

RESEARCH ARTICLE



Fossil papilionoids of the Bowdichia clade (Leguminosae) from the Paleogene of North America

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Abstract

Premise: Understanding the evolutionary history of flowering plants has been enriched by the integration of molecular phylogenies and evidence from the fossil record. Fossil fruits and leaves from the late Paleocene and Eocene of Wyoming and Eocene of Kentucky and Tennessee are described as extinct genera in the tropical American Bowdichia clade of the legume subfamily Papilionoideae. Recent phylogenetic study and taxonomic revision of the Bowdichia clade have facilitated understanding of relationships of the fossil taxa and their evolutionary implications and paleoenvironmental significance.

Methods: The fossils were studied using standard methods of specimen preparation and light microscopy and compared to fruits and leaves from extant legume taxa using herbarium collections. Phylogenetic relationships of the fossil taxa were assessed using morphology and DNA sequence data.

Results: Two new fossil genera are described and their phylogenetic relationships are established. *Paleobowdichia lamarensis* is placed as sister to the extant genus *Bowdichia* and *Tobya claibornensis* is placed with the extant genera *Guianodendron* and *Staminodianthus*.

Conclusions: These fossils demonstrate that the tropical American Bowdichia clade was present in North America during a period when tropical or subtropical conditions prevailed in the northern Rocky Mountains during the late Paleocene and the Mississippi Embayment during the middle Eocene. These fossils also document that the Bowdichia clade had diversified by the late Paleocene when the fossil record of the family is relatively sparse. This result suggests that future work on early fossil legumes should focus on tropical and subtropical climatic zones, wherever they may occur latitudinally.

KEYWORDS

Bighorn Basin, Bowdichia clade, Fabaceae, Genistoid clade, Papilionoideae, samara-like fruits

Our understanding of the evolutionary history of flowering plants has been greatly enriched by the integration of molecular phylogenies with evidence from the fossil record. The abundance and diversity of fossils within some families have provided many insights on the origins and evolution of particular clades in the angiosperm tree of life. One such clade of plants with an exceptionally rich fossil record is the economically important legume family (Leguminosae), where fossils have been key in documenting the rapid radiation of the main legume clades in the early Cenozoic (Lavin et al., 2005; Bruneau, 2008; Koenen et al., 2019, 2021).

The Leguminosae is the third-largest family of flowering plants with ca. 770 genera and ~19,600 species (LPWG, 2017). The family has a cosmopolitan distribution, is exceptionally diverse morphologically, and many species are ecologically important in varied ecosystems (e.g., Doyle and Luckow, 2003; Lewis et al., 2005; Pan et al., 2010, 2012; LPWG, 2013a, 2013b, 2017; Epihov et al., 2017). Legumes also have an abundant and diverse fossil record, with numerous fossil flowers, fruits, and leaves documented from the Cenozoic of every continent except Antarctica (Herendeen, 1992; Herendeen and

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Dilcher, 1992; Herendeen et al., 1992). Temporal and biogeographic patterns in the fossil record of the family were summarized by Herendeen et al. (1992), to which have been added more recent fossil reports from low paleolatitude localities, mainly in Africa and Central and South America (Herendeen and Jacobs, 2000; De Franceschi and De Ploëg, 2003; Jacobs and Herendeen, 2004; Calvillo-Canadell and Cevallos-Ferriz, 2005; Brea et al., 2008; Wing et al., 2009; Pan et al., 2010, 2012; Collinson et al., 2012; Cantrill et al., 2013; Jia and Manchester, 2014; Shukla and Mehrotra, 2016; Herendeen and Herrera, 2019; Herrera et al., 2019; Lyson et al., 2019; Shukla et al., 2019; Jia et al., 2021; Li et al., 2021). By the middle Eocene all major lineages within the family are documented in the fossil record, and many securely identified fossils have been used to calibrate branch ages from molecular phylogenetic analyses (Herendeen et al., 1992; Lavin et al., 2005; Bruneau et al., 2008; Magallon et al., 2015; Estrella et al., 2017; Koenen et al., 2021).

By contrast with the Eocene, the Paleocene fossil record of legumes remains sparse. Lyson et al. (2019) reported what are clearly fossil legume fruits and leaflets from the first million years of the Paleocene in the Denver Basin of Colorado. These fossils represent the earliest definitive records referable to the family though their affinities within the Leguminosae are unknown. Herrera et al. (2019) described eight fossil fruit types and six leaf types from the middle to late Paleocene Cerrejón and Bogotá Formations of Colombia. They placed two bipinnate leaf morphotypes in the Caesalpinioideae, and these are the earliest record of this subfamily. Two of the fruit morphotypes were placed in the Detarioideae and Dialioideae (subfamily names follow LPWG, 2017). The affinities of the other fruit and leaf morphotypes were uncertain.

Paleocene legume fossils mentioned above suggest that divergences among subfamilial lineages were occurring in the first 10 million years of the Cenozoic, but the subfamily Papilionoideae has not yet been definitively documented. In this paper, we describe fossil leaves and fruits referable to the Papilionoideae from the late Paleocene of northwestern Wyoming (United States). Although leaves and fruits have not been found in attachment, they are closely associated with each other at two sites. At each site, only a single type of legume fruit and leaf were found, and the leaves are abundant, suggesting the parent plant was local. At a third nearby site, leaf specimens were found but not fruits. The new fossil fruit specimens described here have been found to be conspecific with two fossil species previously described by Knowlton (1899) and Cockerell (1912). Excellent preservation of the new fossils reveals diagnostic morphological features that are referable to the small Bowdichia clade of the genistoid papilionoid legumes. These fossils represent the oldest known representatives of the Papilionoideae subfamily. The Bowdichia clade includes five extant genera found today in tropical South America (Cardoso et al., 2012b, 2012c, 2013b).

MATERIALS AND METHODS

Location, stratigraphy and environment of deposition

The fossil material described here is from the Willwood Formation of the Bighorn Basin of northwestern Wyoming, United States. Most figured fruits and leaflets are from USNM locality 41643 (=USNM locality 41701), with the exception of one specimen showing attached pinnately compound leaves (USNM509395, Figure 5A) and a second incomplete compound leaf (USNM 509406, Figure 6C), which come from USNM locality 41609, and the leaflet shown in Figure 7E, USNM772323, which comes from USNM locality 42583 (Table 1). All three sites are of the latest Paleocene age, occurring in a stratigraphic interval producing vertebrate fossils belonging to the Clarkforkian 3 biozone (Rose, 1981; Gingerich, 2001; Figure 1). USNM locality 41643/41701 is 56.5 m below the lowest “brown beds” (Gingerich, 2001; Bowen et al., 2001; van der Meulen et al., 2020), which have been shown in nearby stratigraphic sections to coincide with the onset of the carbon isotope excursion marking the base of the Eocene. USNM locality 41609 and USNM locality 42583 are, respectively, 45 m and 35 m below the lowest brown beds. The age of each locality can be estimated from its elevation in the Polecat Bench-Sand Coulee composite section relative to calibration points of known age (Gingerich, 2001; Secord et al., 2006). The base of Chron 24r (57.1 million years ago [Ma]) is at 1058 m in the composite section, and the base of the carbon isotope excursion (55.93 Ma) is at 1500 m (Secord et al., 2006; Bowen et al., 2015). Linear interpolation between these calibration points gives a rock accumulation rate of 0.38 m/thousand years, and estimated ages of 56.08 Ma (USNM locality 41643/41701), 56.049 Ma (USNM locality 41609) and 56.023 Ma (USNM locality 42583). Although the assumption of linear sedimentation rates is an oversimplification, all three sites are likely to be within 150,000 yr of the end of the Paleocene.

USNM locality 41643 was collected in 1998 and 1999 by S. L. Wing (field collections SLW9819, SLW994) and in 2005 by Ellen Currano (field collection EDC0506, also called Daiye Spa; Currano et al., 2008). USNM locality 42583 was collected in 2016 by S. L. Wing (field collection SLW1612). USNM locality 41609 was collected in 1997, 1998, and 2014 by S. L. Wing (field collections SLW9715, SLW9801, SLW1402). The three localities are in Townships 55 and 56 N, R 101 W, Park Co., WY.

The three fossil sites represent similar depositional settings. Each is a lens-shaped body of gray mudstone a maximum of ~2 m thick that overall fines upward from silty sandstone near the base to flat-laminated gray mudstone near the top. The plant fossils are preserved in the silty sandstone near the base of the lens and through the lowest 50 cm of the mudstone. Plant remains are generally concentrated on horizontal bedding surfaces at the top of thin, fining-upward sequences, suggesting that they settled from

T A B L E 1 Stratigraphic levels and ages of *Paleobowdichia* and *Tobyia* localities

Formation	Locality numbers	Field number/name	Meter level ^a	Age (Myr)	Comments
Willwood Fm.	42583	SLW1612, Singendenhammer	1465	56.023	Age estimated by linear interpolation of rock accumulation rates between the base of C24c ^c , and the base of the Eocene (onset of CIE) ^{b,c}
Willwood Fm.	41609	SLW9715, SLW9801, SLW1402, Saddle Mountain	1455	56.049	Age estimated by linear interpolation of rock accumulation rates between the base of C24r ^c , and the base of the Eocene (onset of CIE) ^{b,c}
Willwood Fm.	41643/41701	SLW9819, SLW994, Daiye Spa	1444	56.08	Age estimated by linear interpolation of rock accumulation rates between the base of C24r ^c , and the base of the Eocene (onset of CIE) ^{b,c}
Lamar River Fm.	USGS paleobotany loc 985	Lamar River, between Cache and Calfee creeks.		52–50	Type locality for <i>Acacia lamarensis</i> Knowlton. Radiometric ages from the Washburn and Sunlight Groups are 50–52 Myr ^d
Middle Park Mbr., Coalmont	UCM Loc 74161	N of Whitely Peak			Type locality for <i>Robinia mesozoica</i> Cockerell. Paleocene-Eocene boundary is in the overlying Middle Mbr. of the Coalmont Fm. ^e
Cockfield Fm.	UF15826	Warman clay pit	n.a.	41–38	Type locality for <i>Diploptropis claibornensis</i> Herendeen & Dilcher. Weakley Co., Tennessee ^f
Cockfield Fm.	UF15803	Bell City clay pit	n.a.	41–38	Paratype locality for <i>Diploptropis claibornensis</i> Herendeen & Dilcher. Graves Co., Kentucky ^f

^aMeter level in Polecat Bench composite section (Secord et al., 2006)^bWesterhold et al. (2020)^cSecord et al. (2006)^dHiza (1999), Feeley and Cosca (2003), Smith et al. (2008)^eHail (1968)^fHerendeen and Dilcher (1990a), Wang et al. (2013)

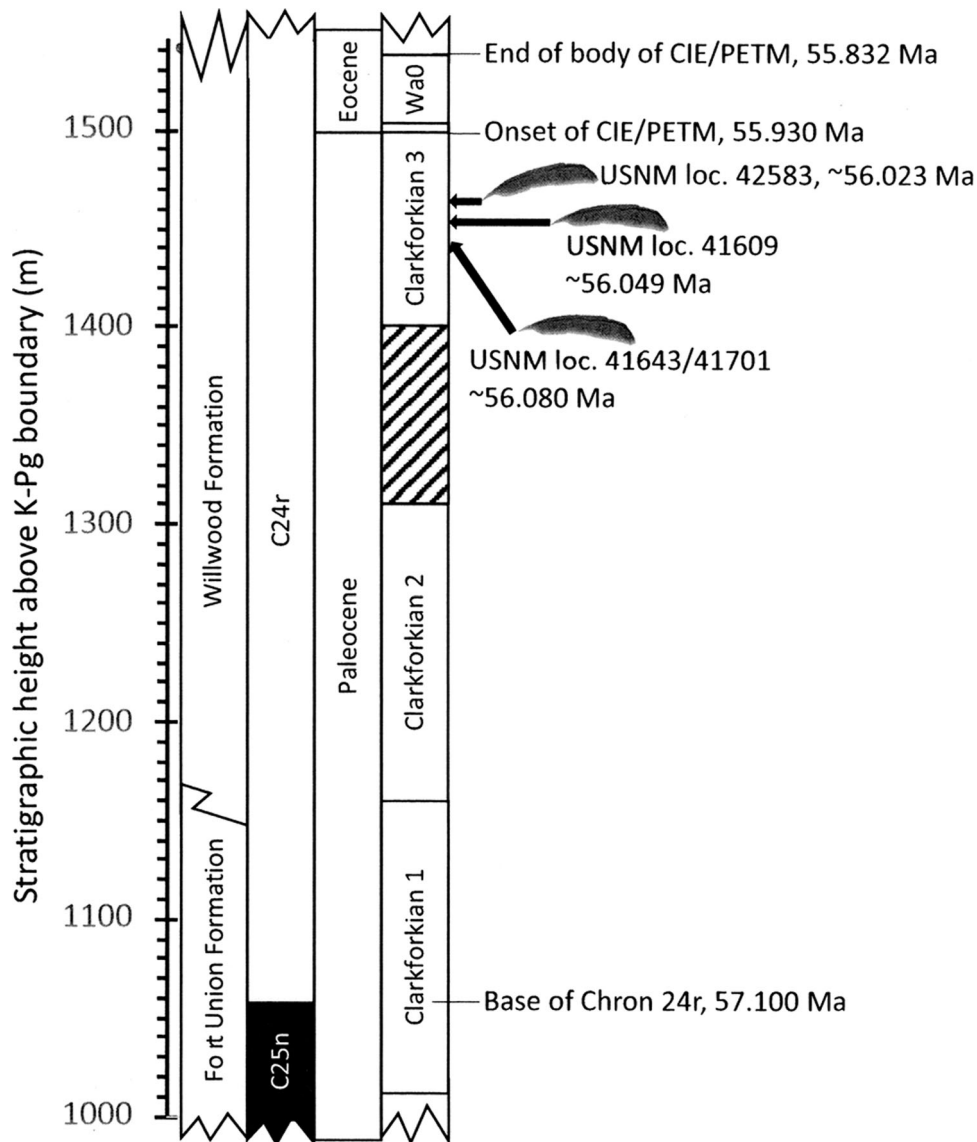


FIGURE 1 Stratigraphic and chronological context for Willwood Formation localities. Meter levels are from the stratigraphic section of Secord et al. (2006). Age estimates for Chron boundary and the onset and termination of the body of the CIE/PETM are from Westerhold et al. (2020). Age estimates for paleobotanical sites are derived by linear interpolation of rock accumulation rates between levels of known age.

suspension in still water. Several features suggest the fossils are preserved in the fine-grained fill of abandoned fluvial channels: the overall lenticular cross section of the deposit, the fining upward from sand to mud, the multiple millimeter-to-centimeter scale, horizontally laminated fining-up sequences, abundant winged fruits, and the presence of aquatic animals such as fish and gastropods (Wing, 1984).

The fossil fruits described here were determined to be conspecific with fruits previously described as *Robinia mesozoica* Cockerell, which were reported to have been collected from a “sandstone on the south side of a yellow cliff a few miles north of Whitley Peak, which is about 25 miles north of Kremmling, Colorado” (Cockerell, 1912, 32–33). An outcrop fitting this description is visible on Google Earth satellite imagery at approximately

40.357387° N, 106.485853° W, and is mapped as being the Middle Park Mbr. of the Coalmont Fm. by Hail (1968). Cockerell thought the specimen came from the Late Cretaceous Laramie Formation, hence the specific epithet. Brown (1962) revised Cockerell's stratigraphy, recognizing the site was likely Paleocene. Hail located the Paleocene–Eocene boundary as being in the Middle Member of the Coalmont Formation (Fm.) (above the Middle Park Member) based on pollen samples containing *Platycarya* from a short distance away from the likely collecting site, making it probable that the *R. mesozoica* site is late Paleocene. This opinion is reinforced by the occurrence on the hand specimen bearing *R. mesozoica* of the base of a leaflet belonging to *Platanites raynoldsii*, a common late Paleocene to early Eocene taxon not known from the Cretaceous.

The new specimens were also determined to be conspecific with a fossil fruit described by Knowlton (1899) as *Acacia lamarensis* Knowlton, which was collected from the east bank of the Lamar River between Cache and Calfee creeks in Yellowstone National Park, Park County, Wyoming on 8/21/1888 by F. H. Knowlton and G. E. Culver (USGS paleobotany locality 985; pp. 655, 730 of Knowlton, 1899). Exposures in this area are mapped as belonging to the Washburn Group of the Absaroka Volcanic Supergroup and likely are in the Sepulcher or Lamar River Formation (Love and Christiansen, 1985). Radiometric ages are not associated directly with the locality collected by Knowlton and Culver, but the Lamar River Fm. in this area is ~52–50 Myr (Feeley and Cosca, 2003; Smith et al., 2008), so 4–6 Ma younger than the Willwood Fm. specimens collected ~80 km to the east.

In addition to the fossils indicated above, in this study we also re-examined the fossil fruits previously described as *Diploptropis claibornensis* Herendeen and Dilcher (1990a) because this species is closely related to the specimens described here and clearly referable to the Bowdichia clade.

Specimen preparation and documentation

Fossil specimens were prepared by degaging with needles and air scribe where necessary to reveal covered portions of leaflets and fruits. Specimens were photographed using a Canon (Tokyo, Japan) EOS 5D MARK II camera with a 60 mm macro lens. Leaflets and fruits of extant legume species were cleared and stained to compare details of venation (see Herendeen and Dilcher, 1990c for details). Leaf descriptive terminology follows that of Ellis et al. (2009). The fossils described here are deposited in the Paleobotanical Collections of the Department of Paleobiology, National Museum of Natural History (Smithsonian Institution).

Phylogenetic analyses

Because the two legume fossil species clearly display a set of morphological traits that are only known in extant genera of the early-branching papilionoid Bowdichia clade (Cardoso et al., 2012c, 2013b), their relationships were evaluated through phylogenetic analyses of morphological and molecular data derived from a data set previously published by Cardoso et al. (2012b, 2013a), where the complete generic composition of that clade was defined. The data set includes nuclear ribosomal internal transcribed spacers (ITS, including ITS1/5.8S/ITS2), two chloroplast DNA regions (*matK*, *trnL* intron), and morphology. The morphological data set from Cardoso et al. (2012b, c) included 29 characters, which was expanded by the addition of four characters that describe aspects of leaf and fruit structure not included in the earlier character set (Appendix S1). Twenty morphological

characters, as well as all molecular data, were treated as missing data for the fossil species and scored exclusively for extant taxa. Missing morphological characters largely involved floral characters, most of which were not preserved in the fossil specimens. Because recent phylogenetic analyses comprehensively sampled across the main genistoid lineages have suggested a sister relationship between the Bowdichia clade and the Brongniartieae clade (Cardoso et al., 2017; Queiroz et al., 2017), here we have used the genus *Poecilanthe*, a representative of the Brongniartieae, as the outgroup.

The combined data set was analyzed with parsimony and Bayesian inference as the phylogenetic reconstruction approaches. The parsimony analysis involved heuristic search strategies implemented in PAUP* version 4.0b10 (Swofford, 2002) that maximized the detection of global optima and clade stability (e.g., random addition sequences with tree-bisection-reconnection branch-swapping, steepest descent, and retention of all most parsimonious trees). Character state transformations were weighted equally and unordered (Fitch, 1971), and maxtrees was set to 10,000. Clade support was estimated through 10,000 bootstrap replicates (Felsenstein, 1985), each analyzed using the heuristic search parameters mentioned above but with only one tree retained per replicate. To evaluate alternative topologies against the most parsimonious relationships of the fossil species, we analyzed trees derived from constraints analyses, which enforced all possible placements of the fossil species as sister to each lineage within the Bowdichia clade, using the Kishino–Hasegawa (Kishino and Hasegawa, 1989) and Templeton (Templeton, 1983) tests as implemented in PAUP*.

Although Bayesian analysis of morphological data has not been as widely used as parsimony methods, empirical and simulation studies have shown that it may perform as well as or even better than parsimony (Nylander et al., 2004; Lee and Worthy, 2012; Wright and Hillis, 2014). The Bayesian analysis was run in MrBayes version 3.2.6 (Ronquist et al., 2012) under mixed models (Nylander et al., 2004), where the best-fit nucleotide substitution models (GTR + I + G for ITS and *matK*; GTR for *trnL* intron) were selected via the Akaike information criterion (AIC) in jmodeltest2 (Darriba et al., 2012). For morphological data, we used the Mk (Markov k) model (Lewis, 2001), which assumes equal or symmetrical state frequencies, that is transition from one state to another has the same probability as transition in the reverse direction. This model was originally developed for estimating phylogenetic trees from discrete morphological data, whether for living or fossil taxa (Lee and Worthy 2012; Wright and Hillis, 2014). In two separate runs of a Metropolis-coupled Markov chain Monte Carlo (MCMC) permutation of parameters, four simultaneous chains run for 8 million generations, sampling one tree at each 10,000th generation. The Bayesian majority-rule consensus tree at 50% was produced after a burn-in of 25%, where the group frequencies represent posterior probabilities (Huelsenbeck et al., 2002).

The software FigTree version 1.4.0 (Rambaut, 2012) was used for visualization of the phylogenetic trees and Adobe Illustrator for final editing. All phylogenetic analyses were run in the CIPRES Science Gateway v. 3.3 online portal (www.phylo.org) (Miller et al., 2010). Original molecular and morphological data sets and associated PAUP* and MrBayes command blocks are at the Dryad Digital Repository (Herendeen et al., 2021; see Data Availability section).

SYSTEMATICS

Family—Leguminosae

Subfamily—Papilionoideae

Bowdichia clade, Genistoid clade

Paleobowdichia Herend., D.B.O.S. Cardoso, F. Herrera & Wing, gen. nov.

Type—*Paleobowdichia lamarensis* (Knowlton) Herend., D.B.O.S. Cardoso, F. Herrera & Wing, comb. nov.

Genus description—Fossil fruits oblong, membranous, placental suture narrowly winged, apex rounded with an abrupt beak at the style base, base stipitate, numerous closely spaced ovules, funiculus attachment subapical, immediately below the radicle lobe. Fossil leaves alternate, compound, imparipinnate, petiole base and petiolules pulvinate, leaflet position variable, opposite to subopposite to alternate, leaflets elliptic, lamina straight to slightly curved, base asymmetrical. *Paleobowdichia* is most comparable to the extant genus *Bowdichia* Kunth and can be distinguished by its longer fruits, which have a greater number of ovules and the leaflet base, which is often unequal as compared to the leaflet base in *Bowdichia*, which is normally symmetrical.

Age—Latest Paleocene to late early Eocene

Etymology—The name *Paleobowdichia* was established to recognize the age, morphological similarity, and close relationship to the extant genus *Bowdichia*.

Paleobowdichia lamarensis (Knowlton) Herend., D.B.O. S. Cardoso, F. Herrera & Wing, comb. nov. Basionym: *Acacia lamarensis* Knowlton, U.S. Geol. Surv. Monogr. 32: 730, Plate 98, Fig. 6. 1899. Type: east bank of the Lamar River between Cache and Calfee creeks in Yellowstone National Park, Park Co., Wyoming (holotype: USNM4413). Figure 3A.

Robinia mesozoica Cockerell, Torreyia 12(2): 32, Fig. 1. 1912. Type: Univ Colorado (holotype: UCM4627a&b). Fig. 3B, C.

Description—The fossil taxon consists of associated fruits (Figures 2–4) and leaves (Figures 5–7) found together in close association at three sites. The fossil fruits are oblong, membranous, and narrowly winged along the placental suture (Figures 2–4); the apex is rounded with an abrupt beak at the style base, straight or hooked toward a non-placental suture (Figures 2A, B, D, 3B). Fruit base is stipitate and obtuse to slightly tapered and acute (Figures 2C, 3B, C).

Fruit length is ca. 10.9 cm (one complete specimen), which includes the ca. 8 mm long stipe; fruit width is 8–14.5 mm, including the 1.75–3 mm wide nonvascularized wing. The wing extends from the base of the fruit valves to the apex. The fruits bear numerous closely spaced ovules (ca. 35 ovules in single complete specimen; 3–4 ovules/cm valve length); ca. 12 apparently mature seeds in the single complete specimen; Figures 2, 4). Abortive ovules are preserved as well as apparently mature seeds (Figure 2B, D). The seeds are transversely oriented, usually with a prominent, curved radicle (Figures 2D, 3). Seeds are 4–5 mm long, 2–3 mm wide. The funiculus attachment (raphe) is lateral, immediately below the radicle lobe (Figures 2D, 3). The funiculus is curved, filiform, ca. 3 mm long. Fruit valve venation is transverse and reticulate (Figures 2B, 2D, 3). The primary veins of the valves are transversely oriented but have an oblique angle of origin on the nonplacental suture; they arise from the suture at an angle of ca. 30–40° and pass into the valve obliquely for 5–7 mm before becoming transverse (Figure 2D). On the placental suture, the primary veins of the fruit valves are essentially perpendicular. Venation in the central portion of the valves is reticulate. The valve venation is best preserved along the margin of the fruit on the nonplacental suture. Small, brown spots are present on the surface of some of the fruit specimens. When present, the spots are irregular in shape, distribution, and abundance (e.g., Figure 2D). The origin of the spots is uncertain but are hypothesized to be fungal.

Leaf arrangement alternate, leaves petiolate with petiole base inflated by presence of a fleshy transversely wrinkled pulvinus (Figure 5A); leaf organization once pinnately compound, imparipinnate (single terminal leaflet; Figure 6A); leaflet attachment petiolulate with fleshy wrinkled pulvinus (Figure 6D, E); petiolule 1–5 mm long, ca. 1 mm wide; leaflet organization variable, opposite to subopposite to alternate (Figures 5, 6). Blade attachment to petiolule marginal. Lamina size microphyll to notophyll; shape elliptic and asymmetrical, straight to slightly curved, L:W ratio 1.7–2.3:1 (35–90 mm long, 17–44 mm wide); leaflet base has width asymmetry. Leaflet margins unlobed and untoothed but with probable nonvascular thickening. Apex acute, straight to convex, neither retuse nor mucronate; base obtuse to acute, convex. Surface texture apparently smooth. Surficial glands not observed. Secondary venation pinnate; basal veins absent; agrophic veins absent. Major secondaries brochidodromous, spacing regular, uniform; attachment excurrent. Interior and minor secondaries absent. Intersecondaries present but uncommon (<1 per intercostal region), proximal course perpendicular to midvein, distal course perpendicular to subjacent major secondary, generally >50% of the length of the subjacent secondary. Intercostal tertiary veins reticulate to opposite percurrent with convex course; when percurrent oriented obtuse to midvein but at inconsistent angles. Epimedial tertiaries percurrent; proximal course perpendicular to midvein; distal course basiflexed. Exterior tertiary course looped. Quaternary vein fabric regular reticulate. Marginal

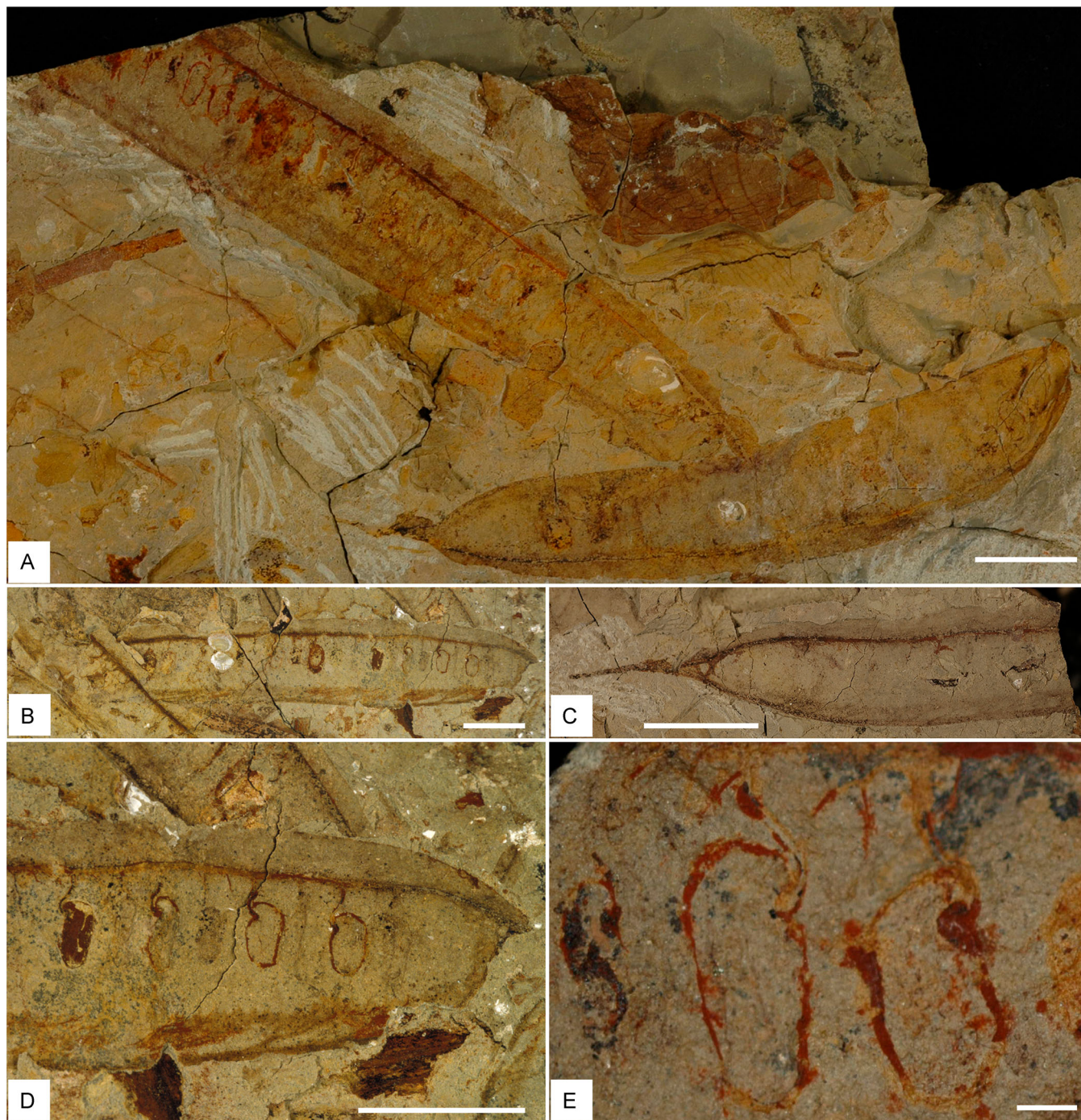


FIGURE 2 Fossil fruits of *Paleobowdichia lamarensis* from the late Paleocene Bighorn Basin of Wyoming. (A) Two winged membranous fruits showing numerous seed outlines. USNM538457A (upper, left), USNM538456 (lower, right). (B) Fruit showing outlines of numerous ovules and presumably mature seeds, many with funiculus preserved. Note well-preserved valve venation on nonplacental suture. Also note freshwater bivalve shell near center of the fruit. USNM509402A. Partial fruit oriented obliquely is USNM509403. (C) Base of fruit showing stipitate structure. USNM509407B. (D) Close-up of fruit shown in B illustrating details of ovules and valve venation. Note slender funiculus attached to ovule on left side below radicle lobe. Also note absence of vascularization in fruit wing. USNM509402A. (E) Close-up of ovule and seeds with funiculus attachment. USNM 538457A. Scale bars A–D = 10 mm, E = 1 mm

ultimate venation looped. Areolation formed by 4th and 5th order veins. Areoles small (~0.1 mm), regular, polygonal to round, with spikey or one-branched freely ending veinlets. Currano et al. (2009) estimated leaf mass per area for 139 specimens from USNM locality 41643/41701 as 128 g/m²

(95% prediction interval 92–179 g/m²) using the method of Royer et al. (2007), indicating moderate lamina thickness.

Remarks—The fossil fruits and leaves described here are thought to be derived from the same plant species based on several lines of evidence. Both fruits and leaflets are



FIGURE 3 Fossil fruits. Type specimens of “*Acacia*” *lamarensis* Knowlton and “*Robinia*” *mesozaica* Cockerell. (A) Holotype of *Paleobodichia lamarensis* (basionym *Acacia lamarensis*), USNM4413. (B) Holotype of “*Robinia*” *mesozaica* Cockerell. University of Colorado Boulder, UCM467. (C) Close-up of (B) to show details of fruit including valve and non-vascularized wing. Scale bars = 10 mm

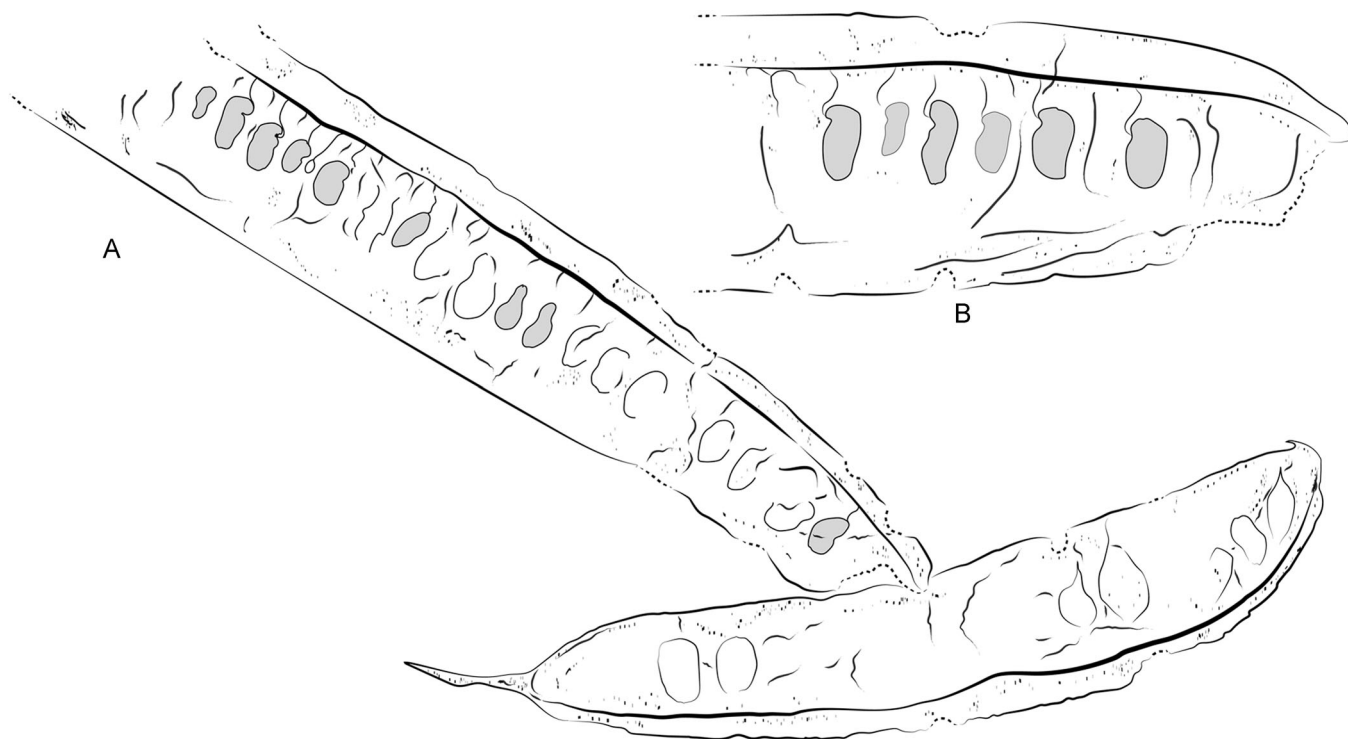


FIGURE 4 Line drawings of fruits of *Paleobowdichia lamarensis* to show venation details and ovule structure. (A) Fruits figured in Figure 2A. (B) Fruit figured in Figure 2D

abundant at USNM loc 41643/41701 and are the only fabaceous fossils at the site. Fruits and leaflets are less abundant but both present at USNM loc. 42583, and as at USNM loc. 41643 they are the only types of fabaceous remains. Leaves are rare, but no fruits were found at USNM loc. 41609. Assessments of systematic relationships of the fruits and leaves were done independently, and in both cases arrived at the papilionoid Bowdichia clade as the most comparable to the fossils (see results of phylogenetic analyses below).

The fossil fruits described here from the Bighorn Basin of Wyoming are essentially identical to fruits that Knowlton (1899) described as *Acacia lamarensis* Knowlton (Figure 3A) from Yellowstone National Park in Wyoming and fruits that Cockerell (1912) described as *Robinia mesozoica* Cockerell (Figure 3B, C) from the “south side of a yellow cliff a few miles north of Whitley Peak, which is about 25 miles north of Kremmling, Colorado”. Brown (1962) refigured Cockerell’s specimens and noted that Cockerell’s assumption that the specimen came from strata of Laramie age (hence the specific epithet) was likely incorrect. Brown argued that the specimen came from the Paleocene to early Eocene Coalmont Formation. Brown (1962) treated *R. mesozoica* as conspecific with *Acacia wardi* Knowlton, *A. lamarensis* Knowlton, and *A. macrosperma* Knowlton under the name *R. wardi* (Knowlton) Brown, but we do not agree that all four of these taxa are conspecific. We found that the type specimens of *Acacia lamarensis* and *Robinia mesozoica* are conspecific and distinct from the other two species described by Knowlton (1899).

Knowlton (1899) suggested that *Acacia lamarensis* might be conspecific with *A. macrosperma* Knowlton, but our examination of the types of both species indicates that they indeed are distinct. In studying the types of these taxa, we found that *Acacia lamarensis* and *Robinia mesozoica* are conspecific with the Bighorn Basin fossils described here. Therefore, according to Art. 11.3 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018), we are obligated to adopt the specific epithet “lamarensis” for this taxon because it is the name with nomenclatural priority. Knowlton (1899) also described fossil leaflets from the same locality as *Leguminosites lamarensis* Knowlton, but preservation is poor, and it is not possible to determine whether they are conspecific with the fossil leaves described here.

The fossil leaves and leaflets reported in this study were previously referred to informally as morphotype FU750 (Currano et al., 2008, 2010, fig. 1C, appendix B, figs. 5E [USNM 509415] and 5F [USNM 509415]).

Tobya Herend., D.B.O.S. Cardoso, F. Herrera & Wing, gen. nov.

Type—*Tobya claibornensis* (Herend. et Dilcher) Herend., D.B.O.S. Cardoso, F. Herrera & Wing, comb. nov.

Genus description—The genus is characterized by fossil fruits that are stipitate, oblong to oblanceolate with a rounded apex and tapering base, thin and membranous, 5.3–7.0 cm long and ca. 2.0 cm wide. The placental suture

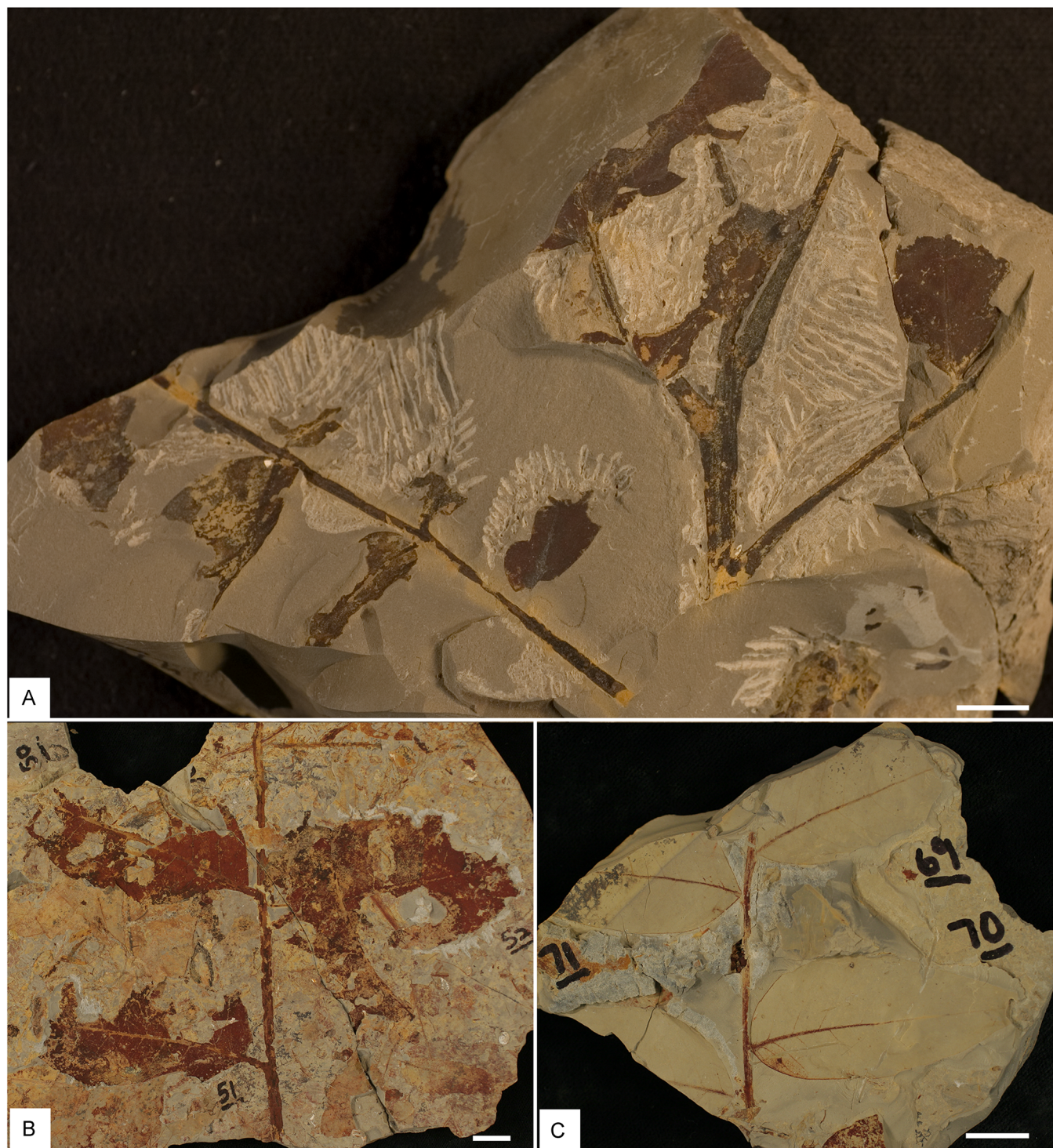


FIGURE 5 Fossil leaves. (A) Stem with at least four attached pinnately compound leaves. USNM509395A. (B) Portion of compound leaf with three attached leaflets. USNM538454. (C) Leaf with four attached leaflets, position subopposite to alternate. USNM538449. Scale bars = 10 mm

supports a narrow (2 mm, maximum width) non-vascularized wing. The fruit body consists of three longitudinal zones: a central thicker zone and two flanking thinner zones. The primary veins of the valves have an oblique and irregular course from the sutures to the fruit center, where they form a fine reticulum. Seed outlines not observed. Leaves not known.

Etymology—The genus is named in honor of R. Toby Pennington (University of Exeter, UK), for his many contributions to understanding the diversity and biogeography of legumes. Professor Pennington grew up in Lyme Regis, on the English Channel coast where he went fossil hunting during his childhood. The region is now recognized as the Jurassic Coast, a World Heritage Site.

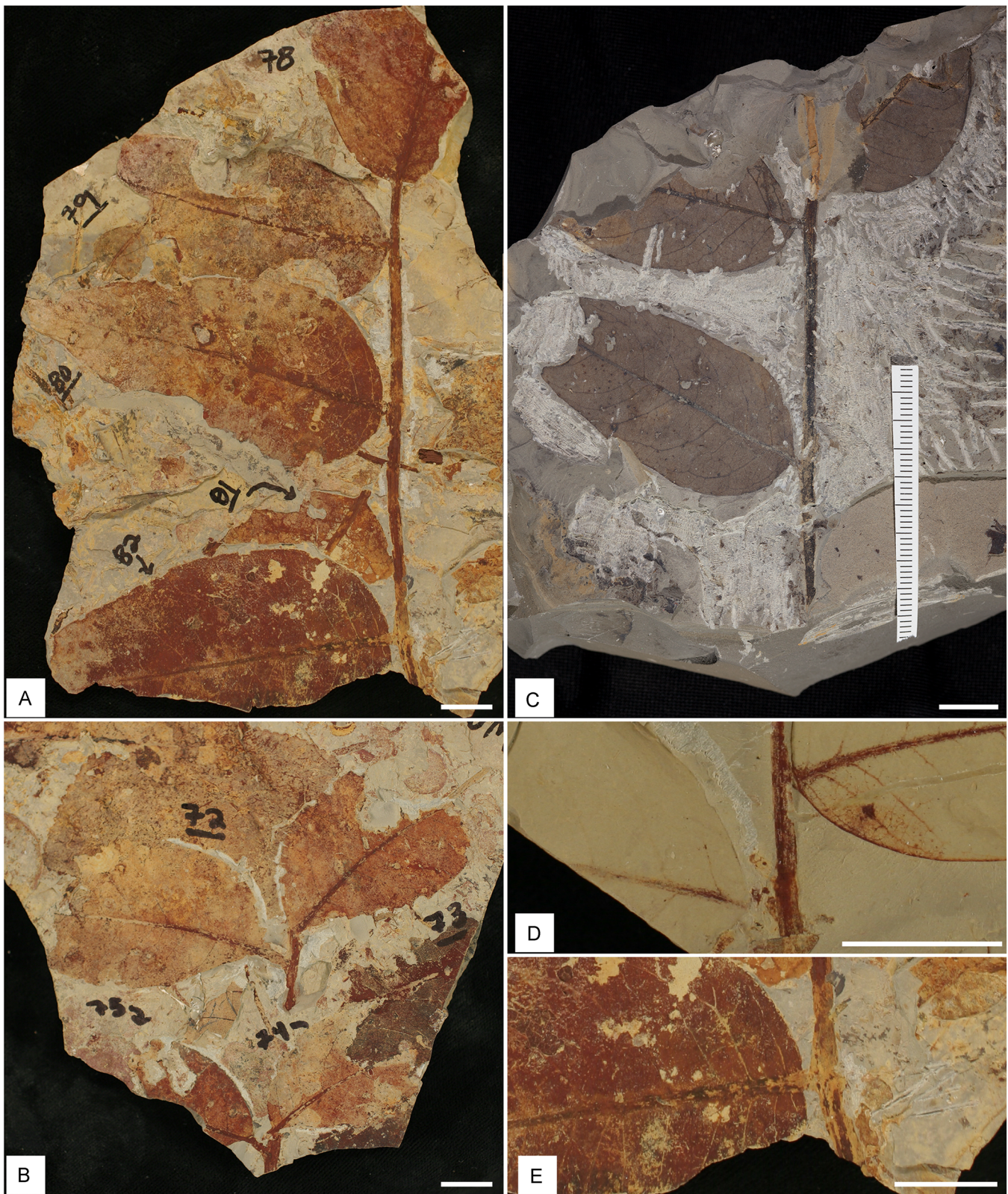


FIGURE 6 Fossil compound leaves. (A) Specimen with four attached leaflets, including a single terminal leaflet. USNM509415A. (B) Specimen with attached leaflets showing subopposite arrangement. USNM538454A. (C) Incomplete leaf showing subopposite leaflet arrangement. USNM509406. (D) Enlargement of Figure 5C to show petiolule with pulvinus. (E) Enlargement of Figure 6A to show petiolule with pulvinus. Scale bars = 10 mm

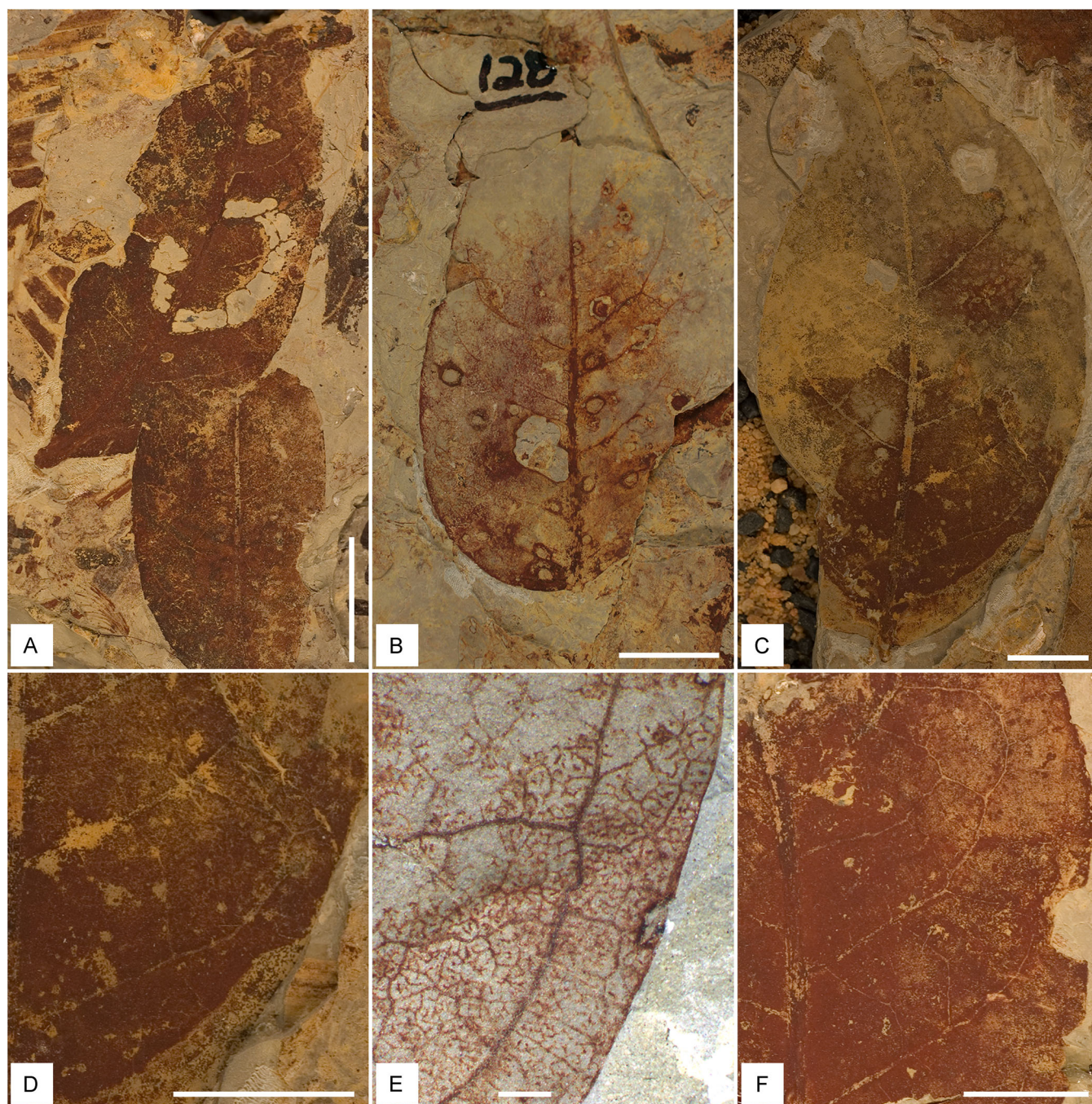


FIGURE 7 Detail of leaflets. (A) Leaflet with circular insect mine in the lamina. USNM538450. Scale bar = 10 mm. (B) Leaflet with circular and irregular feeding damage. USNM538452. Scale bar = 10 mm. (C) Leaflet with circular and irregular feeding damage. USNM538451. Scale bar = 10 mm. (D) Enlargement of base of leaflet shown in C to illustrate venation details. Scale bar = 10 mm. (E) Enlargement of central margin region of leaflet to illustrate venation details. USNM 772323. Scale bar = 1 mm. (F) Enlargement of leaflet to show venation details. USNM538453A Scale bar = 10 mm

Tobyia claibornensis (Herend. & Dilcher) Herend., D.B.O.S. Cardoso, F. Herrera & Wing, comb. nov. Basionym: *Diploptropis claibornensis* Herendeen & Dilcher, Syst. Bot. 15(4): 527, figs. 1-4. 1990. Type: Tennessee, Weakley Co., Warman clay pit, 15826–7235, 7235' (counterpart) (holotype: FLMNH). Paratype: Kentucky, Graves Co., Bell City clay pit, 15803–6085, 6085' (FLMNH).

Remarks—Fruits of *Tobyia claibornensis* are most comparable to those of the extant genera *Staminodianthus* D.B.O.S. Cardoso, H.C. Lima & L.P. Queiroz (Figure 8G) and *Guianodendron* Sch. Rodr. & A.M.G. Azevedo (Figure 8H). *Staminodianthus* includes three species that were previously included in the genus *Diploptropis* Benth. (Cardoso et al., 2013a). *Guianodendron* includes a single species, *Guianodendron praeclarum* (Sandwith) Sch.Rodr. &

A.M.G.Azevedo, which was previously known as *Acosmium praeclarum* (Sandwith) Yakovlev. Rodrigues and Tozzi (2006) noted the similarities between *G. praeclarum* and *Diptotropis*, but they established the genus *Guianodendron* for the species because its actinomorphic flowers and a reduced number of stamens would be inconsistent with the bilateral flowers of *Diptotropis* species. Fruits of *Staminodianthus* (except *S. rosea*, which has water dispersed fruits) and *Guianodendron* are very similar to *Tobya claibornensis* and all of the fruit characters scored for *T. claibornensis* are scored identically for the species of *Staminodianthus* (except *S. rosea*) and *Guianodendron*.

DISCUSSION

Phylogenetic relationships and morphological comparisons

Both parsimony and Bayesian analyses conducted in this study yielded a topology (Figure 9) that is essentially the same as was found by Cardoso et al. (2012b, 2013b). Interrelationships among all genera were strongly supported, except for the sister relationship of the fossil *Tobya claibornensis*. Regardless, *T. claibornensis* was grouped in a clade together with the genera *Guianodendron* and *Staminodianthus* with strong support (Figure 9). *Paleobowdichia lamarensis* was strongly supported as sister to *Bowdichia*, and this clade was grouped as sister to the genus *Leptolobium*, also with strong support (Figure 9).

Constrained trees that enforced *Paleobowdichia lamarensis* outside the clade comprised of *Bowdichia* + *Leptolobium* and as sister to any lineage from within the clade comprised of *Guianodendron* + *Tobya* + *Staminodianthus* significantly differed from the unconstrained most parsimonious tree (Table 2). This result suggests that *P. lamarensis* is robustly supported as sharing at least a most recent common ancestor (MRCA) with *Bowdichia* and *Leptolobium* Vogel. Although only two of the alternative topologies constraining the placement of *Tobya claibornensis* are significantly different (Table 2), the analyses at least strongly support that it is not congeneric with *Paleobowdichia*, and thus, its recognition as new genus is also warranted.

Membranous, samara-like fruits with a narrow non-vascularized wing on the placental margin as seen in *Paleobowdichia lamarensis* and *Tobya claibornensis* occur in a number of legume genera (Herendeen and Dilcher, 1990a). Within the Papilionoideae, the genera *Bowdichia*, *Leptolobium*, *Diptotropis*, *Deguelia* Aubl., *Staminodianthus*, *Robinia* L., and *Calpurnia* E.Mey are most comparable to the fossil fruits. Although fruits of some *Robinia* species (e.g., *R. pseudoacacia* L.) have a narrow nonvascularized wing or a more robust flange on the placental suture, the fruit is more substantial with thicker valves and less prominent venation than observed in the new fossil fruits. The venation of the valves is not similar to that seen in the fossils. Fruits of some species of *Calpurnia* [e.g., *C. aurea*

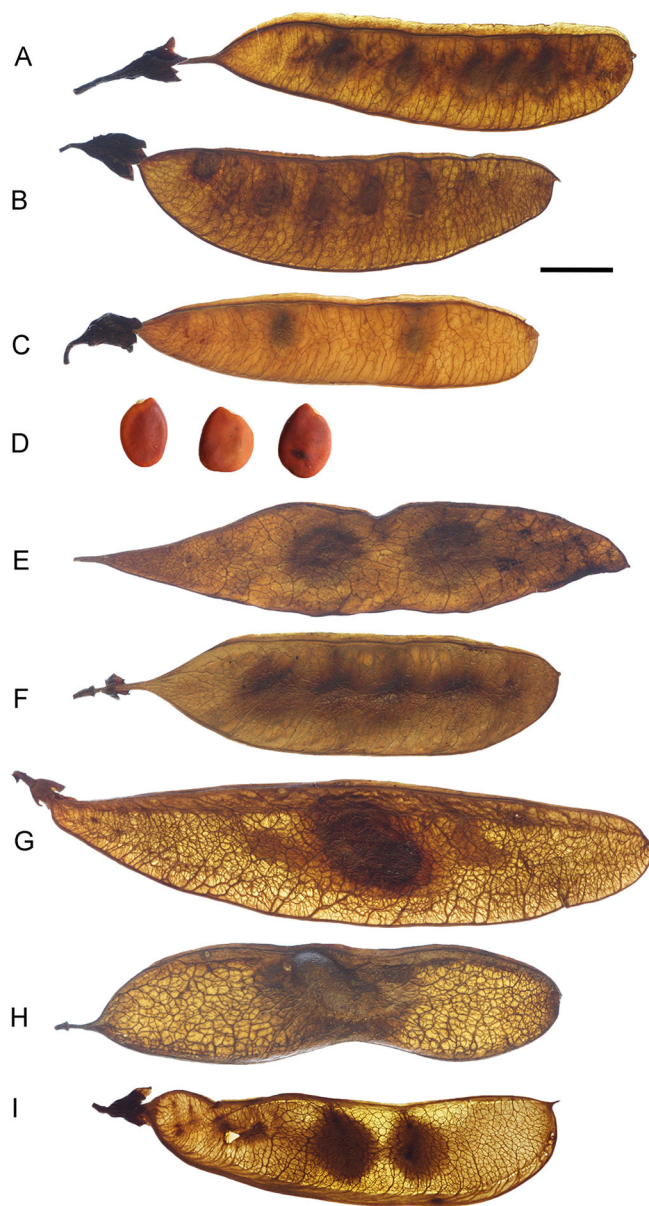


FIGURE 8 Fruits and seeds of *Bowdichia* clade taxa for comparison with *Paleobowdichia lamarensis* and *Tobya claibornensis* fossil fruits. (A–D) *Bowdichia virgilioides* Kunth. (A–C) Fruits. (D) Seeds. (A) L. Croizat s.n., April 3–10, 1950 (F). (B) H.S. Irwin, J.W. Grear, Jr., R. Souza, R. Reis dos Santos 14859, 15 April, 1966 (F). (C, D) B.A.S. Pereira 1110, 7 Aug. 1984 (US). (E) *Leptolobium panamense* (Benth.) Sch. Rodr. & A.M.G. Azevedo. G. S. Bunting 8496, 16 December 1979 (US). (F) *Leptolobium bijugum* (Spreng.) Vogel. R.P. Belem & R.S. Pinheiro 2105, 9.5.1966 (F). (G) *Staminodianthus duckei* (Yakovlev) D.B.O.S. Cardoso & H.C. Lima. A. Ducke 64, June 1932 (F). (H) *Guianodendron praeclarum* (Sandwith) Sch.Rodr. & A.M.G. Azevedo. Forest Dept, 3286, Sept 16, 1940 (US). (I) *Diptotropis brasiliensis* (Tul.) Benth. A. Ducke s.n. (R.B. no. 23355), July 31, 1929 (US)

(Aiton) Benth.] and *Deguelia* [e.g., *Deguelia longifolia* (Benth.) Taub.] are narrowly winged on the placental suture, but the valve venation is not similar to that observed in the fossil fruits. The fossil fruits of *P. lamarensis* exhibit an asymmetrical ovule structure that is characteristic of the Papilionoideae with a subapical hilum and funiculus

TABLE 2 Summary of the parsimony constraints analyses (Kishino–Hasegawa and Templeton tests), which enforced the sister relationship of the fossils *Paleobowdichia lamarensis* and *Tobya claibornensis* with each lineage of the Bowdichia clade. The first topologies in bold show the placement of the fossils in the parsimony unconstrained analysis. *P* values in bold indicate significant difference at $P < 0.05$

Unconstrained/Constrained trees	MPT	<i>L</i>	CI	RI	<i>P</i> (K-H test)	<i>P</i> (<i>t</i> -test)
(Lept,(Plam,Bowd)) and (Guia,(Tclai,Stam))	35	632	0.789	0.884	—	—
(Plam,Lept)	49	633	0.788	0.883	0.3174	0.3173
(Plam,(Bowd,Lept))	35	633	0.788	0.883	0.3174	0.3173
(Plam,(Dipl,(Guia,Tclai,Stam)))	59	634	0.787	0.882	0.1573	0.1573
(Plam,Dipl)	354	636	0.784	0.880	0.0455	0.0455
(Plam,(Guia,Tclai,Stam))	54	636	0.784	0.880	0.0455	0.0455
(Plam,Stam)	86	637	0.783	0.879	0.0253	0.0253
(Plam,Guia)	56	637	0.783	0.879	0.0253	0.0253
(Plam,Tclai)	35	637	0.783	0.879	0.0253	0.0253
(Plam,((Bowd,Lept),(Dipl,(Guia,Tclai,Stam))))	51	634	0.787	0.882	0.1573	0.1573
(Tclai,Lept)	30	634	0.787	0.882	0.1573	0.1573
(Tclai,(Lept,(Plam,Bowd)))	5	634	0.787	0.882	0.1573	0.1573
(Tclai,Plam)	9	636	0.784	0.880	0.0455	0.0455
(Tclai,Bowd)	6	636	0.784	0.880	0.0455	0.0455
(Tclai,(Plam,Bowd))	17	634	0.787	0.882	0.1573	0.1573
(Tclai,(Dipl,(Guia,Stam)))	7	633	0.788	0.883	0.3174	0.3173
(Tclai,Dipl)	53	633	0.788	0.883	0.3174	0.3173
(Tclai,(Guia,Stam))	5	632	0.789	0.884	1.000	—
(Tclai,Guia)	14	632	0.789	0.884	1.000	—
(Tclai,(((Bowd,Plam),Lept),(Dipl,(Guia,Stam))))	15	634	0.787	0.882	0.1573	0.1573

Abbreviations: MPT, number of most parsimonious trees; *L*, length of MPT; CI, consistency index; RI, retention index; K-H test, Kishino–Hasegawa test (Kishino and Hasegawa, 1989); T test, Templeton (Wilcoxon signed-ranks) test (Templeton, 1983); Bowd, *Bowdichia*; Lept, *Leptolobium*; Guia, *Guianodendron*; Dipl, *Diptotropis*; Stam, *Staminodianthus*; Tclai, *Tobya claibornensis*; Plam, *Paleobowdichia lamarensis*.

attachment (Figure 2D, E). All other legume subfamilies have fruits with symmetrical ovules with an apical hilum and funiculus attachment. Ovule structure in *T. claibornensis* is not evident in the fossil specimens.

Paleobowdichia lamarensis and *Tobya claibornensis* are most comparable to several genera of the Neotropical Bowdichia clade (Cardoso et al., 2012b, 2013b), including *Bowdichia*, *Staminodianthus*, *Guianodendron*, *Diptotropis* and some species of *Leptolobium* (Figure 8). These extant genera are generally characterized by the presence of a narrow nonvascular wing on the placental suture, although they vary in size, shape, texture and venation of the valve walls, and ovule number.

The fossil leaves of *P. lamarensis* described here are also most comparable to the genus *Bowdichia*, although a few characters are not satisfactorily documented in the fossils due to inadequate preservation. Like the fossils, leaves of *Bowdichia* are imparipinnate with leaflets that vary in position from opposite to subopposite to alternate, sometimes on the same leaf (Appendix S2). Leaflet shape varies from ovate to oblong, and leaflets are normally straight (symmetrical). The leaflet base is usually obtuse and equal. The base of the fossil leaflets is often unequal, and in this respect, they are more similar to leaflets found in species from the more distantly related extant genus

FIGURE 9 Phylogenetic placement of the legume fossils *Paleobowdichia lamarensis* and *Tobya claibornensis* in the Bowdichia clade, a genistoid early-branching lineage of Papilionoideae that is highlighted in red in the circular *matK*-based Bayesian majority-rule consensus cladogram largely sampled across all major lineages of Leguminosae. Both the Bayesian majority-rule consensus phylogram (top) and parsimony strict consensus tree (bottom) showing the relationships of the fossils within the Bowdichia clade were derived from combined analyses of DNA sequence (ITS/5.8S, *matK*, *trnL* intron) data and 29 morphological characters. Numbers on branches of the Bayesian tree and parsimony trees are the posterior probabilities and parsimony bootstrap support values, respectively. Legume classification of subfamilies follows LPWG's (2017) new system, whereas the general phylogenetic subdivision within Papilionoideae follows Cardoso et al. (2012c). Photographs of the bilaterally symmetrical flowers of *Diptotropis purpurea* and *Bowdichia virgilioides*, and of the radially symmetrical flower of *Leptolobium brachystachyum* are by Domingos Cardoso

Diploptropis within the Bowdichia clade (Figure 9). The apex of most fossil leaflets is not preserved, often due to insect damage, but the shape appears to vary from obtuse to acute.

Genera of the Bowdichia clade are most easily distinguished from each other by floral characters (Cardoso et al., 2012b, 2013a), but unfortunately fossil flowers are not preserved. The fossil fruits and leaves of *P. lamarensis* exhibit the greatest similarities to the genus *Bowdichia*, which includes two species, *B. virgilioides* Kunth and *B. nitida* Spruce ex Benth. The most notable differences between *P. lamarensis* and extant *Bowdichia* include the larger number of ovules in the fossil fruits and the more common occurrence of unequal leaflet bases as compared to what is observed in the extant species of *Bowdichia*. For these reasons, we describe these fossils as a species in the new genus *Paleobowdichia*. The phylogenetic analyses confirmed this relationship in placing *P. lamarensis* as sister to *Bowdichia* (Figure 9).

Tobya claibornensis was originally described as a species of *Diploptropis* by Herendeen and Dilcher (1990a) and found to be most comparable to two species of *Diploptropis* sect. *Racemosa*. Cardoso et al. (2013a) segregated this section from *Diploptropis* as the genus *Staminodianthus*. The phylogenetic analyses placed *T. claibornensis* as sister to *Staminodianthus* (Figure 9). Fruits of *Guianodendron praeclarum* (Figure 8H) are also very similar to *T. claibornensis*, and there are no differences between these taxa in the fruit characters that can be scored in the fossils. *Guianodendron* is grouped as sister to the clade composed of *T. claibornensis* and *Staminodianthus* (Figure 8G), but branch support in this clade is not strong. For these reasons, the new genus *Tobya* was established for the fossil species originally described as *Diploptropis claibornensis*.

Evolutionary transitions from bilateral to radial floral symmetry have been recurrent during the early evolutionary history of papilionoid legumes (e.g., Cardoso et al., 2012a, 2012c, 2013b; Ramos et al., 2016), where monotypic or species-poor genera marked by radial flowers are often sister to more diverse, bilateral-flowered genera. The independent evolution of radial flowers has occurred in multiple papilionoid lineages, including in the Bowdichia clade (Cardoso et al., 2012c). The radial-flowered genera *Guianodendron* and *Leptolobium*, despite being traditionally classified as congeneric (Cardoso et al., 2012a, b; Rodrigues and Tozzi, 2007), are consistently shown as non-sister taxa, and each is phylogenetically closer to a bilateral flowered genus. Unfortunately, fossilized flowers of *Paleobowdichia lamarensis* and *Tobya claibornensis* are completely unknown, which leaves an open question as to whether the tendency for independent evolution of nonpapilionate floral architecture involving radial floral symmetry, undifferentiated petals, and completely exposed reproductive organs has been more common and ancient in the Bowdichia clade than we previously thought.

Early fossil record of Leguminosae and Papilionoideae

The Eocene fossil record of the legume family, particularly of the Papilionoideae, is relatively extensive. Five of the six subfamilies (Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, Papilionoideae; LPWG, 2017) are documented in the fossil record by the end of the Eocene, as are multiple genera of Papilionoideae, including *Tobya*. Only the Duparquetioideae, which includes a single species from West and Central Africa, is unknown in the fossil record. In contrast, fossil legumes from the Paleocene are much less abundant, although they are morphologically diverse (based on leaves and fruits) and with at least three of the subfamilies present at around 60 million years ago (i.e., Caesalpinioideae, Detarioideae, Dialioideae) (Herrera et al., 2019). The earliest taxonomically verified record of the family is represented by fossil fruits and leaflets from the Early Paleocene of the Denver Basin in Colorado (Lyson et al., 2019). The subfamily affinities of these fossils are unknown. Also from the Early Paleocene of Patagonia, Argentina, a permineralized fossil wood (*Paracacioxylon frenguelli*) and an unnamed fossil leaflet were described from the Salamanca Formation (Palacio de los Loros; Iglesias et al., 2007; Brea et al., 2008). From the Middle to Late Paleocene Cerrejón and Bogotá Formations of Colombia, ca. 500 compression/impression specimens with distinctive legume features are known (Herrera et al., 2019). Eight legume fruit and six legume leaf morphotypes were described from the fossil assemblage. Two bipinnate leaf morphotypes were placed in the Caesalpinioideae and are the earliest record of the subfamily. Two fruit morphotypes are placed in the Detarioideae and Dialioideae. All other fruit and leaf morphotypes from Colombia show similarities with more than one subfamily or their affinities remain uncertain. Although the Papilionoideae could be represented by one or more of these unidentified morphotypes, the fossils lack adequate distinctive features to be certain of their affinities. The abundance and diversity of legumes in the fossil floras from northern South America show that the family was the most ecologically important component of the earliest neotropical rainforests in northern South America, ca. 60–58 Ma (Herrera et al., 2019; Carvalho et al., 2021). Centeno-González et al. (2021) reported a legume-like fossil fruit from the Campanian (Late Cretaceous) Olmos Formation in northern Mexico. However, in our opinion, the resemblance of the single fossil fruit to the legume family is only superficial; structural details are not sufficient to be confident of the assignment to the Leguminosae.

This report of fossil fruits and leaves assigned to the Bowdichia clade of the Papilionoideae is significant because it represents the oldest confirmed record of this important subfamily, which is the most diverse clade within the Leguminosae. Papilionoid legumes are prominent members across all major global biomes (Schrire et al., 2005), where the plants range from large trees and woody lianas in tropical rainforests to perennials in many types of habitats, to

tiny desert annuals. The Bowdichia clade (Cardoso et al., 2012b) today comprises about 29 extant species belonging to five genera, the phylogeny of which is structured according to the wet-forest, savanna, and succulent biomes of mainly South America. Species diversity within the Bowdichia clade is about equally distributed among the three biomes. Ratter et al. (2006) cited constituent savanna species *Bowdichia virgilioides* and *Leptolobium dasycarpum* Vogel among the 116 dominant woody species of the cerrado flora. Likewise, *Diplotropis martiusii* Benth. and *Leptolobium nitens* Vogel are among the most common trees throughout the seasonally flooded forests of the Amazon basin (Cardoso et al., 2012b; ter Steege et al., 2013). The Bowdichia clade is a small group, yet it has radiated into three principal biomes of tropical South America, where some members have become ecologically dominant. The fossil record suggests that the clade was previously more widespread, including in North America, and became more geographically restricted since the Eocene. The middle Eocene Mississippi Embayment fossil floras likely lived in a substantially wetter and warmer climate than did the late Paleocene-early Eocene floras of the northern Rocky Mountain region (Frederiksen, 1980; Wing and Greenwood, 1993; Sloan and Morrill, 1998; Kraus et al., 2013). Thus, it is possible that the Bowdichia clade became diverse in both species number and habitat range during the Eocene, and that its current abundance, particularly in the wet-forest and succulent biomes, has been true for a long time. These facts make the ecological history of the Bowdichia clade captivating and worthy of study.

The new fossils of *P. lamarensis* from the Bighorn Basin are found at only three of more than 100 sites of very late Paleocene age (Wing et al., 1995; Wing and Currano, 2013). These very late Paleocene plant fossil sites from the Bighorn Basin occur in three major depositional settings: carbonaceous shales representing extensive floodplain backswamps; carbonaceous siltstones or sandstones representing deposition on point-bars, levees or crevasse splays; and mudstone lenses deposited in abandoned channels (Wing, 1984; Davies-Vollum and Wing, 1998). The absence of *P. lamarensis* from all carbonaceous shale sites of about the same age in this basin ($N > 20$) could indicate the species did not grow in swampy settings. All three sites with *P. lamarensis* are also in the northwestern part of the Bighorn Basin, where red, variegated paleosols caused by seasonal fluctuations in water table began to form earlier (late Paleocene) than in other parts of the Bighorn Basin (early Eocene) (Wing and Bown, 1984). This occurrence pattern could indicate that *Paleobowdichia lamarensis* preferred riparian settings in areas with seasonal precipitation or seasonal changes in soil moisture related to flooding.

The *Paleobowdichia lamarensis* fossils occur together with winged fruits of *Acer* sp., *Deviacer* sp., and *Lagokarpus lacustris* McMurran & Manchester, and leaves of *Trochodendroides genetrix* (Newberry) Manchester. Other leaves at these sites include *Browniea serrata* (Newberry) Manchester

& Hickey, *Davidia antiqua* (Newberry) Manchester, cf. *Gyrocarpus* sp., *Macginitiea gracilis* (Lesquereux) Wolfe & Wehr, *Metasequoia occidentalis*, *Platanites raynoldsii* Newberry (Manchester), cf. *Populus wyomingiana* (Berry) MacGinitie, *Populus wilmattae* Cockerell, *Ternstroemites aureavallis* Hickey, *Zizyphoides flabella* (Newberry) Crane, Manchester & Dilcher, cf. *Corylus acutertiaryaria* Hickey, and many other undescribed species of non-monocot angiosperms.

The fossils of *Paleobowdichia lamarensis* occur in the very late Paleocene and early Eocene, the peak of Cenozoic warm climates locally, regionally and globally (Wing, 1998; Currano et al., 2005; Westerhold et al., 2020). Mean annual temperature at the *Paleobowdichia* sites has been estimated at $15.7 \pm 2.4^\circ\text{C}$ based on leaf margin analysis (Currano et al., 2005). The presence of palms in the megafloora is inconsistent with sustained sub-freezing temperatures and probably indicates a cold month mean $>5.2^\circ\text{C}$ (Greenwood and Wing, 1995; Reichgelt et al., 2018). The combination of warm temperatures and drained soils at the Willwood Fm. sites producing *P. lamarensis* sites is consistent with a seasonal subtropical climate in the area during the latest Paleocene. The paleoclimate under which these earliest members of the Bowdichia clade grew was thus more similar to that of extant species in the clade than might be expected from the mid-latitude location.

The two fossil species described here, combined with the diversity of fossil legumes described from the middle to late Paleocene Cerrejón and Bogotá Formations in Colombia (Herrera et al., 2019) and the early Paleocene legume fruit and leaf from the Denver Basin of Colorado (Lyson et al., 2019), and fossil wood and leaflet from Patagonia (Iglesias et al., 2007; Brea et al., 2008) demonstrate that the family had undergone substantial diversification in the Americas during the Paleocene. In addition, fossil legume fruits from the late Paleocene Reading Beds in England (Herendeen and Crane, 1992) provide evidence that the family was also present in other parts of the world by that time. These fossil records represent relatively few data points for documenting the diversity of the family through this important early stage of diversification, but they are consistent with the conclusion based on phylogenomic analyses of extant legumes and molecular dating analyses that all six subfamilies originated nearly simultaneously (Koenen et al., 2021).

The rarity of Paleocene legume fossils in the Paleocene of the Rocky Mountains has not attracted much comment previously, but now that the family is well documented in the earliest and latest Paleocene, it is interesting that abundant and well-collected Paleocene floras from the region have few legume fossils (e.g., Brown, 1962; Manchester, 2014). Given hundreds of collecting sites from the Paleocene of the northern United States and south to Colorado and New Mexico, the rarity of legumes is unlikely to result from undersampling alone. We suggest that climate is likely to have been an important factor. The first and last part of the Paleocene were globally warmer than the middle (Westerhold et al., 2020), and the same trend has been

observed in the northern Rockies (Hickey, 1980; Wing et al., 1995; Wing, 1998). If legumes were diversifying during the Paleocene primarily in tropical to subtropical climates (which would hardly be surprising given the distribution of diversity in the family today), their abundance and diversity in mid-latitudes may have been enabled by periods of global warmth. If this is correct, Paleocene floras from the Mississippi Embayment, which are generally less well studied and less well constrained temporally, may record higher legume diversity than other areas of North America. Indeed, several types of undescribed fossil legume fruits and leaflets are known from the earliest Eocene of northwestern Wyoming, but are only present there during the Paleocene–Eocene Thermal Maximum (PETM) event (Wing et al., 2005; Wing and Currano, 2013). The fossils described in this paper provide strong evidence for the presence of a tropical-subtropical papilionoid lineage in this region immediately before the PETM, in the latest Paleocene, and again near the time of peak Cenozoic warmth in the late early Eocene.

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AUTHOR CONTRIBUTIONS

P.S.H. and S.L.W. led conception and design of project. S.L.W. directed fieldwork. D.B.O.S.C. and P.S.H. assembled the morphological matrix. D.B.O.S.C. assembled the molecular data set and led the combined phylogenetic analyses. P.S.H. wrote the initial manuscript draft; all authors contributed, reviewed, and edited further drafts.

DATA AVAILABILITY STATEMENT

Fossil material is housed in the Paleobotanical Collections of the National Museum of Natural History (Smithsonian Institution). Precise fossil locality coordinates are available to qualified researchers from the Dept. of Paleobiology, NMNH, Smithsonian Institution. Phylogenetic data matrices and other supplemental materials are available at the Dryad Digital Repository (Herendeen et al., 2021; <https://doi.org/10.5061/dryad.8sf7m0cng>).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Morphological character definitions and data for the phylogenetic analysis focusing on the genistoid Bowdichia clade. Morphological characters 14–33 are present only in extant lineages.

Appendix S2. Photographs of selected members of the Bowdichia clade for comparison with *Paleobowdichia la-marensis* and *Tobya claibornensis*. All photos by D.B.O.S. Cardoso unless otherwise indicated. A. *Bowdichia virgilioides* Kunth. B. *Bowdichia nitida* Spruce ex Benth. C. *Leptolobium bijugum* (Spreng.) Vogel. D. *Leptolobium dasycarpum* Vogel. Photo by L.P. Queiroz, by permission. E. *Staminodianthus duckei* (Yakovlev) D.B.O.S. Cardoso & H.C. Lima. F. *Diplotripsis peruviana* J.F. Macbr.

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