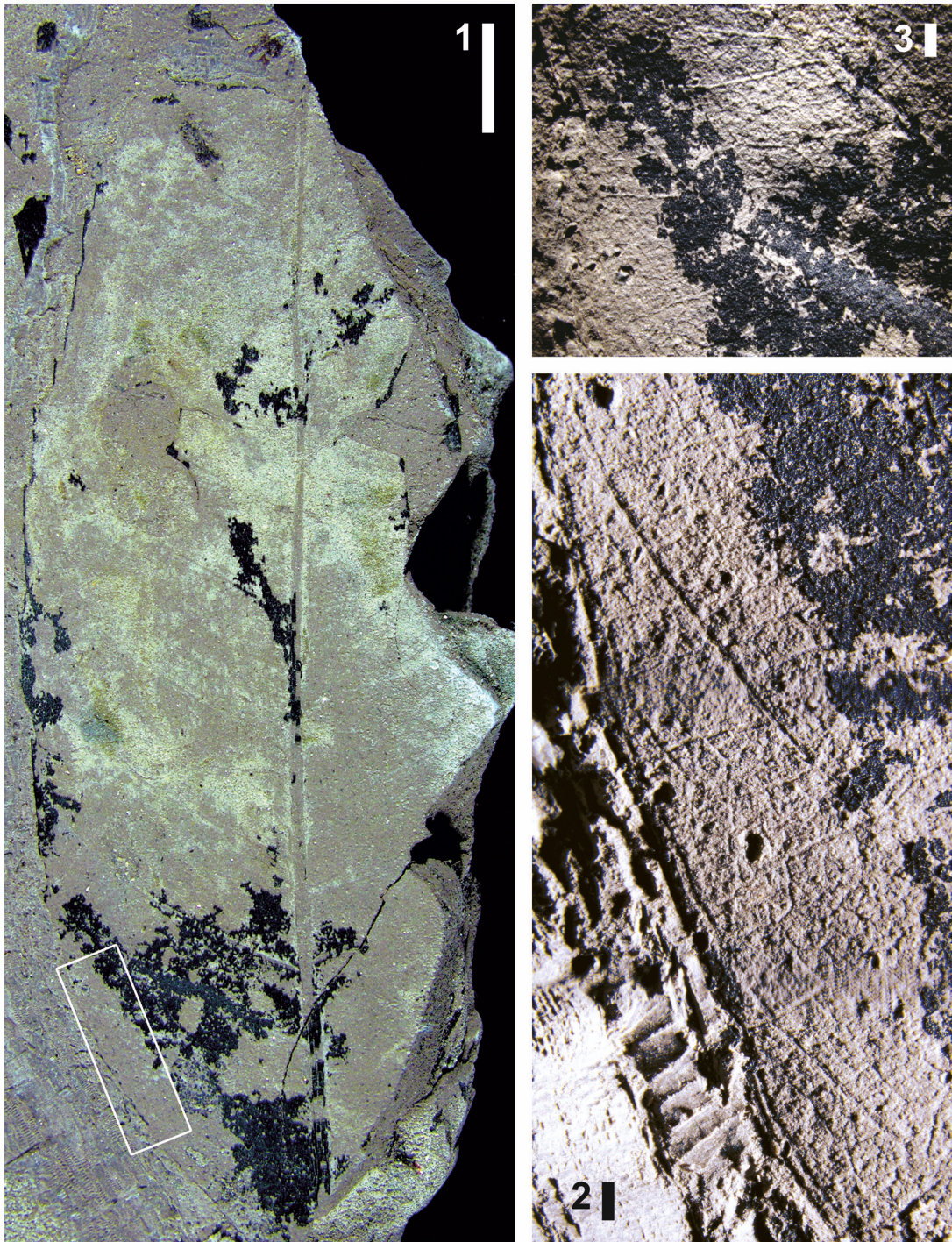
*Rhabdophyllites diapyros* sp. nov.

**Type material and illustration.** Holotype: USNM 535054 (Figure 6), USNM loc. 43409 (= site 1). Paratypes: USNM 535055 (Figure 7.1–3), USNM loc. 43409 (= site 1) and USNM 535056 (Figure 7.4, 7.5), USNM loc. 41312 (= site 2). [Morphotype RH01]

**Etymology.** Greek, “red-hot, fiery” (Brown 1956). Named in memory of the Red Hot Truck Stop, a popular local landmark, 1955–2000.

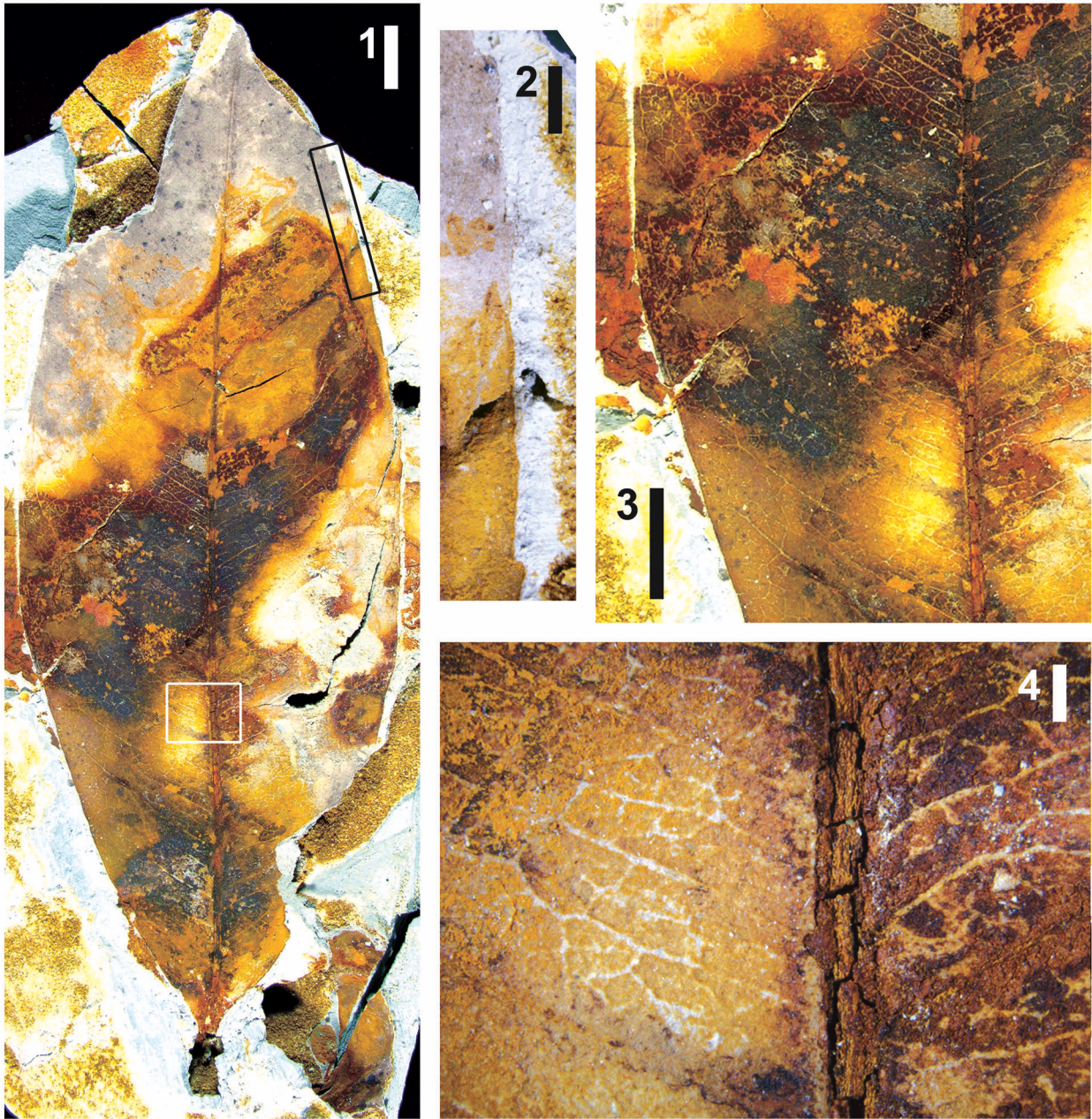
**Distinguishing features.** Elliptic leaf with single primary vein. Secondary veins numerous, thin, closely spaced (3–8 mm apart along primary), eucamptodromous; intersecondary veins well developed, closely spaced (2–3 mm apart along primary), but both secondaries and intersecondaries vary and intergrade in distance covered from mid-





**Figure 5.** *Platycarya* sp., USNM 535053. **(1)** Complete specimen, showing course of secondary veins, turning distally near margin, and small, irregularly spaced teeth. Scale bar equals 1 cm. Note two large, circular insect-feeding holes distal to middle left of blade. Inset for **(2)** detail of margin near base of blade, showing opposite percurrent, straight to sinuous tertiary veins joining subjacent secondaries mostly at perpendicular angles, and some quaternary veins. Scale bar equals 0.5 mm. The small blurry areas result from stitching of this composite image; dark areas are coal remnants not removed, to avoid damage. **(3)** Detail taken immediately distal to **(2)** along left margin of blade, showing secondaries (ascending and curving towards upper left) and opposite percurrent, straight to sinuous tertiary veins. Scale bar equals 1 mm. Dark areas are coal remnants not removed, to avoid damage.





**Figure 6.** *Rhabdophyllites diapyros*, holotype, USNM 535054. **(1)** Complete specimen, showing closely spaced, thin, numerous secondaries and intersecondaries ("*Clusia*" venation) and small teeth developed towards apex. Scale bar equals 1 cm (petiole not recovered, apparent petiolar area is a hole in the thin matrix), with insets from top to bottom for **(2)** detail of apical margin with small teeth. Scale bar equals 1 mm, **(3)** close-up of left margin showing secondary, intersecondary, and tertiary venation. Scale bar equals 1 cm, and **(4)** detail of venation diverging from midvein, showing closely spaced secondary and intersecondary veins as well as reticulate tertiary veins. Scale bar equals 1 mm.



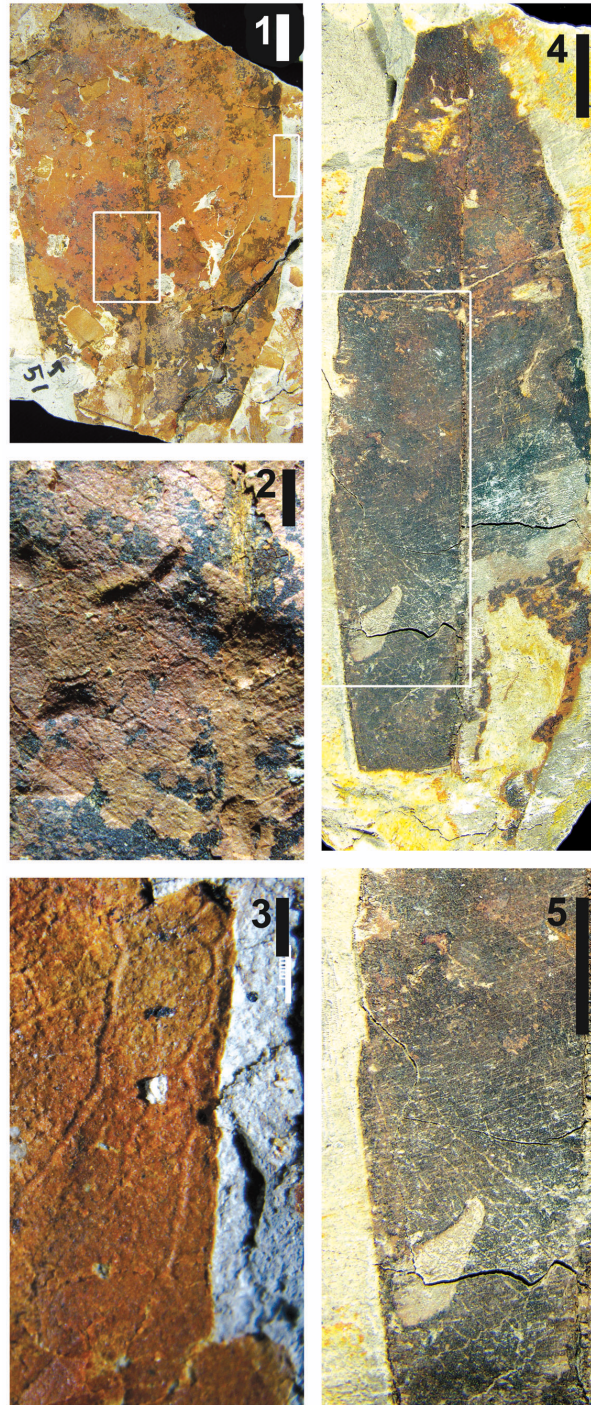
vein to margin before branching or deflection; thus, individual intersecondaries are difficult to distinguish from secondaries as well as tertiaries. Tertiary veins random reticulate; teeth cryptic to conspicuous, best developed towards the apex.

**Description.** Lamina elliptic, symmetrical. Estimated length 10.5–14.5 cm, width 4.5 cm; preserved l:w ratio 2.5:1; estimated l:w ratio ~3:1. Base convex, base angle acute; apex angle acute, apex shape unknown; margin crenate to serrate. Petiole not preserved. Venation pinnate; primary vein straight, thick, apparently well lignified. Secondary veins eucamptodromous, straight to slightly curved, curving distally approaching margin, 3–8 mm apart along primary, angle 50–65°, spacing irregular, course infrequently deflected at tertiary vein junctions. Intersecondary veins well developed, 2–3 mm apart along primary, one or more intersecondary per secondary, but highly variable in strength and thus difficult to distinguish from secondaries and tertiaries. Tertiary and fourth order veins random reticulate. Teeth small, blunt, best developed towards leaf apex, possibly glandular but not diagnostic due to preservation; looped accessory veins present in larger teeth (Figure 7.3).

**Comments.** The distinctive, closely spaced, parallel, thin secondaries and intersecondaries mark the “*Clusia*” venation type (Gentry 1993; Keller 2004) found within many Clusiaceae Lindley (1836b) and certain genera of Sapotaceae, such as *Manilkara* Adanson (1763), *Micropholis* (Grisebach) Pierre (1891), and many others; Vochysiaceae Saint-Hilaire (1820), including *Qualea* Aublet (1775) and *Ruizterania* Marcano-Berti (1969); and Ochnaceae de Candolle (1811a) such as *Blastemanthus* Planchon (1846), *Elvasia* de Candolle (1811b), *Euthemis* Jack (1820), *Philacra* Dwyer (1944), *Rhabdophyllum* van Tieghem (1902a), *Schuurmansiella* Hallier (1913), and *Tyleria* Gleason (1931). All four groups are characteristically tropical in distribution (e.g., Heywood 1993). Leaves in Ochnaceae are often toothed, whereas the three other families listed uniformly have untoothed leaves (Gentry 1993). An extremely rare exception is the Sapotaceae species *Chrysophyllum imperiale* (Linden) Bentham and Hooker (1876), which has vein architecture completely unlike this fossil. Thus, the combination of “*Clusia*” venation and a toothed margin diagnoses the fossils to Ochnaceae, the only other possibility being an extinct toothed genus from one of the families mentioned above.

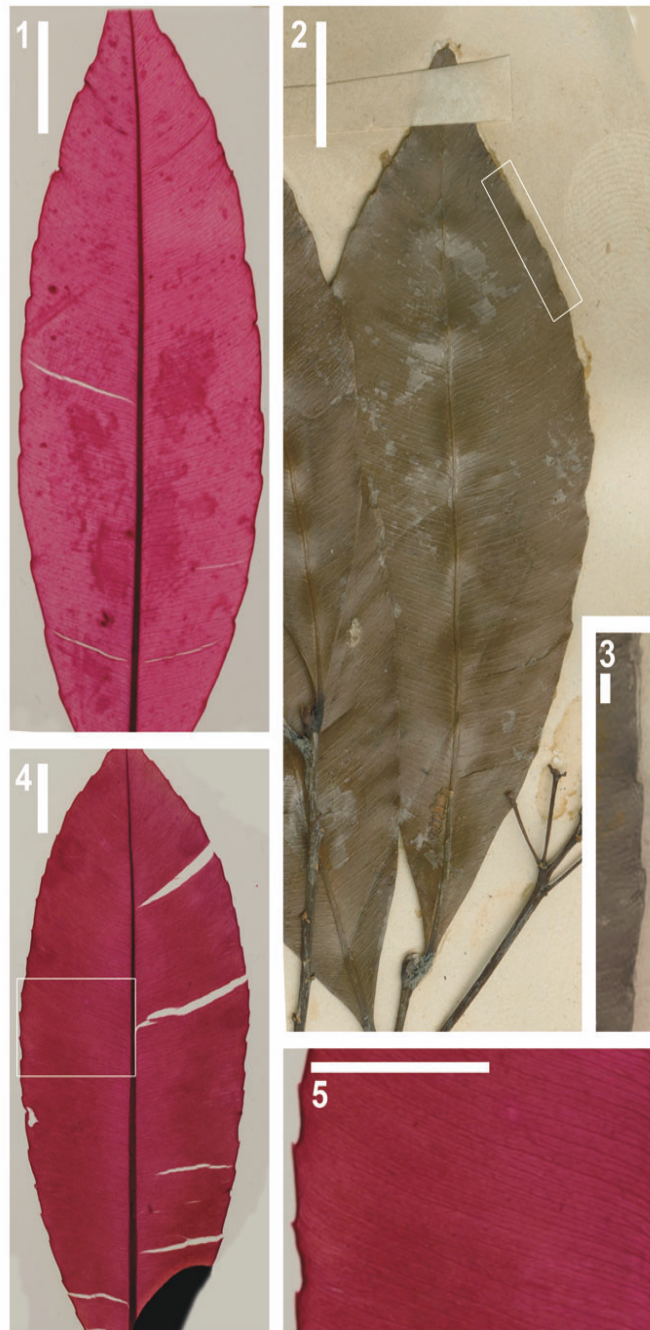
Of the extant genera we observed, those most similar to the fossil are *Philacra*, *Rhabdophyllum*, and *Schuurmansiella*, which all have toothed margins and distinct intersecondaries. Of these, *Rhabdophyllum* has the least regular teeth and the most visibly distinct intersecondaries, additional attributes of the fossil species. Good comparative examples are *R. arnoldianum* van Tieghem (1902a) (Figure 8.1), *R. penicillatum* van Tieghem (1902a) (Figure 8.2, 8.3), *R. affine* van Tieghem (1902a), *R. refractum* van Tieghem (1902a), and *R. welwitschi* van Tieghem (1902b) (Figure 8.4, 8.5). However, the fossil species differs from *Rhabdophyllum* in having intersecondaries of more variable and generally lower strength (weaker course), as well as secondary veins that turn distally more strongly inside the margin. We also note the Eocene Gulf Coast species *Clusiaphyllum eocenicum* (Berry 1930, type specimen USNM 316794), whose venation does not resemble *R. diapyros* in that its secondaries are strongly upturned near the margin and join either a fimbrial vein or a strong ascending secondary vein; this single specimen is fragmentary and is not toothed along the preserved margin.

The fossil record of other Malpighiales groups, as well as molecular clock divergence estimates, suggests a Cretaceous origin for all Malpighiales families (Davis et al. 2005). Fossil fruits that resemble the extant genus *Ochna* Linnaeus (1753) have recently been found in the Late Paleocene of North Dakota and are currently being described (Pigg and DeVore 2005). However, to our knowledge, the distinctive specimens reported here are the most reliable fossil leaves of Ochnaceae, a family with approximately 30 extant genera and 500 species, of mostly trees and shrubs, having tropical South America as its major center of diversity within a pantropical distribution (Heywood 1993). Berry described middle Eocene leaves from Tennessee (Berry 1930) and Río Negro, Argentina (Berry 1938; dated in Wilf et al. 2005) as species of *Ouratea* Aublet (1775), but neither bears close resemblance to the extant genus. Although there are scattered reports of fossil Ochnaceae pollen in the literature (Gruas-Cavagnetto 1976; Barbin 1992), these must be considered unreliable, until more detailed analyses are done, because the extant pollen morphology is unspecialized and thus very difficult to distinguish from similar groups (e.g., Muller 1969). There appear to be no reliable pollen records of Ochnaceae older than Holocene (e.g., Muller 1981).



**Figure 7.** *Rhabdophyllites diapyros*, paratypes. (1–3) USNM 535055. (1) Complete specimen, closely spaced secondaries faintly visible. Scale bar equals 1 cm. (2) Detail of inset in box 1 from approximate center of blade, of midvein (at right, running bottom to top), secondary and intersecondary veins of the “*Clusia*” type (running towards upper left from the left side of the midvein and towards upper right from the right side of the midvein), and random reticulate tertiary veins. Scale bar = 2 mm. (3) Detail of teeth corresponding to inset box in (1) along the leaf margin, showing looped accessory venation and apex (dark areas at apex are remnant coal flakes probably unrelated to glands). Scale bar equals 0.5 mm. (4, 5) USNM 535056. (4) Complete specimen, showing teeth and faintly visible, closely spaced, thin secondary veins. Note conspicuous insect-feeding hole bordered by dark reaction tissue at lower left of blade. Scale bar equals 1 cm. (5) Detail of area near insect-feeding hole in (4), showing faintly preserved secondary and intersecondary veins (running from midvein, at right, towards upper left) and some tertiary veins. Scale equals 1 cm.





**Figure 8.** Extant *Rhabdophyllum* taxa. Herbarium specimen supplied by the Royal Botanic Gardens, Kew, and cleared leaves supplied from the Jack A. Wolfe United States Geological Survey Cleared Leaf Collection, housed at USNM. Images depict the similarities between the extant genus *Rhabdophyllum* and the new genus *Rhabdophyllites* (Figure 6 and Figure 7) including numerous, thin, closely spaced secondary and intersecondary veins, reticulate tertiary veins, and small teeth along the margin (see text). **(1)** *Rhabdophyllum arnoldianum* (USGS cleared leaf number 3198, herbarium source voucher UC 1327293, Congo, collected Gilbert). Scale bar equals 1 cm. **(2)** Type number of *Rhabdophyllum penicillatum* (specimen K000431306, Angola, collected Welwitsch). Scale bar equals 1 cm. Reproduced with the consent of the Board of Trustees of the Royal Botanic Gardens, Kew. **(3)** Detail of margin from (2) showing small teeth along the margin. Scale bar equals 1 mm. **(4)** *Rhabdophyllum welwitschi* (USGS cleared leaf number 4836, herbarium source voucher MO 1643896, Angola, collected Carisso and Mendonça), scale bar equals 1 cm. **(5)** Detail of venation from (4) showing venation diverging from midvein and converging along the margin. Scale bar equals 1 mm.

Order SAPINDALES Dumortier, 1829  
Family ANACARDIACEAE Lindley, 1830  
Genus *RHUS* Linnaeus, 1753  
*Rhus* sp.

**Specimen.** USNM 535057 (Figure 9.1, 9.2; site 1).  
Morphotype RH09.

**Distinguishing features.** Large, compound, irregular teeth; craspedodromous, nearly cladodromous secondary veins branch conspicuously and terminate into both tooth orders and into sinuses; thin but prominent intersecondary veins; secondaries and intersecondaries irregularly angled.

**Comments.** Conspicuously forking to cladodromous secondary veins, irregularly angled secondaries and intersecondaries, large and irregular to compound teeth, and termination of secondary veins or branches thereof in pointed tooth apices and sinuses comprise the characteristic architecture for toothed *Rhus* leaflets (e.g., Wolfe and Wehr 1987; Martínez-Millán and Cevallos-Ferriz 2005). A few other genera in Anacardiaceae show some components of this venation syndrome, including *Loxopterygium* Bentham and Hooker (1862) and *Schmaltzia* Desvaux ex Small (1841), but it is best expressed and most widely prevalent in *Rhus*. Harrington (2003a, 2003b) reported possible Anacardiaceae pollen from the Red Hot Truck Stop section.

**Description.** Lamina narrow (size data not available due to fragmentation), shape and angles of apex and base unknown; margin serrate, fimbrial vein present. Venation pinnate, primary vein straight. Secondary veins craspedodromous to cladodromous, 6–8 pairs preserved, thickness and angle irregular. Intersecondaries thin, ~parallel to secondaries, angle irregular. Tertiary veins random reticulate. Teeth in two orders, ~four teeth/cm; teeth large, glandular; sinuses angular; tooth apices pointed; secondary vein branches terminate in sinuses and compose principal veins.

*Incertae sedis*, morphotype RH15

**Specimens.** USNM 535064 (Figure 9.3; site 1).

**Distinguishing features.** Strongly asymmetrical base; irregularly spaced secondary veins that diverge off primary vein with a different divergence angle on either side of the primary vein.

**Description.** Lamina (probable leaflet fragment), oblong, wide (preserved l:w ratio 1.6:1, estimated l:w ratio ~2:1), base asymmetrical, decurrent, angle acute, petiole attachment marginal. Margin entire, fimbrial vein present. Venation pinnate; pri-

mary vein thick, curved basally; basal veins three. Secondary veins craspedodromous, 8–10 pairs spaced irregularly, arising from midvein decurrently at ~55°, curving distally near margin. Intersecondaries weak. Tertiary veins random reticulate; fourth order veins regular polygonal reticulate; fifth order veins random reticulate, FEVs unbranched where preserved.

*Incertae sedis*, morphotype RH16

**Specimen.** USNM 535065 (Figure 9.4; site 1).

**Distinguishing features.** Thick primary vein with strongly decurrent secondary veins and prominent intersecondaries.

**Description.** Leaf fragment, base and apex characteristics unknown, preserved lamina width ~2.5 cm; observed margin entire. Venation pinnate, primary vein stout, tapering distally; secondary veins eucamptodromous or craspedodromous, curved, thin, numerous (4 pairs in small exposed area), decurrent on midvein with divergence 45–60°. Intersecondaries present, conspicuous. Tertiary veins random reticulate; higher order venation not preserved.

*Incertae sedis*, morphotype RH04

**Specimen.** USNM 535058 (Figure 10.1, 10.2; site 1).

**Distinguishing features.** Two primary veins (probably three or more originally) diverging from each other and connected by interior secondary veins. Leaf possibly palmately lobed. High order venation and areolation unusually well-preserved (Figure 9.2) for this flora, suggesting well-lignified veins.

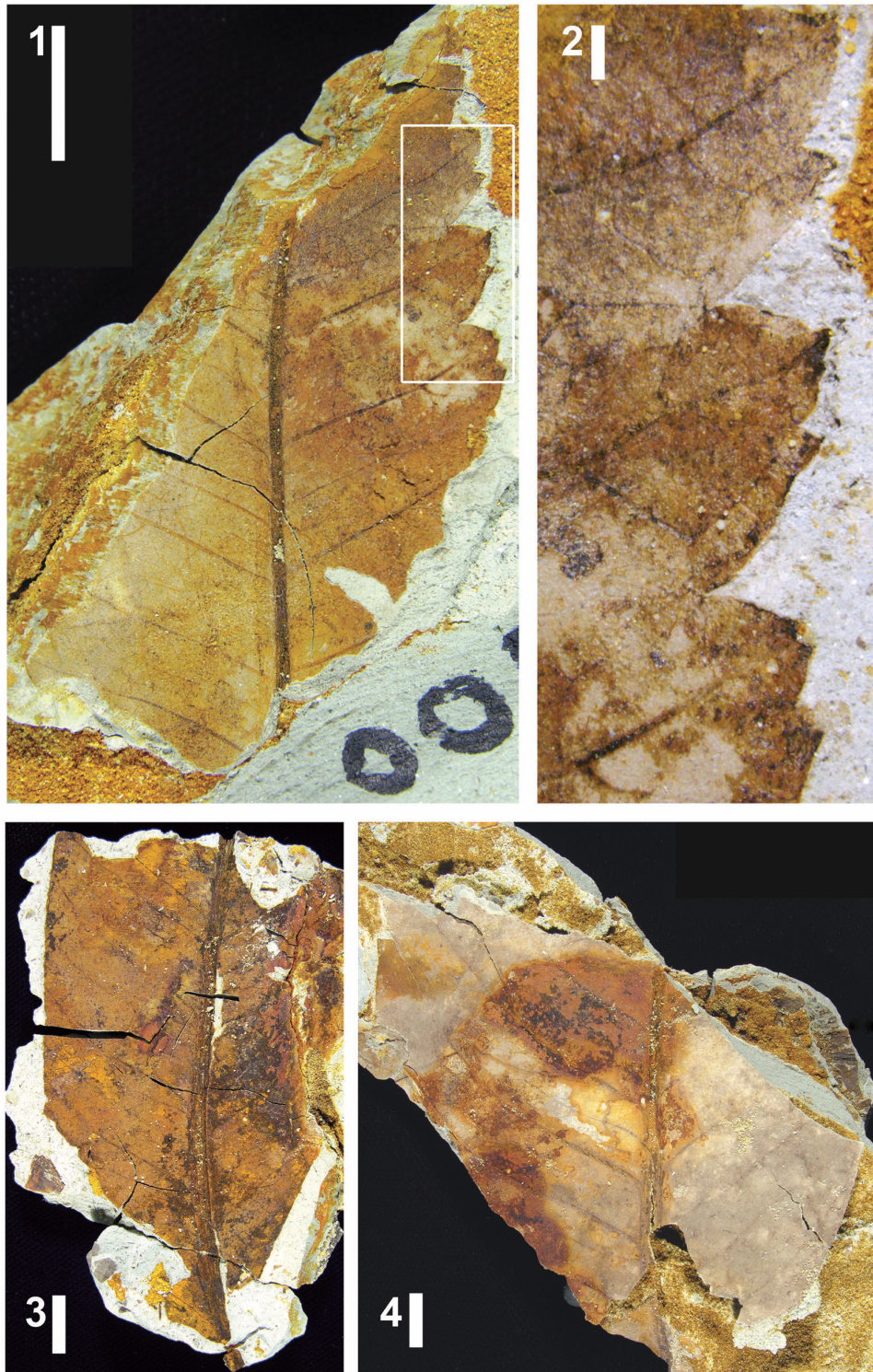
**Description.** Fragment; lamina size, base, apex, and margin features unknown. Primary venation apparently actinodromous or palinactinodromous; preserved secondary venation interior, spacing decreasing basally, perpendicular to primaries. Tertiary veins random reticulate, spacing close (1.5–3 mm). Fourth and fifth order veins random reticulate; areolation moderately developed, five or more sided; FEVs unbranched or one-branched.

*Incertae sedis*, morphotype RH05

**Specimen.** USNM 535059 (Figure 10.3, 10.4; site 1).

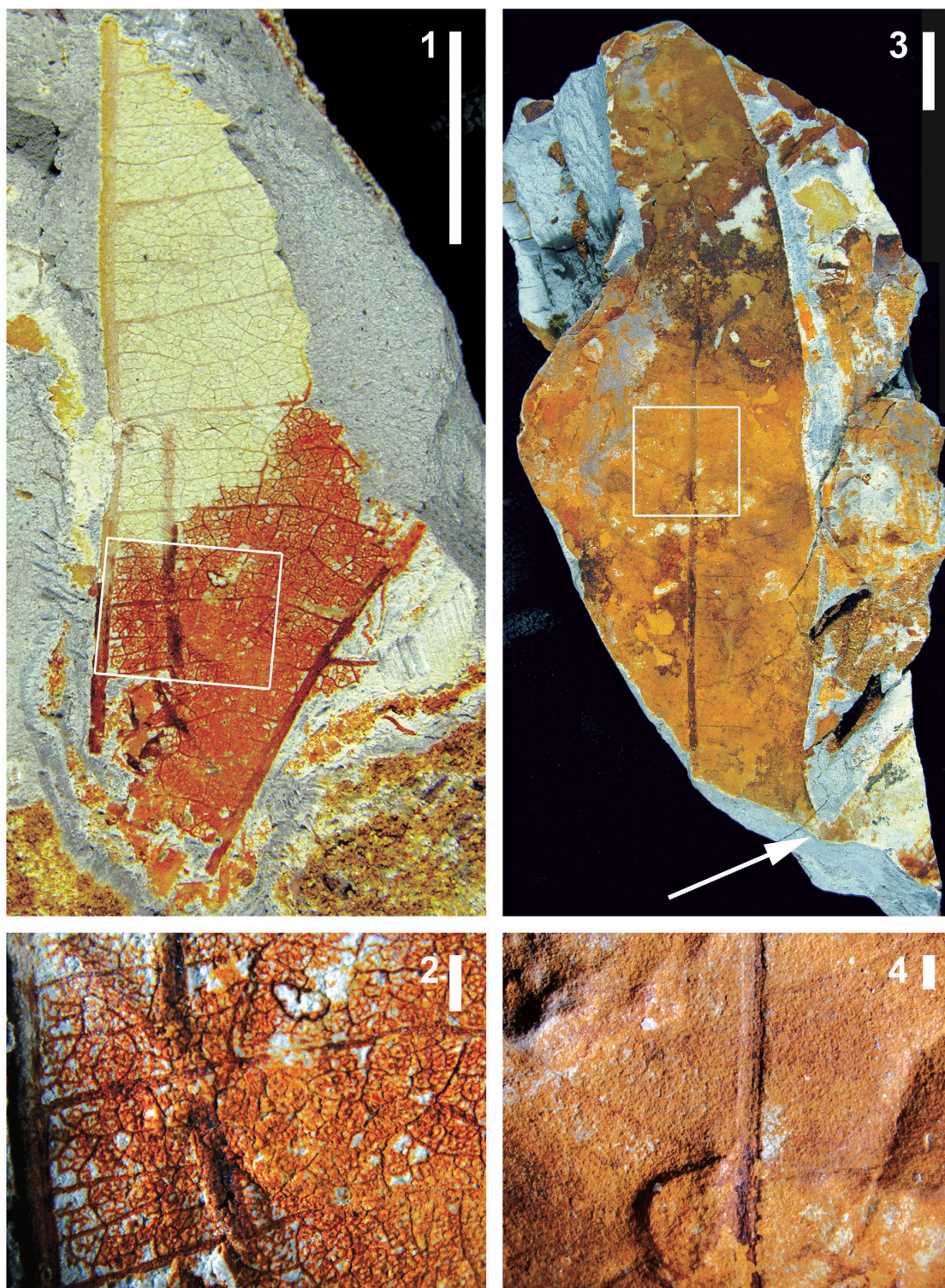
**Distinguishing features.** Rounded sinus (Figure 9.3, arrow), which indicates this is a lobed leaf, and thick tertiary veins arising perpendicular to the primary vein that join the subjacent secondary vein.





**Figure 9.** (1-2) *Rhus* sp., USNM 535057. (1) Complete specimen showing compound teeth, strong but irregularly spaced secondaries and intersecondaries, branching of secondaries near margin, and terminations of secondaries in tooth sinuses and apices. Scale bar equals 1 cm. Inset for (2) detail of teeth and venation at margin. Scale bar equals 1 mm. (3) Leaf morphotype RH15, USNM 535064, showing asymmetrical base and irregularly spaced secondaries with different divergence angles on either side of midvein. Scale bar equals 1 cm. (4) Leaf morphotype RH16, USNM 535065, showing wide midvein, markedly decurrent secondary veins, and intersecondary veins between each set of secondary veins. Scale bar equals 1 cm.





**Figure 10.** Leaf morphotypes RH04 and RH05. **(1)** Leaf morphotype RH04, USNM 535058, showing convex, interior secondary veins between two primary veins. Scale bar equals 1 cm. **(2)** Inset for venation detail, showing unusually good preservation of higher venation for this flora; the tertiary and quaternary veins are random reticulate. Scale bar equals 1 mm. **(3)** Leaf morphotype RH05, USNM 535059, presumed to be a left lateral lobe. Note the difference in secondary vein divergence angle on either side of the primary, and the lobe sinus portion indicated by arrow. Scale bar equals 1 cm. **(4)** Inset for detail of primary vein with departing secondaries, showing greater divergence angle to right than to left of primary. Scale bar equals 0.2 mm.

The marked difference in secondary vein divergence angle on either side of the lobe primary (Figure 9.4) indicates that this is a left lateral lobe. From same locality as RH04 but lacking the distinctive impressed areolation (Figure 9.2).

**Description.** Preserved lobe narrow, lobe sinus rounded; margin entire, fimbrial vein present. Venation presumably actinodromous or palinactinodromous. Secondary veins eucamptodromous. Tertiaries arising from midvein thick, divergence from primary perpendicular, then deflecting to subadjacent secondary; tertiary veins arising from secondary veins. Higher-order venation present but indeterminate.

*Incertae sedis*, morphotype RH08

**Specimens.** USNM 535060 (Figure 11.1; site 1). Additional deposited specimens: five from site 1.

**Distinguishing features.** Ovate blade, entire margin, and eucamptodromous or weak brochidodromous, irregularly spaced secondary veins, diverging from the midvein at  $\sim 40^\circ$ , and then curving towards the margin with few, weak intersecondary veins.

**Description.** Lamina elliptic to ovate, symmetrical, narrow (preserved and estimated l:w ratio  $\sim 3:1$ ; preserved length 1.2–6.5 cm, estimated 3.5–7 cm; preserved width 1.0–3.0 cm, estimated 1.3–3.2 cm); margin entire, fimbrial vein present. Venation pinnate; primary vein straight. Secondary veins eucamptodromous to weakly brochidodromous,  $\sim 2$ – $3$  secondaries per cm, divergence angle  $\sim 40^\circ$ , gently to sharply curving off primary vein and curving apically near margin; spacing irregular. Intersecondary veins few to absent. Tertiary veins random reticulate, oriented nearly perpendicular to primary vein near margin where secondaries are closely spaced; fourth order veins random reticulate.

*Incertae sedis*, morphotype RH14

**Specimen.** USNM 535063 (Figure 11.2, 11.3; site 2). Additional deposited specimens: five from site 2.

**Distinguishing features:** Poorly preserved morphotype with eucamptodromous or weakly brochidodromous secondary veins, which diverge from the midvein at  $45^\circ$ . Although very generalized in appearance, RH14 is distinct from other morphotypes presented here in the combination of eucamptodromous or weakly brochidodromous

secondary venation, entire margin, and a high length:width ratio.

**Description.** Lamina elliptic, probably symmetrical prior to preservation, narrow (preserved l:w ratio  $\sim 5:1$ , estimated l:w ratio  $\sim 3.5:1$ ; preserved length 5.7–10 cm; preserved width 2.5–4.5 cm); base angle acute, apex rounded, apex angle obtuse; margin entire, fimbrial vein present. Venation pinnate; primary vein straight, width decreases distally. Secondary veins eucamptodromous or weakly brochidodromous, straight-slightly curved, divergence angle  $\sim 45^\circ$ . Higher order venation not preserved.

*Incertae sedis*, morphotype RH10

**Specimens.** USNM 535061 (Figure 12.1, site 2). Additional deposited specimen: one from site 2.

**Distinguishing features.** Acute base and apex angles, and secondary veins diverging off the midvein at  $\sim 65^\circ$ .

**Description.** Lamina elliptic, narrow (preserved l:w ratio  $\sim 3.3:1$ , estimated l:w ratio  $\sim 3.5:1$ ; preserved length 12.5–13.5 cm; width 3.5 cm); base apparently asymmetrical, base angle acute; apex straight and acute; margin entire, fimbrial vein present. Venation pinnate; primary vein width decreasing distally. Secondary veins eucamptodromous to weakly brochidodromous, slightly curved, divergence angle  $65^\circ$ ; agrophic veins absent; intersecondary veins weak if present. Tertiary veins random reticulate.

*Incertae sedis*, morphotype RH11

**Specimen.** USNM 535062 (Figure 12.2, 12.3; site 2).

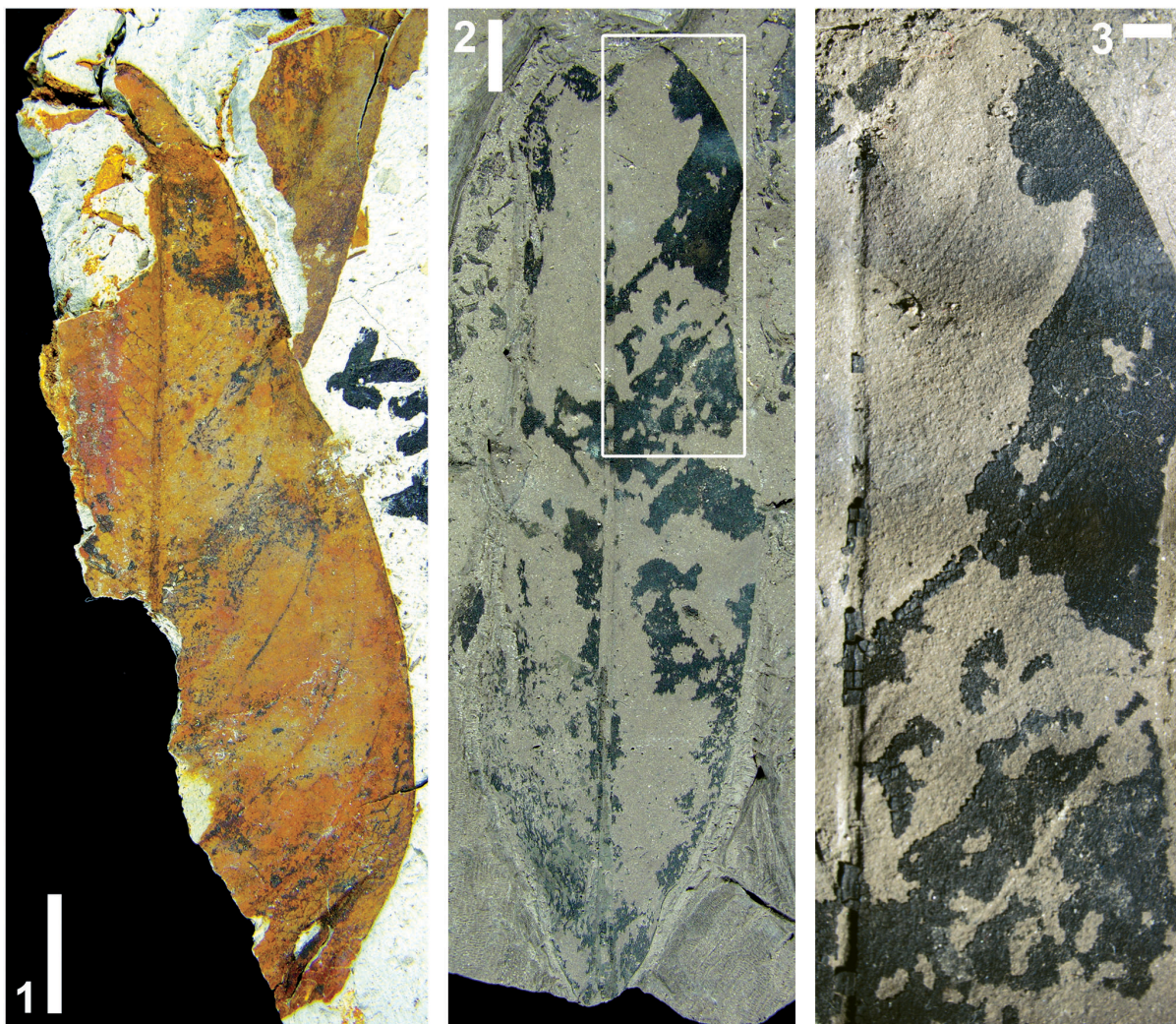
**Distinguishing features.** Large, blunt, widely spaced, semitriangular teeth, concave on both flanks; craspedodromous secondary veins lose gauge as they enter teeth.

**Description.** Lamina apparently elliptic; margin serrate, fimbrial vein absent. Preserved length 5.6 cm (estimated 9 cm); preserved width 2.8 cm (estimated 3 cm). Venation pinnate; secondary veins craspedodromous, spacing irregular, angles uniform. Intersecondary veins absent. Tertiary veins opposite percurrent. Teeth of one order, spacing  $\sim 1$  tooth/cm, large, concave on both flanks, sinuses angular, apices glandular; secondaries lose gauge, or decrease in width, entering teeth.

*Incertae sedis*, morphotype RH18

**Specimen.** USNM 535067 (Figure 12.4; site 1).





**Figure 11.** (1) Leaf morphotype RH08, USNM 535060. Complete specimen showing ovate blade and eucamptodromous secondary veins that turn sharply distally as they approach the margin. Scale bar equals 1 cm. (2) Leaf morphotype RH14, USNM 535063. Complete specimen showing combination of elliptic blade, high length-width ratio, entire margin, eucamptodromous secondaries, and secondary departure angle near  $45^\circ$ . Scale bar equals 1 cm. (3) Inset for margin detail. Scale bar equals 2 mm.

**Distinguishing features.** Basally eucamptodromous and apically brochidodromous secondary veins that turn upwards sharply along the margin towards the apex of the leaf, and well-developed opposite percurrent tertiary veins that change course with the secondary veins.

**Description.** Lamina elliptic, symmetrical; narrow (preserved l:w ratio 2.4:1; estimated l:w ratio ~2.1:1; preserved length 6 cm, estimated 7 cm; preserved width 2.2, estimated 3 cm), base and apex angle acute but shape indeterminate; margin entire. Venation pinnate, primary vein slightly sinuous. Secondary veins brochidodromous apically, eucamptodromous basally, extend straight towards

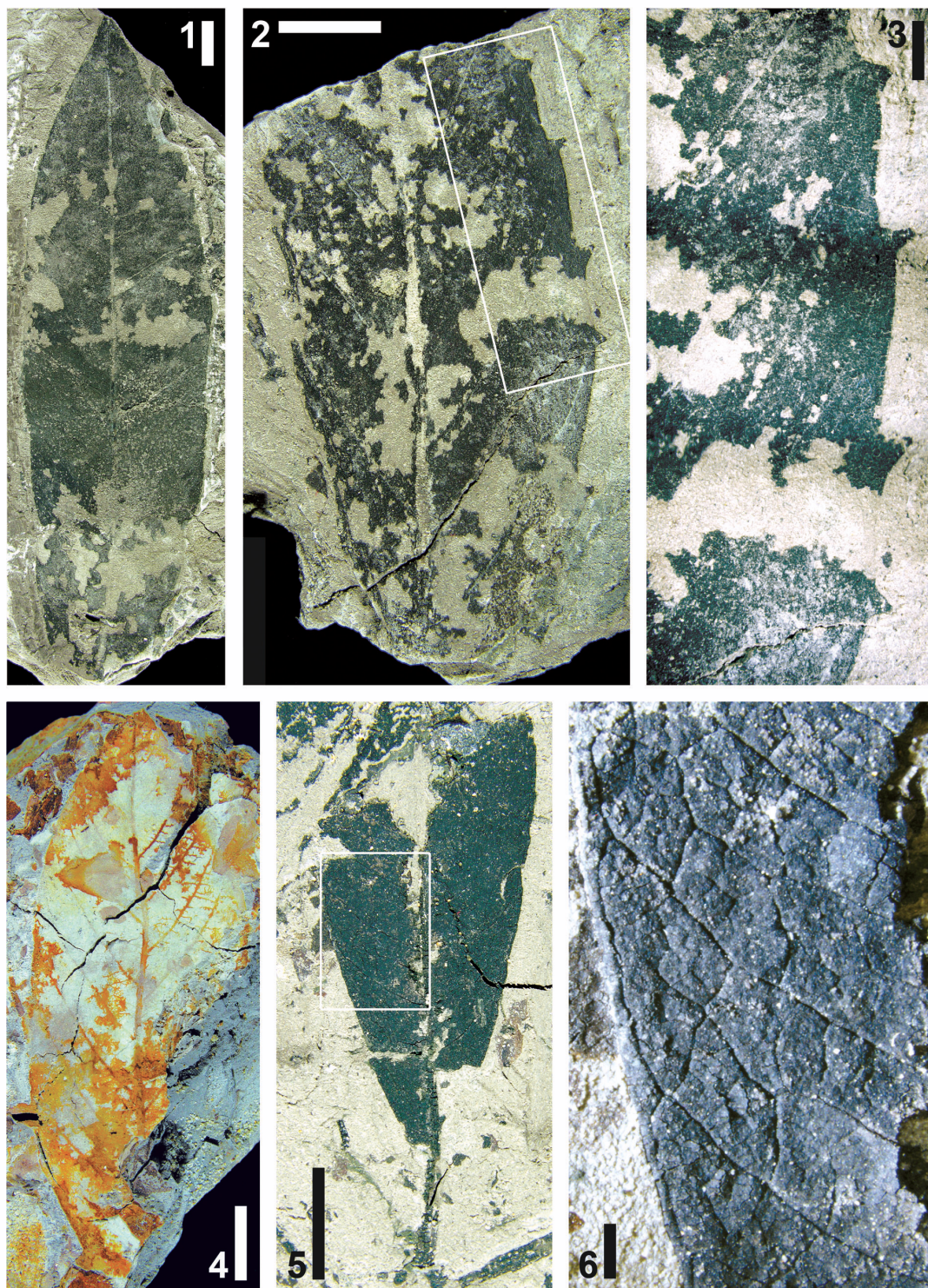
the margin, turning steeply near margin, 9 pairs, divergence angle  $\sim 50^\circ$ , spacing regular. Tertiary veins opposite percurrent; angle to midvein obtuse admedially, perpendicular to midvein near margin. Higher order venation present but poorly preserved.

*Incertae sedis*, morphotype RH17

**Specimen.** USNM 535066 (Figure 12.5, 12.6; site 2).

**Distinguishing features.** Entire margin, acute base. Weakly brochidodromous, thin secondary





**Figure 12.** (1) Leaf morphotype RH10, USNM 535061, showing elliptic, narrow blade with entire margin and acute base and apex. Scale bar equals 1 cm. (2) Leaf morphotype RH11, USNM 535062, showing large, blunt, widely spaced, semitriangular teeth with concave flanks. Scale bar equals 1 cm. (3) Inset for details of teeth. Scale bar equals 2 mm. (4) Leaf morphotype RH18, USNM 535067, showing basally eucamptodromous and apically brochidodromous secondary venation and well-developed, opposite percurrent tertiary veins. Scale bar equals 1 cm. (5-6) Leaf morphotype RH17, USNM 535066. (5) Complete specimen, scale bar equals 1 cm. (6) Detail, scale bar equals 1 mm, of RH17, showing thin, brochidodromous secondary veins and random reticulate tertiary veins.

veins diverging from the midvein at  $\sim 55^\circ$ ; random reticulate tertiary veins.

**Description.** Lamina apparently elliptic, narrow (preserved l:w ratio 2.5:1, estimated l:w ratio 2.25:1; preserved length 2.5 cm, estimated 4.5 cm; preserved width 1.5, estimated 2 cm); base cuneate, base angle acute; margin entire, fimbrial vein present; petiole attachment marginal. Venation pinnate; secondary veins weakly brochidodromous, looping close to margin, 5 pairs observed, divergence angle  $\sim 55^\circ$ , spacing increasing basally. Intersecondary veins well developed; tertiary veins random reticulate.

*Incertae sedis*, cuticle morphotype 1  
probable monocot

**Specimen.** USNM 535049 (Figure 13; site 2). Numerous additional specimens present in matrix but not inventoried.

**Distinguishing features.** The strap-shaped cuticle fragments are often preserved yellow to orange. Cells are visible under stereoscope (Figure 13.1), with both epidermis and hypodermis preserved. The epidermal surface is striated, and stomata are present.

**Description.** Strap-shaped cuticle,  $\sim 5.5$  mm width. Epidermal cells elongate (width 14–26  $\mu$ m), with surface striations, cells more elongate along leaf margin. Hypodermis thick-walled, cells less elongate than those of epidermis. Stomatal areas sunken in relation to surrounding epidermis, guard cell pairs (24–28  $\mu$ m in polar length) oriented obliquely to long axis of surrounding epidermal cells; subsidiary cell arrangement paracytic. Venation absent.

**Comments.** Paracytic stomata and strap-shaped leaves are suggestive of Monocots. This cuticle morphotype may have been produced by the same source species as monocot compression morphotype RH03 described above, but without preserved venation, this is impossible to establish.

*Incertae sedis*, cuticle morphotype 2  
probable liverwort

**Specimen.** USNM 535888 (Figure 14; site 2). Numerous additional specimens present in matrix but not inventoried.

**Distinguishing features.** The cuticle is preserved in fragments of variable shape that are dark brown. Cells are difficult to distinguish under stereoscope, and only epidermis is preserved. The epidermis

lacks surface striations and bears densely distributed pore-like structures with raised rims.

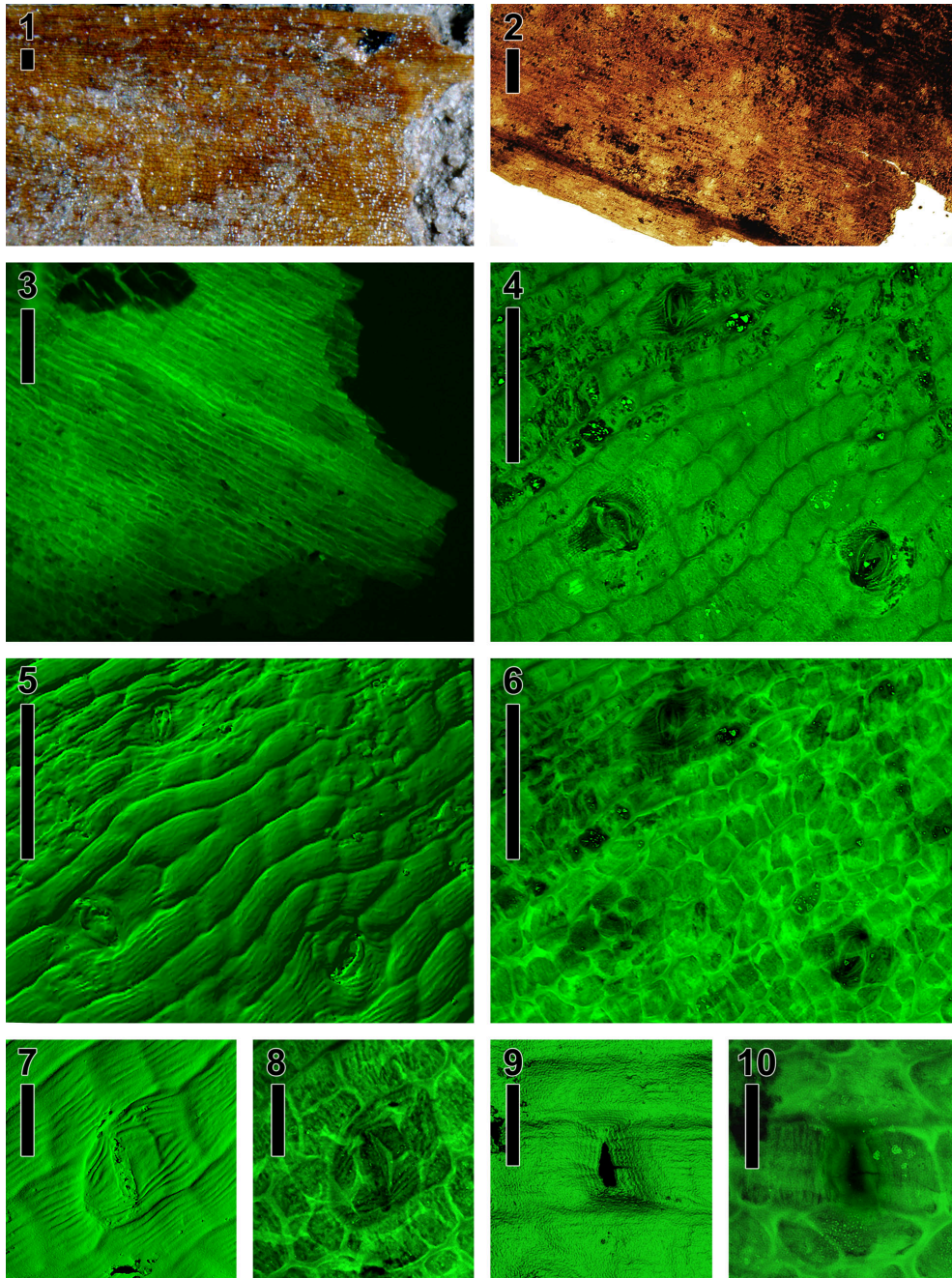
**Description.** Cuticle fragments, epidermal cells elongate, surface striations lacking, surface rough to smooth under ESEM. Hypodermis and stomata not present. Epidermis bears densely distributed pore-like structures with raised rims, pores filled with debris (visible under ESEM).

**Comments.** The pores consistently lack remnants of guard cells or trichome bases. Thus, the pores appear to be a true feature of the cuticle, rather than sites of detached or degraded stomatal areas. Open pores of varying morphology are produced by thalloid liverworts (Ligrone et al. 2007).

## DISCUSSION

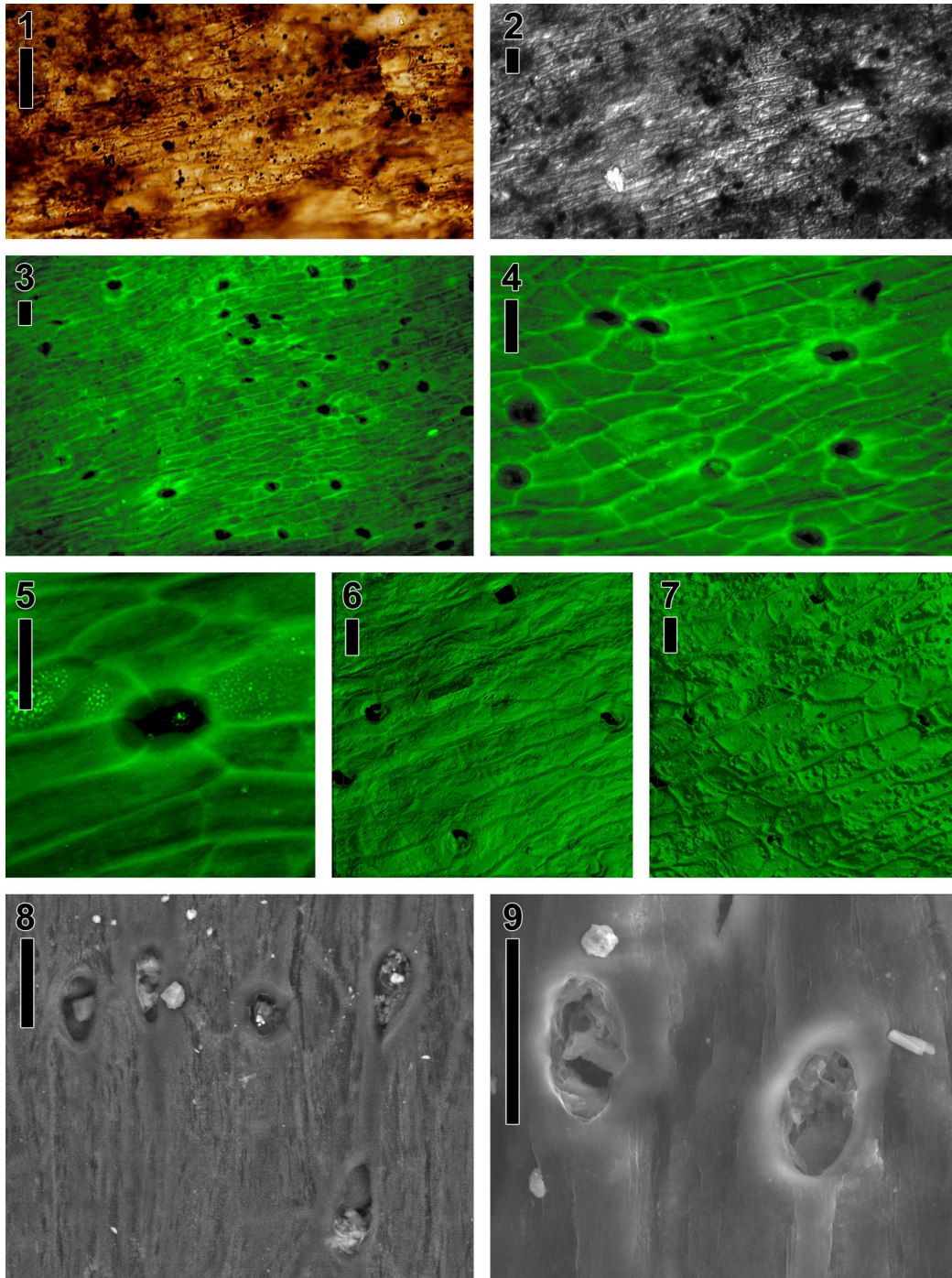
Nearly all the identified plant taxa in the Red Hot flora represent groups with predominant or exclusive distribution in tropical to subtropical biomes (e.g., Gentry 1993; Heywood 1993), indicating warm temperatures at this time in the Gulf Coast. A majority of identifiable taxa also have close relatives from well constrained early Eocene localities in the western USA, showing that these groups were widespread in North America shortly after (and possibly during) the PETM. *Lygodium kaulfussi* appears just above and possibly within the PETM in Wyoming (Wing 1998; Wing et al. 2005); the modern genus is known for its diverse reproductive strategies, including selfing, that appear to expedite long-distance dispersal and colonization (Lott et al. 2003). Lauraceae are known continuously from the late Paleocene and early Eocene of Wyoming (Wing 1998; Wilf 2000). Myrtaceous fruits (*Paleomyrtinaea* Pigg et al. 1993) are known from the late Paleocene of North Dakota and southern Wyoming and from the Eocene of British Columbia (Crane et al. 1990; Pigg et al. 1993; Wilf 2000); myrtaceous leaves (*Syzygioides americana* [Lesquereux] Manchester et al. 1998) appear in the Wyoming fossil record about 2 m.y. after the PETM (Manchester et al. 1998; Wing 1998; Wilf 2000) and extend to the middle Eocene Green River floras (MacGinitie 1969; Manchester et al. 1998). Legumes, not similar to those at the Red Hot leaf flora, are found in the early Eocene of Wyoming including the PETM (Wing 1998; Wilf 2000; Wing et al. 2005). In the Bighorn Basin, *Platycarya* pollen occurs in the lowermost Eocene, and its foliage occurs about 2 m.y. later (Wing 1984, 1998; Wilf 2000). The *Platycarya* specimen from the Red Hot leaf flora (Figure 5) is the first macrofossil of the genus from eastern North Amer-





**Figure 13.** Cuticle morphotype 1, probable monocot, USNM 535049. **(1)** Strap-shaped cuticle viewed directly on rock (note adhering sand grains) under stereomicroscope, showing margin at top, broken at right; cells visible. **(2)** Light micrograph of mounted cuticle, margin at bottom, broken at right. **(3)** Cuticle under light microscope with epifluorescence showing elongate epidermal cells; square hypodermal cells at bottom. **(4)** Maximum brightness projection view of stacked confocal images, showing rectangular epidermal cells and sunken paracytic stomata. Note striated pattern on subsidiary cells. **(5)** Three-dimensional surface rendering of stacked confocal images, showing epidermal cells with striated surfaces and sunken stomatal areas. **(6)** Sum projection view of stacked confocal images, showing faint striated pattern from epidermal cells, thick-walled, square hypodermal cells, and stomatal areas. **(7)** Three-dimensional surface rendering of stacked confocal images showing epidermal cells with striated surface and a single stomatal area. **(8)** Sum projection view of previous figure showing guard cells, thick-walled hypodermal cells, and striated subsidiary cells. **(9)** Three-dimensional surface rendering of stacked confocal images, showing epidermal cells with striated surfaces, and a single stomatal area. **(10)** Sum projection view of previous figure showing guard cells, thick-walled hypodermal cells, and striated subsidiary cells. (1-6): Scale bars equal 100  $\mu\text{m}$ ; (7-10): Scale bars equal 30  $\mu\text{m}$ .





**Figure 14.** Cuticle morphotype 2, probable liverwort, USNM 535888. **(1)** Light micrograph of mounted cuticle; cells elongate, containing brown to black organic matter and minerals. **(2)** Sum projection view of stacked differential interference contrast images (light microscope); view similar to (1) but minerals and sediment more prominent. **(3)** Extended depth-of-focus image of stacked epifluorescence light micrographs; epidermal cells elongate and bearing pores. **(4)** Higher magnification, extended depth-of-focus image of stacked epifluorescence light micrographs; epidermal cells elongate and bearing pores with raised margins. **(5)** Enlarged sum projection view of stacked confocal images. The end walls between epidermal cells are visible to the bottom of the single raised pore. Note the brightly fluorescing pyrite in pore and in cells adjacent to pore. **(6)** Three-dimensional surface rendering of stacked confocal images, showing epidermal cells and open pores. **(7)** Same rendering as in (6), showing reverse side. Note minerals (rough ‘bumps’) and protruding epidermal end walls. All scale bars equal 20  $\mu\text{m}$ .

ica. *Rhus* is well represented in late early Eocene floras of the western USA (e.g., MacGinitie 1969; Wolfe and Wehr 1987; Wilf 2000), and the genus is probably present in Wyoming during the PETM (Wing and Lovelock 2007). To our knowledge, those here presented are the first reliable fossil leaves of Ochnaceae, a diverse pantropical group concentrated in today's Neotropics with a possible fruit record from the late Paleocene of North Dakota (Pigg and DeVore 2005)

## CONCLUSIONS

Lowstand deposits from the basal Bashi Formation at the Red Hot Truck Stop locality date to the first ~1.6 million years of the Eocene and may lie within the Paleocene-Eocene Thermal Maximum. From two sites we collected and analyzed 113 fossil leaf specimens, which included 18 discrete morphological groups (morphotypes). Despite generally poor preservation, we recognize the following botanical entities as well as 10 undiagnosed morphotypes: *Lygodium kaulfussi* (a climbing fern), Lauraceae (laurel family), Monocots, Myrtaceae (guava family), Fabaceae (legumes), *Platycarya* (a member of the walnut family, Juglandaceae, currently endemic to East Asia), *Rhus*, a sumac or sumac relative (Anacardiaceae), and a new genus and species of Ochnaceae (ochna family); all are consistent with tropical to subtropical climates. Additionally, we recognize two cuticle morphotypes suggestive of monocots and liverworts, respectively. *Platycarya* is an Eocene index taxon here represented for the first time as a macrofossil in the eastern USA. The new Ochnaceae, *Rhabdophyllites diapyros*, apparently is the only leaf record of this major extant pantropical group. Most of the groups found in the Red Hot leaf flora are also found in western North America during the earliest Eocene, showing that they were widespread in North America at this time. The Red Hot flora indicates the potential to rebuild the stratigraphic context of the classic paleobotanical record of the U.S. Gulf Coast, leading to improved understanding of plant migration and evolution during the Early Cenozoic.

## NOTE ADDED IN PROOF

A fragment from a leaf-bearing rock from site 1 has revealed two fossil fruit specimens (Fig. 15.1-15.4). Also, a new cuticle morphotype was found from site 2, due to improved fluorescence equipment (Fig. 15.5-15.6). These specimens were discovered after manuscript acceptance. The fruits

are preserved as compression-impressions with some three-dimensionality. These occurrences include the following three specimens. All scale bars in Figure 15 equal 0.2 mm; all photographs were taken on the Nikon SMZ-1500 stereomicroscope.

USNM 536213 (Fig 15.1, 15.2, part and counterpart). Icacinaceae cf. *Palaeophytocrene* (Reid, E.M., and Chandler, M.E.J. 1933. The London Clay Flora. British Museum [Natural History], London, England, 561 p.). Oval, tuberculate endocarp. Tubercles extend towards center of fruit, tubercles in vertical rows. Dimensions preserved: 2.7 mm length, 1.2 mm width.

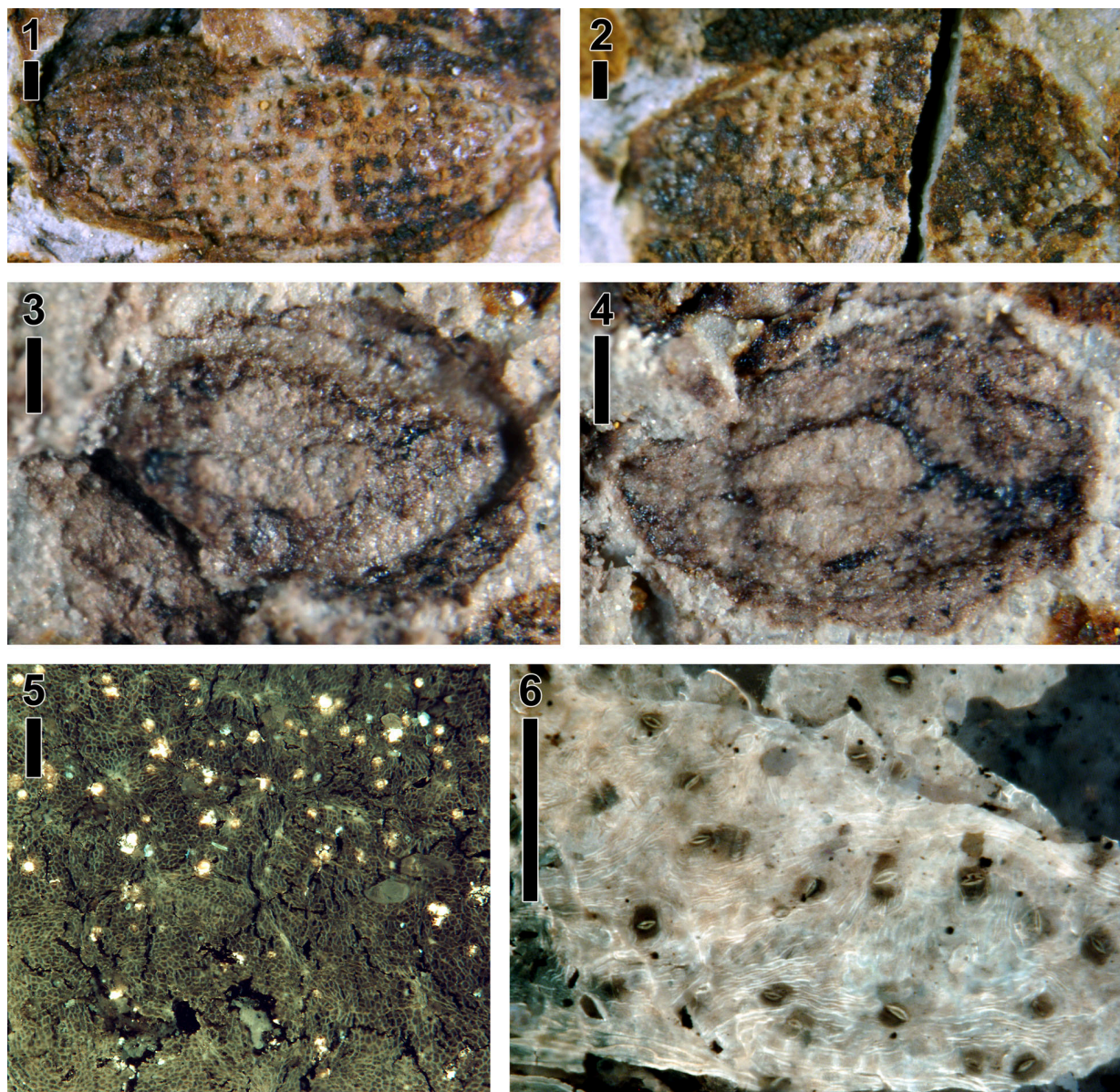
USNM 536214 (Fig 15.3, 15.4, part and counterpart). Juglandaceae sp., endocarp. The single specimen is ovoid and basally lobed internally. The endocarp is apparently without a wing and two-lobed, but more specimens would be needed to determine these characters and better assign this fruit taxonomically. Dimensions preserved: 1.3 mm length, 0.8 mm width.

USNM 536215 (Fig. 15.6; Fig. 15.5 shows a separated fragment of the same morphotype, on the same rock). Dicot cuticle morphotype with densely spaced, diffuse paracytic stomata and trichome bases, visible under fluorescence microscopy with long-pass green filter. Spherical resin bodies are also visible in the carbon film between cuticle layers (Fig 15.5), and these are probably organically preserved oil/mucilage idioblasts common in tissues of Laurales, Magnoliales and basal 'ANITA' grade angiosperms. These resin bodies are also visible, under fluorescence, in the Lauraceae leaf morphotype exemplar (Fig. 2.3), further confirming that specimen as Lauraceae.

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**Figure 15.** Additional specimens added in proof (see text). (1-2) Icacinaceae cf. *Palaeophytocrene*, part and counterpart, USNM 536213. (3-4) Juglandaceae sp., part and counterpart, USNM 536214. (5-6) Dicot cuticle morphotype with densely spaced, diffuse paracytic stomata, trichome bases, and spherical resin bodies; USNM 536215 applies to panel (6). All scale bars equal 0.2 mm; all photographs were taken on the Nikon SMZ-1500 stereomicroscope.

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