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LAURACEOUS FLOWERS FROM THE EOCENE OF VANCOUVER ISLAND: *TINAFLORA BEARDIAE* GEN. ET SP. NOV. (LAURACEAE)

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Premise of research. Twenty-one permineralized fossil flowers assignable to Lauraceae from the Eocene Appian Way locality on Vancouver Island, British Columbia, Canada, provide important anatomical and morphological data for interpreting evolutionary patterns in this diverse magnoliid family.

Methodology. Consecutive anatomical sections were prepared using the cellulose acetate peel technique. Morphology and anatomy of the flowers were determined from anatomical sections, and three-dimensional reconstructions were rendered from serial sections using the software Amira.

Pivotal results. Fossil flowers with oil bodies, trichomes, pollen, ovary anatomy, and other characters have allowed for the reconstruction of actinomorphic, pedicellate, and trimerous flowers with tepals in two whorls adnate to a shallow hypanthium. Nine fertile stamens occur in three whorls, the innermost of which bears paired glandular appendages, and a fourth whorl of sagittate staminodes surrounds the carpel. Anthers are tetrasporangiate. Stamens of the two outer whorls have median pollen sacs that are shorter than the two marginal pollen sacs. Third-whorl stamens have median pollen sacs that are longer than the marginal pollen sacs. Anthers of the first and second whorls are introrse, while the third-whorl anthers are extrorse. The fossil flowers have diagnostic characters of Lauraceae and are compared to flowers of extinct and extant taxa.

Conclusions. The Eocene floral remains are assigned to *Tinaflora beardiae* gen. et sp. nov. We infer some aspects of floral biology based on different stages of development preserved among the fossils. The combination of well-preserved floral organs and in situ pollen is rare in the fossil record, allowing *T. beardiae* to expand the diversity of lauraceous floral morphology and provide further evidence for an Eocene radiation of the family in Laurasia.

Keywords: Eocene, flowers, fossils, Lauraceae, *Neocinnamomum*.

Online enhancement: video.

Introduction

With 50 genera and 2500–3500 species, the Lauraceae is one of the most diverse magnoliid families (Rohwer 1993*a*). The fossil record of this family is rich and dates back to the Early Cretaceous (Eklund 1999; von Balthazar et al. 2007). Due to a dynamic evolutionary history (Renner 2005), a large number of species, and high levels of extinction, the evolutionary patterns within Lauraceae are not fully understood. Furthermore, the most common fossils known from this family are biased toward leaves and wood, while the systematically significant reproductive structures (e.g., inflorescences, flowers, pollen, and fruits) are relatively uncommon (discussed in Eklund 1999; Friis et al. 2011). Therefore, more work is needed on lauraceous flower structure and development as well as the fossil record to elucidate the evolutionary patterns among diverse lauraceous lineages.

Over several decades, discoveries of fossil flowers and dispersed floral organs from Cretaceous sediments have revealed important data about the early evolution of Lauraceae (Drinnan et al. 1990; Herendeen et al. 1994, 1999; Eklund and Kvaček 1998; Eklund 2000; Takahashi et al. 2001, 2014; Kvaček and Eklund 2003; Frumin et al. 2004; von Balthazar et al. 2007; Viehofen et al. 2008). Molecular studies suggest that lineages leading to the most diverse clades of Lauraceae (e.g., the Perseeae-Laureae clade) underwent an evolutionary radiation early in the Eocene in Laurasia, followed by a second radiation during the Miocene in South America (Chanderbali

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et al. 2001; Renner 2005). However, there are too few fossil flowers or pollen grains from the Cenozoic of Laurasia to adequately test molecular clock hypotheses.

In this study, we describe a new genus and species, *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell et Bolton, from the Eocene Appian Way locality of British Columbia, based on anatomically preserved flowers with in situ pollen. These flowers are compared to those of extinct and extant taxa of Lauraceae. Flowers of *T. beardiae* provide important data regarding the evolution of lauraceous flowers and provide additional evidence of an Eocene Laurasian radiation.

Material and Methods

Twenty-one permineralized flowers were recovered from the Appian Way fossil locality (lat. 49°54′42″N, long. 125°10′40″W; UTM 10U CA 5531083N, 343646E) on the east coast of Vancouver Island, British Columbia. This locality is situated on the northern edge of the Tertiary Georgia Basin (Mustard and Rouse 1994). The Appian Way fossils are found in large calcareous concretions bearing permineralized fossil plants, gastropods, decapods, corals, echinoderms, bivalves, and foraminifera. These concretions are embedded in a silty-sandy graywacke matrix with trace fossils of crab burrows, which, in combination with the fossil assemblage, indicate a shallow marine paleoenvironment (Haggart et al. 1997). Mollusks, decapods (Schweitzer et al. 2003), and shark teeth support an Eocene age for the fossils (Haggart et al. 1997; Cockburn and Haggart 2007). Sweet (2005) compiled an inventory of pollen from the site and has found both late Paleocene and early Eocene elements present. The biostratigraphy of the area is currently being examined (J. W. Haggart, personal communication).

Appian Way locality plant fossils are represented by roots, stems, wood, leaves, flowers, fruits, pollen, pollen cones, seed cones, and fungi (Mindell 2008). Thus far, fruits of Juglandaceae (Elliott et al. 2006), Fagaceae (Mindell et al. 2007*a*, 2009), and Icacinaceae (Rankin et al. 2008); inflorescences of Platanaceae (Mindell et al. 2006*a*); cupressaceous pollen cones (Hernandez-Castillo et al. 2005); schizaeaceous (Trivett et al. 2006) and gleicheniaceous (Mindell et al. 2006*b*) ferns; and leafy liverworts (Steenbock et al. 2011) have been described from this locality. A basidiomycete polypore and an ascomycete pleosporalean fungus (Smith et al. 2004; Mindell et al. 2007*b*) have also been described.

Concretions were cut with a water-cooled saw, and slabs were subsequently peeled using the cellulose acetate peel technique (Joy et al. 1956). For LM, peel sections were mounted on slides using Eukitt (O. Kindler, Freiberg, Germany) mounting medium. Images were captured using a Better Light camera (Precision Digital Imaging System, Placerville, CA). One peel section that contained pollen was prepared for SEM by mounting with double sticky tape on a stub and coating with 9 nm of Au-Pd on a Cressington 108 sputter-coater. Images of pollen were obtained using a Quanta 600 FEG SEM (Oregon State University Electron Microscopy Facility, Corvallis, OR). Images were processed using Photoshop CS 5.0 (Adobe, San Jose, CA) and Pixelmator 4.0 (Vilnius, Lithuania). One flower was three-dimensionally reconstructed using Amira 5.6 (FEI, Hillsboro, OR). Specimens and microscope slides are housed in the University of Alberta Paleobotanical Collections, Edmonton, Alberta (UAPC-ALTA).

Systematics and Results

Order—Laurales

Family—Lauraceae Jussieu

*Genus—*Tinaflora *Atkinson, Stockey, Rothwell, Mindell et Bolton gen. nov.*

*Type Species—*Tinaflora beardiae *Atkinson, Stockey, Rothwell, Mindell & Bolton sp. nov.*

Generic diagnosis. Flowers pedicellate, trimerous, bisexual; perianth perigynous, with tepals equal sized. Androecium of nine fertile stamens in three alternating whorls; three staminodes in inner fourth whorl. Anthers tetrasporangiate; stamens of first and second whorls with introrse median pollen sacs and introrse-latrorse marginal pollen sacs; anthers of third whorl with extrorse median pollen sacs and extrorse-latrorse marginal pollen sacs. Filaments of third staminal whorl with paired glandular appendages. Staminodes sagittate and stipitate. Pollen psilate; carpel with superior ovary.

Specific diagnosis. Tepals lanceolate, fleshy, with up to seven vascular bundles. Filament up to twice as long as anther and tomentose. Oil cells ellipsoidal to ovoid. Hypanthium inner surface tomentose with unicellular trichomes. Pollen spherical, psilate, ca. 17 μm diameter.

Etymology. *Tinaflora* is named in honor of Tina Beard of Qualicum Beach, British Columbia, for help in collecting, field logistics, and providing a base camp for a large number of field crews for more than a decade.

Holotype. UAPC-ALTA AW641 G top (figs. 1*A*, 2*B*, 2*C*, 3*C*, 3*F*, 4*B*–4*D*).

Paratypes. UAPC-ALTA AW104 C top (fig. 2*A*); AW108 B bot (figs. 1*C*, 2*D*, 3*D*, 3*E*, 4*A*); AW130 D top; AW132 G top; AW144 G bot; AW260 C bot, D top; AW264 C top (fig. 1*B*); AW277 B bot, C top; AW279 D top; AW321 B top; AW374 E bot, F top; AW384 C top; AW391 B bot; AW541 J bot; AW546 B top (fig. 3*A*, 3*B*); AW613 C (fig. 1*D*); AW660 B top; AW665 I top; AW 668 C top.

Type locality. Appian Way, shoreline beach exposure on the eastern coast of Vancouver Island, south of Campbell River (lat. 49°54′42″N, long. 125°10′40″W; UTM 10U CA 5531083N, 343646E).

Stratigraphy. Oyster Bay Formation.

Age. Eocene.

Description. Twenty-one isolated flowers were found in the calcium carbonate concretions from the Appian Way fossil locality. Flowers are small, pedicellate, bisexual, actinomorphic, trimerous, perigynous, and somewhat fleshy (figs. 1, 2*A*, 2*B*; see video 1, available online). Flowers are up to 4.0 mm long and 3.0 mm in diameter, with a pedicel that is 2.0–3.0 mm long. Tepals, stamens, and staminodes are fused at the base, forming a shallow hypanthium that is up to 1.0 mm long.

Perianth. The perianth consists of six equal-sized tepals that are in two alternating whorls (figs. 1*A*, 5*A*). The tepals

Fig. 1 *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell, et Bolton gen. et sp. nov. *A*, Cross section of flower at ovary apex showing two alternate whorls of tepals (three per whorl), three whorls of stamens (three per whorl), stalks of staminal appendages, single whorl of three staminodes, and single carpel. AW 641 G top #1 ×34. *B*, Longitudinal section of flower showing elongate pedicel. AW 264 C top #11 ×11. *C*, Longitudinal section of flower displaying pedicel and various appendages. Note acute tip of tepal (arrow) and pubescence on various floral organs. AW 108 B bot #6 ×21. *D*, Tangential section of flower with shallow hypanthium showing large oil cells (arrow). Note vascular tissue diverging into hypanthium from pedicel. AW 613 C #3 ×23.

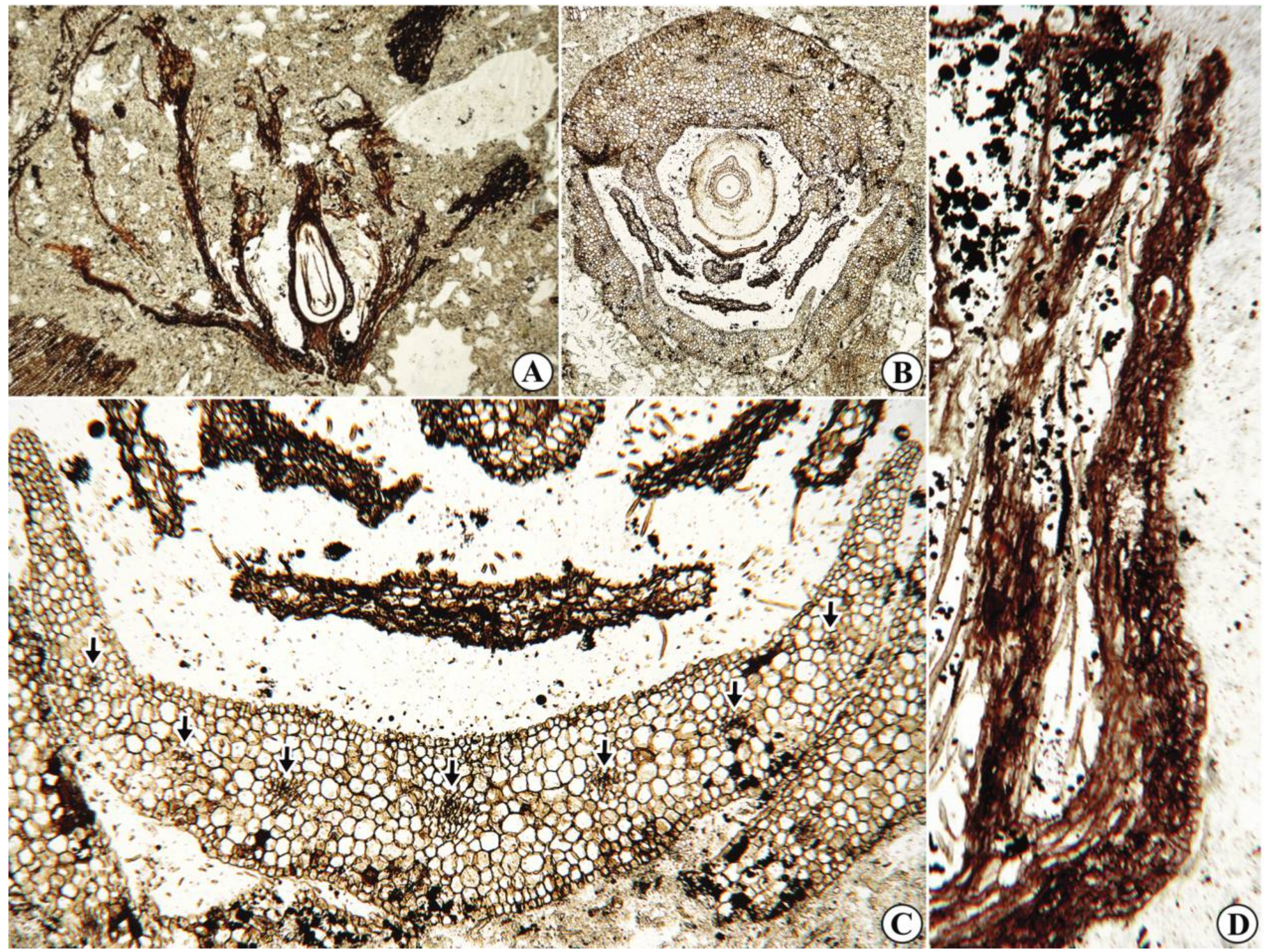


Fig. 2 *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell, et Bolton gen. et sp. nov. *A*, Longitudinal section of flower showing open perianth. AW 104 C top #1 ×17. *B*, Oblique cross section of flower showing androecium and perianth merging into hypanthium (top). AW 641 G top #51 ×17. *C*, Cross section of tepal showing parenchymatous ground tissue, seven vascular bundles (arrows), and epidermis. AW 641 G top #46 ×110. *D*, Longitudinal section of tepal with scattered oil bodies and trichomes. AW 108 B bot #3 ×115.

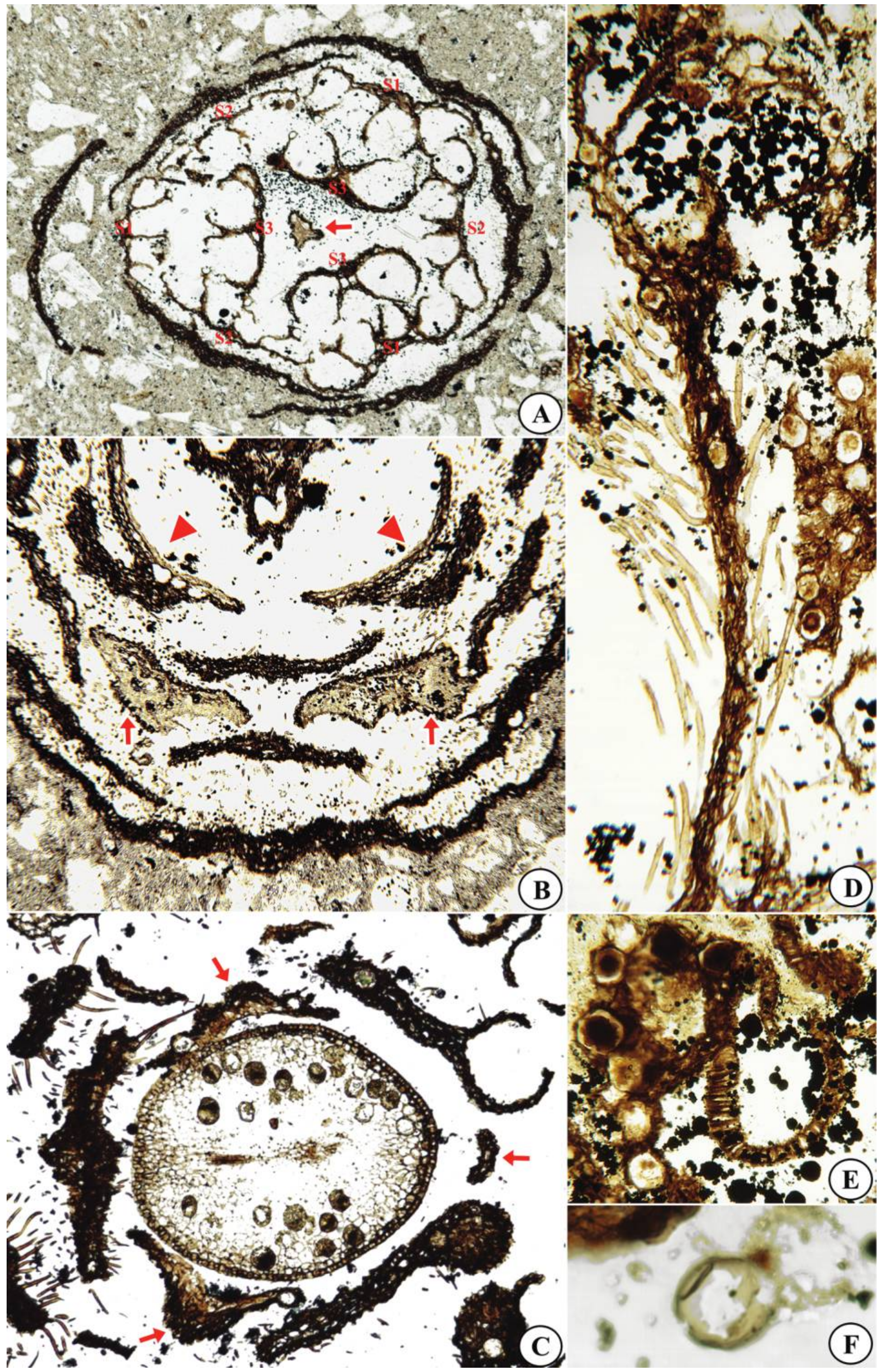


Fig. 3 *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell, et Bolton gen. et sp. nov. Holotype. *A*, Cross section of flower showing tepals, four locules per anther, and anther dehiscence orientation with outer two whorls (S1 and S2) introrse and inner third whorl (S3) extrorse. Note style at arrow. AW 546 B bot #5 × 28. *B*, Slightly lower section of specimen in *A* showing glandular appendages (arrows) attached to third-whorl stamen. Note fourth whorl of sterile staminodes (arrowheads). AW 546 B bot #63 × 56. *C*, Cross section of flower showing staminodes (arrows) clasping ovary. Note scattered oil bodies and trichomes. AW 641 G top #4 × 53. *D*, Tangential section of stamen showing oil cells and trichomes. AW 108 B bot #3 × 85. *E*, Longitudinal section of anther valve with endothecium composed of thick-walled cells. AW 108 B bot #3 × 128. *F*, Psilate pollen grain. AW 641 G top #14 × 1047.

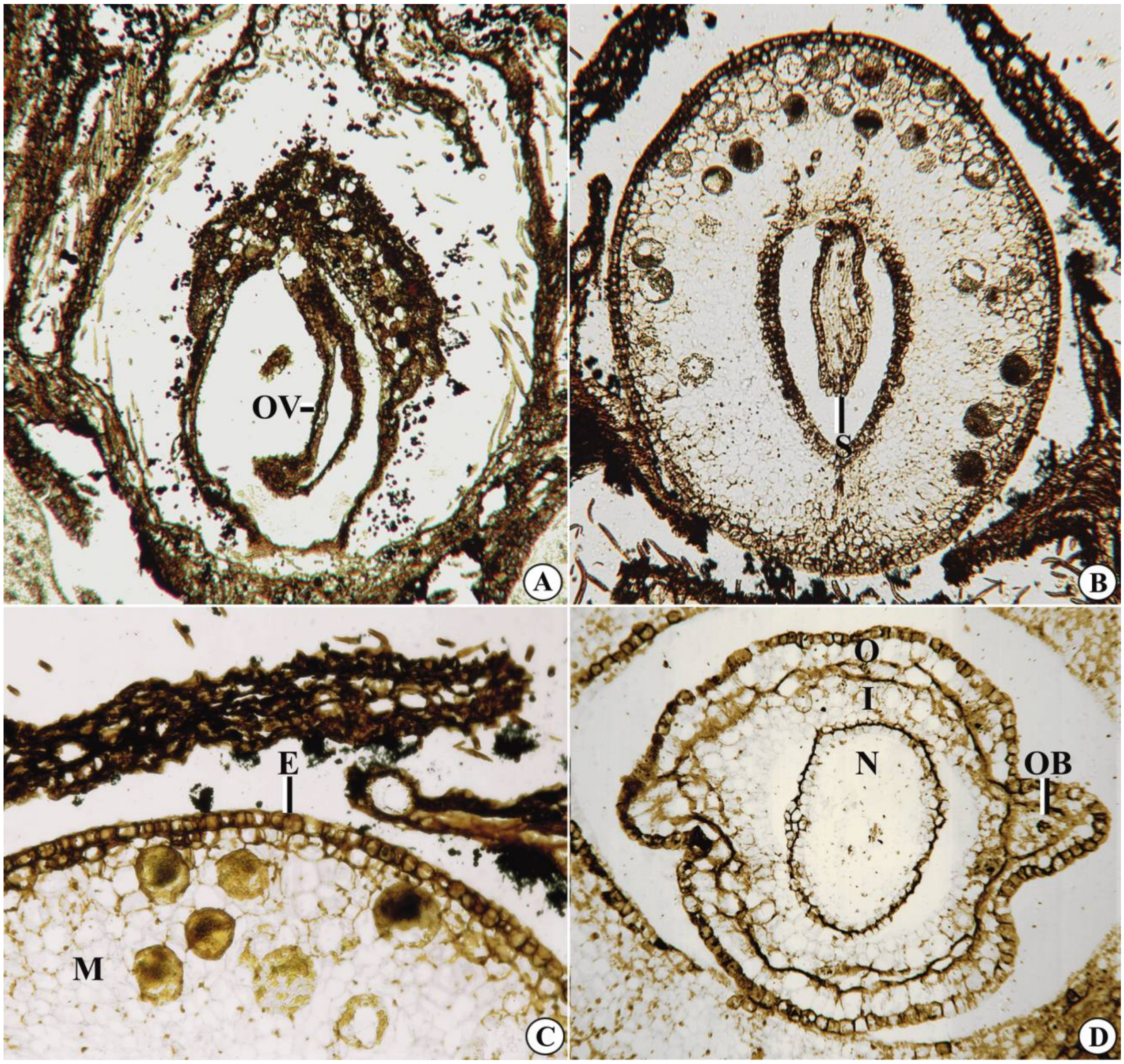
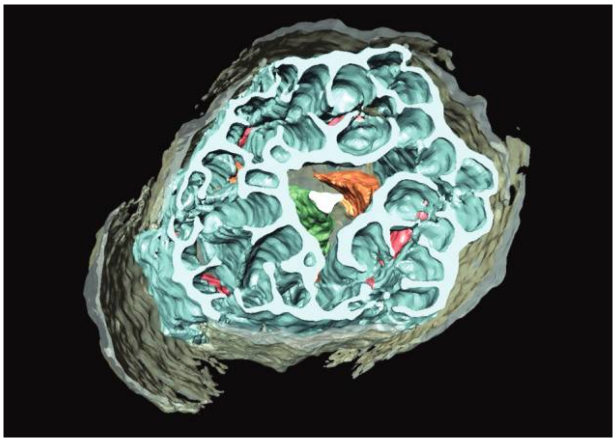


Fig. 4 *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell, et Bolton gen. et sp. nov. *A*, Longitudinal section of ovary showing apically attached ovule (OV). Note scattered oil bodies in carpel wall tissue and a lack of trichomes. AW 108 B bot #12 ×54. *B*, Cross section of ovary showing fleshy carpel wall, a single locule, and one seed (S). AW 641 G top #10 ×92. *C*, Magnification of carpel wall displaying parenchymatous mesocarp (M) with oil bodies and epidermis (E) consisting of cuboidal cells. AW 641 G top #4 ×153. *D*, Cross section of seed showing outer (O) and inner (I) integuments, ovular bundle (OB), and nucellus (N). AW 641 G top #33 ×127.

taper to a slightly rounded tip (fig. 1*C*) and are up to 2.0 mm long, 1.0 mm wide, and ca. 0.75 mm thick. In most flowers, the perianth is closed (figs. 1*B*, 1*C*, 5*A*); however, in some specimens, the perianth is more open (figs. 1*D*, 2*A*). The inner surfaces of tepals bear unicellular trichomes (fig. 2*D*). There are up to seven vascular bundles in each tepal (fig. 2*C*), and oil cells are occasionally found scattered throughout the ground tissue (fig. 1*D*). The epidermis consists of a single layer of distinctly smaller cells (fig. 2*C*) that contain dark-colored contents, most likely tannins, which have also been observed in extant Lauraceae (Buzgo et al. 2007).

Androecium. The androecium contains nine fertile stamens in three alternating whorls (figs. 1*A*, 3*A*) and three staminodes that comprise an innermost fourth whorl (figs. 1*A*, 3*B*). Stamens are up to 3.5 mm long and 1.0 mm wide. More specifically, filaments measure up to 2.5 mm long, while anthers are about 1.0 mm long. Anthers are tetrasporangiate (figs. 1*A*, 3*A*, 5*B*, 5*C*) and dehisce by apically hinged flap-like valves that consist of thick-walled endothecial cells (fig. 3*E*).

Anthers of first and second whorls have introrse median pollen sacs and introrse-latrorse marginal pollen sacs, while the anthers of the third whorl have extrorse median pollen sacs



Video 1 *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell, et Bolton gen. et sp. nov. Still photograph from a video (available online) showing AMIRA three-dimensional reconstruction of flower. AW 546 B Bot.

and extrorse-latrorse marginal pollen sacs (figs. 1*A*, 3*A*, 5*A*–5*C*). The pollen sac arrangement also differs between stamens of the outer two whorls and the inner third whorl. Marginal pollen sacs of the first- and second-whorl stamens are longer than the median pollen sacs (fig. 5*B*; tables 1, 2). The anthers of the third whorl have median pollen sacs that are longer than the marginal pollen sacs (fig. 5*C*).

The filaments and anthers are of about equal width (fig. 5*B*, 5*C*). A number of specimens have stamens with filaments that are up to twice the length of the anthers. Filaments are covered by unicellular trichomes (fig. 3*D*, 3*C*, at left), and both filaments and anthers contain oil cells (fig. 3*C*–3*E*). The third whorl of stamens bears glandular appendages that are attached to filament bases by a short pubescent stalk (figs. 3*B*, 3*C*, 5*C*). The glandular heads of the appendages consist of thin-walled cells that are surrounded by a uniseriate layer of epidermal cells with dark contents that may represent secretory cells (fig. 3*B*), as are reported in *Persea* Mill. (Buzgo et al. 2007). Scattered trichomes are also found on the epidermis of the glandular appendages (fig. 3*B*).

The innermost whorl of staminodes clasps the pistil (figs. 1*A*, 3*B*, 3*C*, 5*A*, 5*D*). Staminodes are sagittate, roughly triangular in cross section, stipitate, and bear scattered unicellular trichomes (figs. 1*A*, 3*B*, 3*C*, 5*A*, 5*D*–5*F*). Staminode tissue consists of a thin layer of light-colored, thin-walled cells that extends along the inner adaxial surface (fig. 3*B*, 3*C*). The outer abaxial surface consists of darker-colored cells (fig. 3*C*). Furthermore, scattered oil cells are found throughout staminode tissue (fig. 3*C*).

Most pollen sacs have dispersed all of their pollen; however, a single pollen grain was found in situ (figs. 3*F*, 6*B*). Through SEM imaging, the pollen grain is partially collapsed, with a depressed outer surface (fig. 6*B*). The grain is spherical and psilate (fig. 6*B*, 6*C*) and is 17.2 μm in diameter, with no apertures visible.

Gynoecium. The gynoecium consists of a single carpel with an elongate style (figs. 1, 2*A*, 2*B*, 3*A*, 3*C*, 4*A*, 4*B*, 5*A*, 5*D*, 6*A*). The carpel is at least 2.0 mm long and 1.0 mm wide. The style is at least 0.7 mm long and ca. 3.0 mm wide. The ovary is up to 1.3 mm long and 1.0 mm wide. The ovary is superior and contains a single locule (figs. 1*A*, 1*C*, 1*D*, 2*A*, 2*B*, 4*A*, 4*B*, 4*D*, 5*A*, 6*A*). The carpel is constricted at the base (stipitate; figs. 2*A*, 4*A*). Ground tissue of carpels consists of thin-walled parenchyma and scattered large oil cells (figs. 4*B*, 4*C*, 6*A*). The ovary epidermis is made up of a single layer of cuboidal cells with dark contents (fig. 4*C*) that may be tanniferous, as has been reported in several lauraceous species (Endress and Igersheim 1997). The locule lining is composed of smaller cells with dark contents that may also have been tannins (fig. 4*B*, 4*D*).

There is one pendulous, anatropous ovule/seed per carpel with apical placentation (figs. 2*A*, 2*B*, 4*A*, 4*B*, 4*D*, 5*A*). Ovules are at least 1.0 mm long and 0.6 mm wide and bitegmic, in which the outer integument is two cells thick and the inner integument is two or three cells thick (fig. 4*D*). The epidermis of the ovule contains cells with dark contents that probably represent tannins (fig. 4*D*). Ovules are crassinucellar, and the nucellus is composed of thin-walled, light-colored cells (fig. 4*D*).

Discussion

Based on a trimerous organization, two alternating whorls of tepals, three alternating whorls of fertile stamens, paired glandular appendages on third-whorl stamens, pollen sacs dehiscing by apically hinged valves, an inner fourth whorl of sterile staminodes, and a single one-seeded carpel with a superior ovary, the fossil flowers described in this study are assignable to Lauraceae (Cronquist 1981; Endress and Hufford 1989; Rohwer 1993*a*). Unsurprisingly, this general floral design is shared with a number of lauraceous taxa (Rohwer 1993*a*, 2000). However, when analyzing certain other floral features across all extant lauraceous genera (Rohwer 1993*a*; table 5.1 in Little 2006), taxa are distinguished by unique combinations of characters.

Floral Biology

The fossil flowers described in this study display remarkable preservation, which allows us to infer several aspects of floral biology, including developmental traits and rarely preserved floral anatomy. Among the Appian Way fossil flowers, some specimens were found to have a closed perianth, while in others, the perianth is open. In Lauraceae, many species have two flowering stages (Kaspaspligil 1951; Ravindran et al. 2004; Buzgo et al. 2007; Rohwer 2009). During the first stage, the flower opens with the perianth and androecium spreading outward while the carpel is pollinated. At this point, the pollen sacs have not yet dehisced. Afterward, the flowers close. On the following day, a second stage begins with the flower opening a second time (Kasapligil 1951; Ravindran et al. 2004; Buzgo et al. 2007; Rohwer 2009). During this stage, the androecium is more appressed to the carpel. The outer stamens may elongate and the pollen sacs dehisce (Buzgo et al. 2007), whereas the stigma, style, and staminodes begin to wither (Rohwer 2009). After some time, the flower closes again, at which time it may abort and abscise (Buzgo et al. 2007), or the fruit begins to develop. Despite having been washed out to sea before deposition, it is clear that all of the flowers described in this study had released

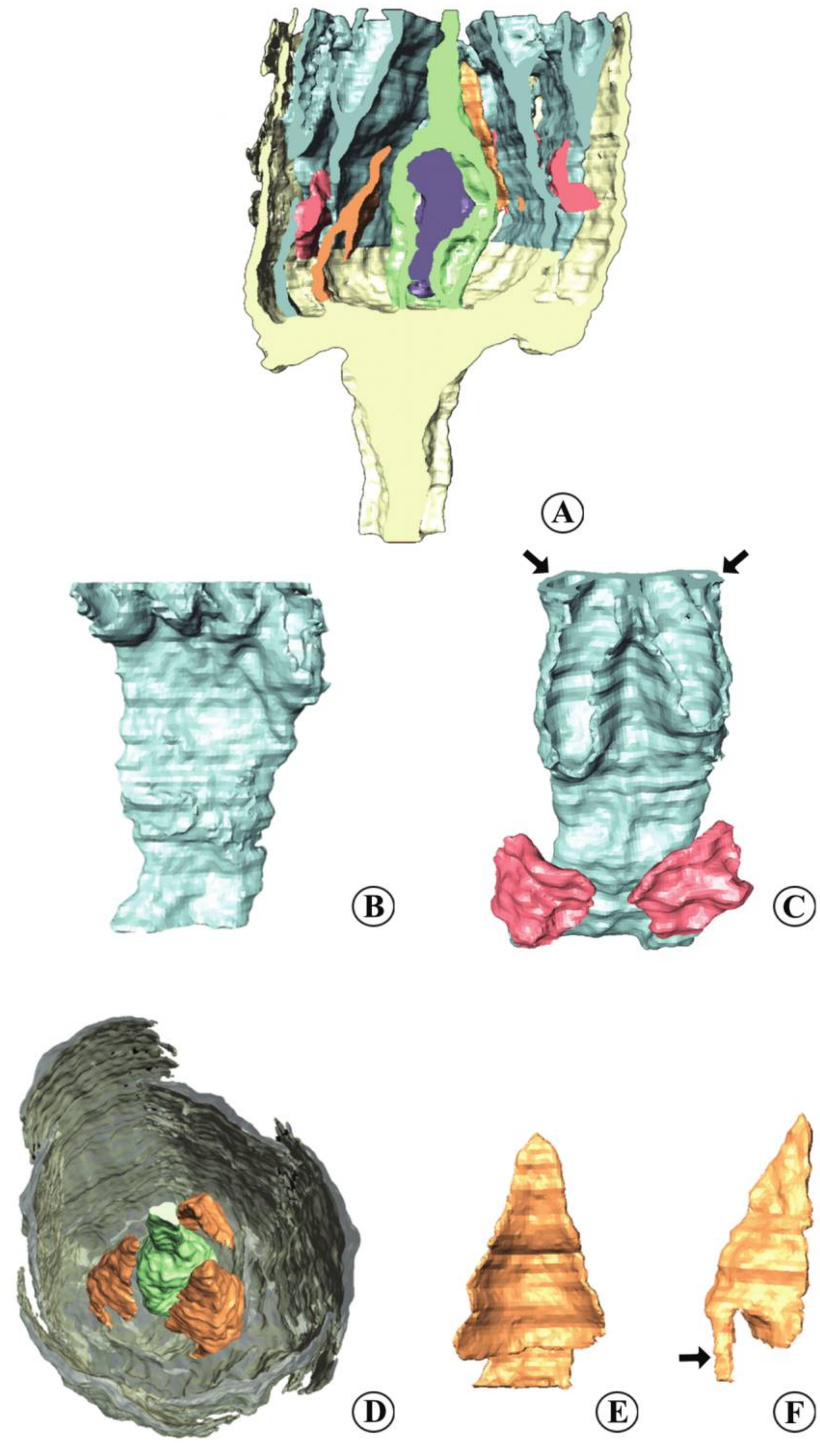
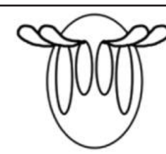
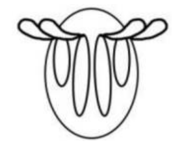
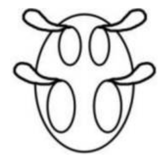
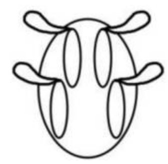
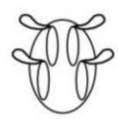
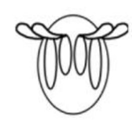
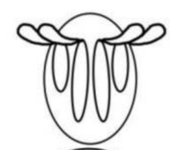
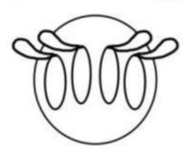
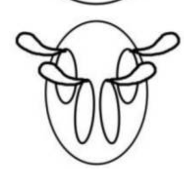
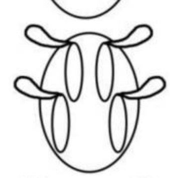
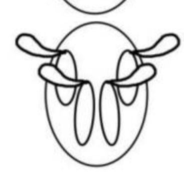
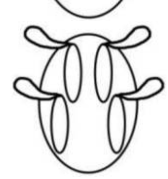
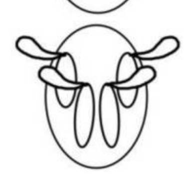
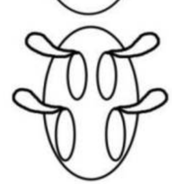
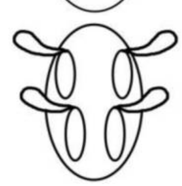


Fig. 5 *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell, et Bolton gen. et sp. nov. AMIRA three-dimensional reconstructions of flower and floral parts. AW 546 B bot. *A*, Longitudinal section of three-dimensional reconstructed flower displaying general features. ×25. *B*, Stamen showing general morphology of stamens of first and second whorls. ×33. *C*, General morphology of third inner-whorl stamen with glandular appendages attached at base of filament. Note longer median pollen sacs and the smaller lateral pollen sacs (arrows). ×42. *D*, Top view of flower without stamens showing staminodes clasping carpel. ×26. *E*, Front view of staminode showing sagittate morphology. ×58. *F*, Side view of staminode showing head and stipe (arrow). ×58. White/cream = tepals and hypanthium; blue = stamens; red = glandular appendages; orange = staminode; green = carpel; purple = seed.

Table 1

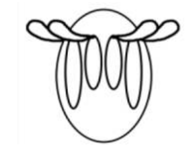
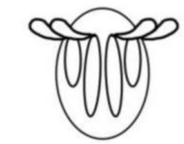
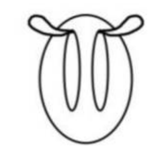
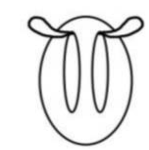
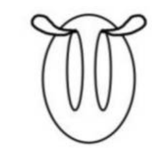
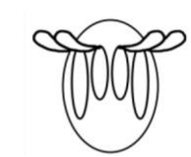
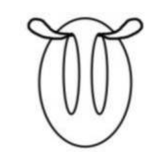
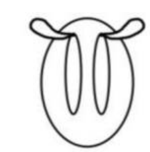
Floral Characters of Similar Extant Lauraceae Taxa with Bisexual Trimerous Flowers with Nine Tetrasporangiate Stamens, Paired Glandular Appendages, Staminodes, and a Shallow Hypanthium

Character taxon	Staminode shape	Staminode sessile or stipitate	Pollen sac arrangement (first two whorls)	Pollen sac arrangement (third whorl)	Pollen ornamentation
Tinaflora beardiae	**Sagittate**	**Stipitate**			**Psilate**
Alseodaphne	Heart shaped	**Stipitate**			Echinate
Cinnamomum	**Sagittate**	**Stipitate**			Echinate, clavate
Neocinnamomum	Deltoid/ovoid	**Stipitate**	 		**Psilate**
Nectandra	Columnar/conical	Sessile			Echinate
Ocotea (bisexual grade)	Clavate	**Stipitate**/sessile			Echinate
Persea (p.p.)	**Sagittate**	**Stipitate**			Echinate
Phoebe	**Sagittate**	**Stipitate**			Echinate
Umbellularia	Lanceolate	**Stipitate**			Echinate, clavate

Sources. Data from Kasapligil 1951; Rohwer 1993*a*, 1993*b*, 1994; Shang and Tang 1995; Eklund 2000; Little 2006; Li et al. 2008*a*, 2008*b*.
Note. Boldface indicates characters that are similar to *Tinaflora*.

Table 2

Floral Characters of Extinct Lauraceae Species

Character taxon	Age	Bisexual or unisexual	Mery	Hypanthium	No. fertile stamens	Glandular appendages	No. pollen sacs/anther	Innermost staminodal whorl	Staminode shape	Staminode sessile or stipitate	Pollen sac arrangement (first two whorls)	Pollen sac arrangement (third whorl)
Tinaflora beardiae	**Eocene**	**Bisexual**	3	**Shallow**	9	**Third whorl**	4	**Present**	**Sagittate**	**Stipitate**		
Cohongarootonia hispida[a]	Early Cretaceous	**Bisexual**	3	**Shallow**	3–6?	First and third whorls	2	**Present**	Columnar	?		?
Powhatania connata[a]	Early Cretaceous	?	3	**Shallow**	3?	First whorl	?	?	?	?	?	?
Potomacanthus lobatus[b]	Early Cretaceous	**Bisexual**	3	Flat?	6	**Third whorl**	2	Absent	na	na		
Neusenia tetrasporangiata[c]	Late Cretaceous	**Bisexual**	3	**Shallow**	9	**Third whorl**	4	**Present**	**Sagittate**	Sessile		
Pragocladus lauroides[d]	Late Cretaceous	**Bisexual**	3	Shallow	**9?**	**Third whorl**	2	Absent?	na	na		
Lauranthus futabensis[e]	Late Cretaceous	Unisexual?	3	Absent?	9	Absent?	4	Absent?	na	na		

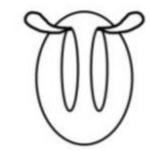
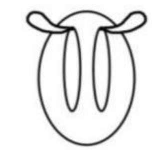
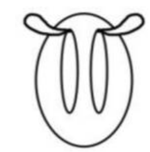
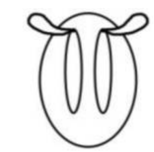
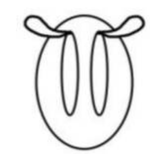
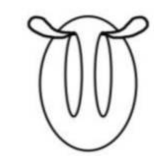
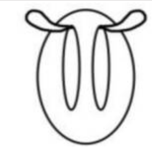
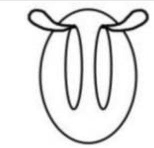
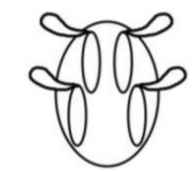
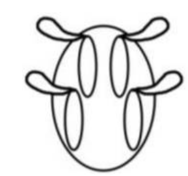
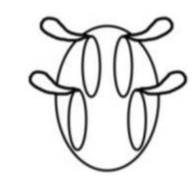
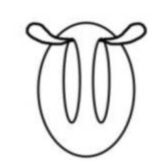
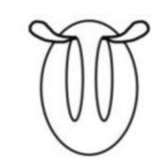
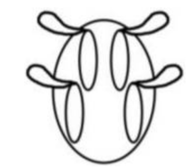
Microlaurus perigynus[f]	Late Cretaceous	**Bisexual**	3	**Shallow**	9	First whorl	**4?**	**Present**	**Sagittate**	**Stipitate**		
Perseanthus crossmanensis[g]	Late Cretaceous	**Bisexual**	3	**Shallow**	9	**Third whorl**	?	**Present**	Clavate	Sessile	?	?
Mauldinia mirabilis[h]	Late Cretaceous	**Bisexual**	3	?	9	**Third whorl**	2	**Present**	Lingulate	**Stipitate**		
Mauldinia bohemica[i]	Late Cretaceous	**Bisexual**	3	**Shallow**	9	**Third whorl**	2	**Present**	Lingulate	**Stipitate**		
Mauldinia hirsuta[j]	Late Cretaceous	**Bisexual**	3	**Shallow**	9	**Third whorl**	?	**Present**	Short-cuspidate	Sessile?	?	?
Mauldinia angustiloba[k]	Late Cretaceous	**Bisexual**	3	**Shallow**	9	**Third whorl**	2	**Present**	Lingulate	**Stipitate**		
Mauldinia sp.[l]	Late Cretaceous	Unisexual	3	?	3	?	?	?	?	?	?	?
Androglandula tennessensis[m]	**Eocene**	Unisexual	3	**Shallow**	?	Present?	**4**	?	?	?		

Table 2 (*Continued*)

Character taxon	Age	Bisexual or unisexual	Mery	Hypanthium	No. fertile stamens	Glandular appendages	No. pollen sacs/anther	Innermost staminodal whorl	Staminode shape	Staminode sessile or stipitate	Pollen sac arrangement (first two whorls)	Pollen sac arrangement (third whorl)
Princeton chert flowers[n]	**Eocene**	**Bisexual**	2 or 3	**Shallow**	6 or 9	**Third whorl**	2	Absent	na	na		
Cinnamomum felixii[o]	**Eocene-Oligocene**	**Bisexual**	3	**Shallow**	**9**	Absent	**4**	?	?	?		
Cinnamomum prototypum[o]	**Eocene-Oligocene**	**Bisexual**	3	**Shallow**	**9**	**Third whorl**	**4**	**Present**	Lanceolate	?		
Trianthera eusideroxyloides[o]	**Eocene-Oligocene**	**Bisexual**	3	**Shallow**	3	Absent	**4**	**Present**	Orbiculate	**Stipitate**		
Litseopsis rottensis[p]	Oligocene	**Bisexual?**	3	?	6	Present?	**4**	Absent	na	na		
Lindera rottensis[p]	Oligocene	Unisexual	3	?	6	?	2	**Present**	?	?		

Persea avita[q]	Oligocene-Miocene	**Bisexual**	**3**	Flat	**9**	**Third whorl**	**4**	**Present?**	?	?		
Treptostemon domingensis[r]	Oligocene-Miocene	**Bisexual**	**3**	Flat	**9**	**Third whorl**	**4**	Absent?	na	na		
Umbellularia californica[s]	Pleistocene	**Bisexual**	**3**	**Shallow?**	6	First whorl	**4**	Absent	na	na		

Sources. a = von Balthazar et al. 2011; b = von Balthazar et al. 2007; c = Eklund 2000; d = Kvaček and Eklund 2003; e = Takahashi et al. 2001; f = Takahashi et al. 2014; g = Herendeen et al. 1994; h = Drinnan et al. 1990; i = Eklund and Kvaček 1998; j = Frumin et al. 2004; k = Viehofen et al. 2008; l = Herendeen et al. 1999; m = Taylor 1988; n = Little 2006; o = Conwentz 1886; p = Weyland 1938; q = Chambers et al. 2011; r = Chambers et al. 2012; s = Chaney and Mason 1933.

Note. Several character states are coded from our own observations of original descriptions. na = not applicable. Boldface indicates characters that are similar to *Tinaflora*.

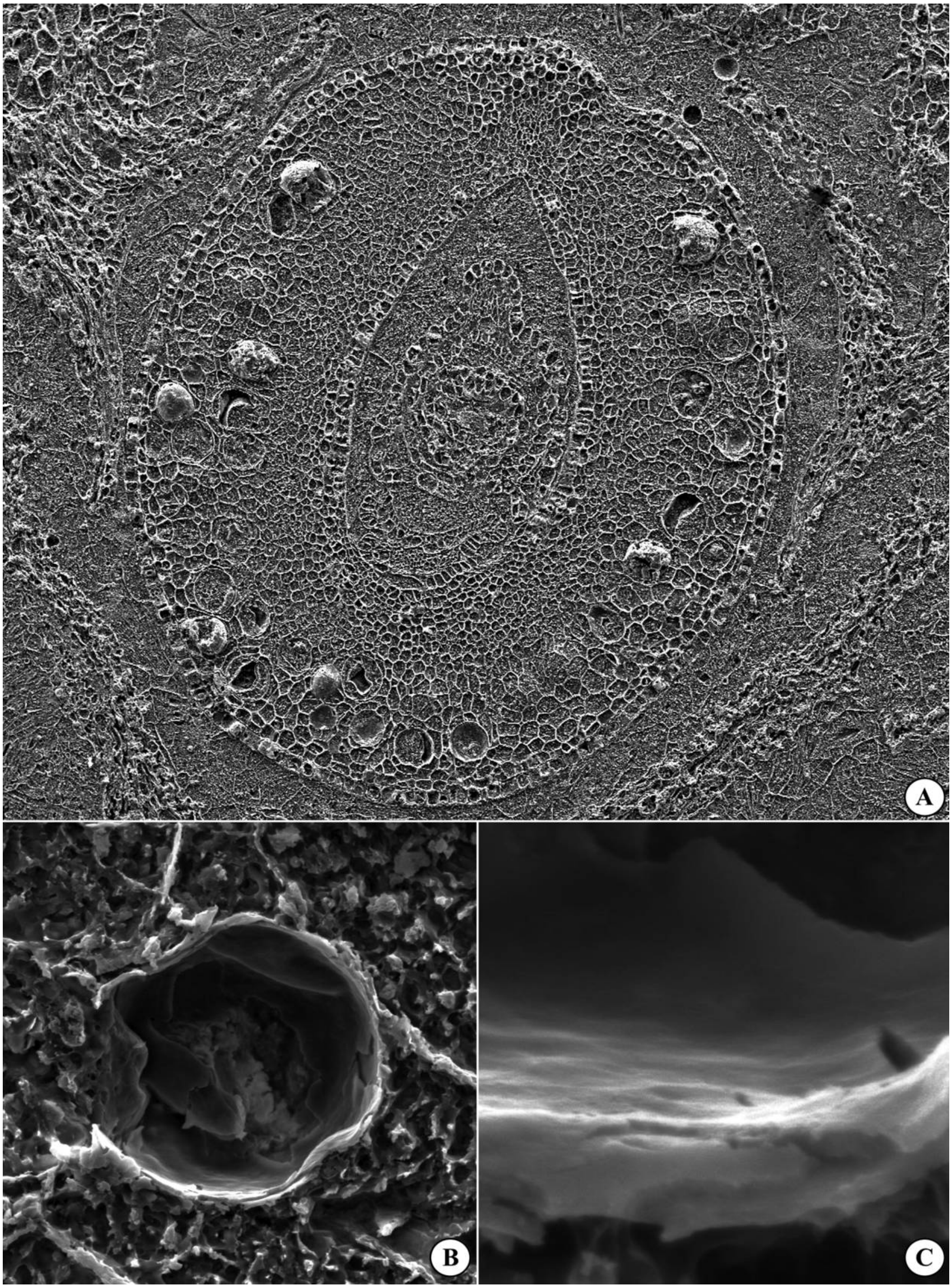


Fig. 6 *Tinaflora beardiae* Atkinson, Stockey, Rothwell, Mindell, et Bolton gen. et sp. nov. SEM photographs of AW 641G top. *A*, Cross section of carpel showing conspicuous oil cells in ground tissue. ×215. *B*, View of collapsed pollen grain showing psilate and spherical morphology. ×3197. *C*, Magnified view of psilate pollen grain wall in *B*. ×16,500.

their pollen prior to deposition. Therefore, all of the specimens probably represent the second flowering stage just after pollen sac dehiscence.

Tannins are known to be present in epidermal cells of the tepals in *Persea americana* (Buzgo et al. 2007) and in carpels and ovules of a number of other lauraceous taxa (Endress and Igersheim 1997). In these extant plants, such tanniniferous cells often appear dark and opaque. Epidermal cells of tepals, carpels, and ovules in the Appian Way flowers also have dark contents and appear to be comparable to cells with tannins in the living taxa. Tannins in leaf epidermal cells have been studied in two extant lauraceous species and are thought to defend against herbivores (Simon et al. 2007). Therefore, it is possible that the tannins observed in the Appian Way flowers might have deterred herbivores as well. As has been suggested by Robbins et al. (1987), it is likely that epidermal cell tannins would deter herbivores from damaging important floral structures.

Comparisons with Extant Lauraceae

Phylogenetic analyses based on molecular data have produced a general understanding of subfamilial relationships within Lauraceae (Rohwer 2000; Chanderbali et al. 2001; Li et al. 2004, 2011; Rohwer and Rudolph 2005; Rohwer et al. 2009, 2014; Wang et al. 2010). While the results of these analyses resolve the Lauraceae as monophyletic, polyphyly within the family is common, with species of large genera appearing in several different clades. A significant amount of homoplasy occurs throughout the family, thus making it difficult to understand useful morphological synapomorphies of subfamilies and genera (Rohwer 1993*a*; Chanderbali et al. 2001; Li et al. 2004).

Of the 50 extant lauraceous genera, eight have species with flowers bearing the following combination of characters: (1) bisexuality, (2) trimerous organization, (3) nine fertile stamens, (4) paired glandular appendages on third-whorl stamens, (5) presence of a fourth staminodal whorl, (6) tetrasporangiate anthers, and (7) a shallow hypanthium. *Alseodaphne* Nees, *Cinnamomum* Schaeff, *Neocinnamomum* Liou Ho, *Nectandra* Rolander ex Rottb., *Ocotea* Aubl., *Persea* Mill., *Phoebe* Nees, and *Umbellularia* Nutt. share these floral characters with the Appian Way flowers (Kostermans 1957; Rohwer 1993*a*, 1994; van der Werff 1997; table 5.1 in Little 2006; table 1). These genera are scattered across the phylogeny of Lauraceae (highlighting the homoplasy). Therefore, without fruit and/or inflorescence characters, these fossil flowers cannot be assigned to a living genus or species.

The dustbin genus *Ocotea*, with around 350 species (Rohwer 1993*a*), forms a paraphyletic complex with largely unresolved relationships (Rohwer 2000; Chanderbali et al. 2001). There are around 300 species of *Ocotea* that are dioecious (having unisexual flowers), forming an *Ocotea* sensu stricto clade (Chanderbali et al. 2001). Those species of *Ocotea* that have unisexual flowers typically lack staminodes (Rohwer 1986), while those with bisexual flowers are described as having club-shaped to columnar staminodes (Rohwer 1993*a*; table 1) and the Appian Way flowers have sagittate staminodes. Furthermore, pollen grains of *Ocotea* are echinate and ornamented with small and distinct spinules (Shang and Tang 1995), contrasting with the psilate surface of the pollen grain described here (table 1).

Nectandra contains around 115 species (Rohwer 1993*b*) and forms a clade with the genus *Pleurothyrium* Nees ex Lindl. (Chanderbali et al. 2001). *Nectandra* is divided into two groups. The first (100 species), *Nectandra* sensu stricto, has flowers with conspicuously papillose tepals and stamens (Rohwer 1993*b*; Chanderbali et al. 2001), whereas papillae are not seen in the Appian Way flowers. The second group of *Nectandra*, about 20 species, designated as the *Nectandra coriacea* species group (Chanderbali et al. 2001), has flowers more similar to those described in this study. However, the staminodes of *Nectandra* are columnar and typically papillate (Rohwer 1993*b*; table 1), rather than sagittate and nonpapillate as seen in the Appian Way fossil flowers. In addition, *Nectandra* has pollen grains with distinct spinules (Raj and van der Werff 1988), which contrast with the psilate pollen grain described in this study.

Cinnamomum, a representative of the subfamily Cinnamomeae (sensu Chanderbali et al. 2001), contains about 350 species (Rohwer 1993*a*). The Appian Way flowers and *Cinnamomum* are similar in many respects (table 5.1 in Little 2006); differences are minor. The anthers of *Cinnamomum* have four pollen sacs that are in a stronger arc than those of the Appian Way flowers (Rohwer 1993*a*; table 1). *Cinnamomum* has pollen grains with spinules (Shang and Tang 1995), as opposed to the psilate grain seen in the Appian Way flower (table 1).

Alseodaphne contains about 50 species, with a tropical Asian distribution (Rohwer 1993*a*). In many respects, the flowers of this extant genus are similar to the Appian Way fossils, but the outer tepals of most species of *Alseodaphne* are slightly smaller than the inner tepals (Rohwer 1993*a*), whereas the tepals of the fossil flowers are of equal size. Furthermore, the staminodes of *Alseodaphne* are reported to be heart shaped rather than distinctly sagittate, as found in the Appian Way flowers. The pollen of *Alseodaphne* is echinate (Shang and Tang 1995), while the fossil pollen grain is psilate.

The flowers of *Phoebe*, *Persea* (subg. *Persea* and *Persea indica* (L.) Spreng.), and *Umbellularia* are similar to the Appian Way flowers in many respects (Rohwer 1993*a*). However, these taxa have echinate pollen (Shang and Tang 1995), while the pollen grain in the Appian Way flower is psilate.

Neocinnamomum is an Asian endemic with five species (Wang et al. 2010) and flowers similar to those of Appian Way (table 1). Shang and Tang (1995) reported that *Neocinnamomum* is the only extant genus with spherical psilate pollen grains; however, this needs to be confirmed since acetolysis often destroys the delicate exine (J. G. Rohwer, personal communication, 2015). In some species of *Neocinnamomum*, the pollen sacs are arranged in a horizontal row or in a shallow arc (Rohwer 1993*a*; Li et al. 2008*b*). The pollen sac arrangements in *Neocinnamomum fargesii* (Lecomte) Kostermans and *Neocinnamomum caudatum* (Nees) Merrill are similar to those in the fossil flowers, where anthers of the outer two whorls have marginal pollen sacs that extend lower than the median pollen sacs and the anthers of the third whorl have median pollen sacs that extend lower than the marginal pollen sacs (Xin et al. 2008; table 1). However, *N. fargesii* and *N. caudatum* can be distinguished from the Appian Way flowers in having staminodes that are deltoid to ovoid rather than sagittate (table 1).

Comparisons with Extinct Lauraceae

Most lauraceous fossil flowers, including those described in this study, are trimerous (table 2). There is one species from the Eocene Princeton Chert locality that has trimerous and dimerous flowers born on the same inflorescence (Little 2006). There are few taxa with unisexual flowers: *Lauranthus futabensis* Takahashi Herendeen et Crane (2001); *Androglandula tennessensis* Taylor (1988); *Lindera rottensis* Weyland (1938); and an undescribed species of *Mauldinia* Drinnan, Crane, Friis et Pedersen (Herendeen et al. 1999) all have unisexual flowers (table 2). Therefore, we eliminated these taxa from detailed comparison to the Appian Way flowers (table 2). Furthermore, there are several fossil species that differ from the Appian Way flowers in having bisporangiate anthers: *Cohongarootonia hispida* von Balthazar, Crane, Pedersen et Friis (2011); *Potomacanthus lobatus* von Balthazar, Pedersen, Crane, Stampanoni et Friis (2007); *Pragocladus lauroides* Kvaček et Eklund (2003); three species of *Mauldinia* (Drinnan et al. 1990; Eklund and Kvaček 1998; Viehofen et al. 2008); the Princeton Chert flowers (described in Little 2006); and *Lindera rottensis* Weyland (1938; table 2).

There are nine fossil species with trimerous bisexual flowers and tetrasporangiate anthers like those from the Appian Way locality (table 1). These include *Neusenia tetrasporangiata* Eklund (2000); *Microlaurus perigynus* Takahashi, Herendeen, Xiao et Crane (2014); *Cinnamomum felixii* Conwentz (1886); *Cinnamomum prototypum* Conwentz (1886); *Trianthera eusideroxyloides* Conwentz (1886); *Litseopsis rottensis* Weyland (1938); *Persea avita* K.L. Chambers, Poinar et A.E. Brown (2011); *Treptostemon domingensis* Chambers, Poinar et A.S. Chanderbali (2012); and a flower described as *Umbellularia californica* Nutt. (Chaney and Mason 1933; table 2).

Chaney and Mason (1933) described a single compressed flower as *U. californica* from the Pleistocene of California (Chaney and Mason 1933). The Appian Way flowers can be distinguished from this specimen by having nine stamens as opposed to only six (table 2). In addition, glandular appendages can be found on first-whorl stamens of the California fossil flower (Chaney and Mason 1933), whereas the flowers described here have appendages on the third-whorl stamens. The California fossil flower also lacks staminodes, while the Appian Way flowers have staminodes in the fourth whorl. It should be noted that the fossil flower from California differs from extant *U. californica* in several characters (Chaney and Mason 1933; see Kasapligil 1951), and this fossil specimen should probably be removed from this extant species.

Litseopsis rottensis is a lauraceous species of compression fossils from the Oligocene of Germany (Weyland 1938). Weyland (1938), however, stated that what appeared to be the pistil of the *L. rottensis* flower might actually be debris, so it may actually be unisexual. There are only six stamens in *L. rottensis*, while Appian Way flowers have nine (table 2). Furthermore, Weyland (1938) did not identify any staminodes in *L. rottensis*, whereas staminodes are conspicuous in the flowers described in this article.

Persea avita and *Treptostemon domingensis* are two fossil species described from flowers that were recovered from Oligocene-Miocene Dominican amber (Chambers et al. 2011, 2012). *Persea avita* flowers have a flat hypanthium (Chambers et al. 2011), while the hypanthium of the Appian Way flowers is a shallow cup. Unlike the glabrous pistil of the Appian Way flowers, the pistil of *P. avita* is pubescent (Chambers et al. 2011). *Treptostemon domingensis* also differs from the Appian Way flowers in having a flat hypanthium (table 2). All three stamen whorls of *T. domingensis* have extrorse anther dehiscence (Chambers et al. 2012), whereas the first two staminal whorls of *Tinaflora beardiae* are introrse. Furthermore, flowers of *T. domingensis* differ from Appian Way flowers in lacking a fourth whorl of staminodes (table 2).

Cinnamomum felixii, *C. prototypum*, and *T. eusideroxyloides* are three extinct tetrasporangiate species of Lauraceae preserved in the Eocene Baltic amber (Conwentz 1886). *Cinnamomum felixii* differs from the Appian Way fossil flowers in having stamens that lack paired glandular appendages (Conwentz 1886). Flowers of *C. prototypum* have staminodes that are lanceolate, while the Appian Way flowers have sagittate staminodes (table 2). *Trianthera eusideroxyloides* has flowers with only three stamens that lack glandular appendages and have orbiculate staminodes, thereby differing from those of the Appian Way flowers (table 2).

There are a number of Cretaceous lauraceous flowers that are similar to those described here (table 2). The Late Cretaceous species *Perseanthus crossmanensis* was described from charcoalified flowers from New Jersey (Herendeen et al. 1994). Because the anthers of *P. crossmanensis* were abraded, the number of pollen sacs per anther is unknown for that species. Flowers of *P. crossmanensis* have clavate and sessile staminodes, whereas the staminodes of Appian Way flowers are sagittate and stipitate (table 2).

Microlaurus perigynus, another species described from Cretaceous charcoalified floral material (Takahashi et al. 2014), is in many respects similar to the Appian Way flowers (table 2). However, the outer tepals of *M. perigynus* are significantly smaller than the inner tepals (Takahashi et al. 2014), whereas the tepals are of equal size in the Appian Way specimens. Takahashi et al. (2014) reported that the glandular appendages in the flowers of *M. perigynus* might be attached toward the base of first-whorl (outer) stamens (however, this is not certain). The glandular appendages in the fossil flowers of Appian Way are clearly attached to the third-whorl stamens.

Among the extinct lauraceous fossil species with tetrasporangiate anthers, Cretaceous *Neusenia tetrasporangiata* is most similar to the Appian Way fossil flowers in having bisexual and trimerous flowers with nine stamens, paired glandular appendages on third-whorl stamens, a fourth whorl of sagittate staminodes, a shallow hypanthium, and spherical psilate pollen grains (Eklund 2000; table 2). However, there are also several differences between these two taxa. The staminodes of *N. tetrasporangiata* are sessile, while those of the Appian Way flowers are stipitate. Stamens of all three whorls in *N. tetrasporangiata* flowers have longer marginal pollen sacs and shorter median pollen sacs (Eklund 2000), whereas the third-whorl stamens of the Appian Way flowers have median pollen sacs that are longer than the marginal pollen sacs (table 2).

Affinities

A unique combination of characters distinguishes the Appian Way flowers from all other currently known lauraceous taxa.

Therefore, these fossil flowers are described as a new taxon, *Tinaflora beardiae* gen. et sp. nov. Eklund (2000) mentioned the similarities between flowers of *Neusenia tetrasporangiata* and extant *Neocinnamomum*, and these flowers are strikingly similar to those of *T. beardiae* (tables 1, 2). These extinct and extant flowers differ only in staminode morphology and pollen sac arrangement. It is difficult to classify lauraceous flowers to living or extinct taxa based mostly on staminal characters (van der Werff and Richter 1996). However, *Neocinnamomum*, *Neusenia tetrasporangiata*, and *T. beardiae* are the only lauraceous taxa described so far to have psilate pollen grains. We propose that *T. beardiae* and *Neusenia tetrasporangiata* may share close affinities with living *Neocinnamomum*.

Neocinnamomum and *Caryodaphnopsis* are the two extant genera of Lauraceae that are thought to be relicts of Cretaceous lineages (Chanderbali et al. 2001; Renner 2005). Although the phylogenetic relationships among genera in Lauraceae are not well resolved, morphology suggests that these two genera are closely related (Rohwer and Rudolph 2005; Wang et al. 2010). Therefore, flowers and pollen of *Neusenia tetrasporangiata* provide supporting evidence of a Cretaceous origin for the *Neocinnamomum* lineage. If correct, then *T. beardiae* reveals that this clade was also present in North America during the Eocene.

Dynamics in Floral Evolution

The earliest accepted record of Lauraceae is the fossil flower *P. lobatus* from the Early Cretaceous of North America (von Balthazar et al. 2007). *Potomacanthus lobatus* flowers are interesting because they have bisporangiate stamens and lack glandular appendages and staminodes. If staminodes are plesiomorphic in the family, this morphology demonstrates that reduced floral morphologies were present early in the evolution of Lauraceae (von Balthazar et al. 2007). Some early fossil flowers, such as those of *Cohongarootonia hispida* and *Powhatania connata* von Balthazar, Crane, Pedersen and Friis (2011), share many similarities with the closely related families Hernandiaceae and Monimiaceae (von Balthazar et al. 2011). These early fossil flowers illustrate that the floral diversity in Laurales was already rich during the mid-Cretaceous, providing additional paleobotanical evidence that Lauraceae was rapidly diversifying during the Cretaceous (see table 2).

Concordant with the fossil record, divergence estimates based on molecular clock analyses infer that the Lauraceae initially radiated during the Cretaceous but that the bulk of extant diversity is due to two radiations that occurred during the Eocene and Miocene (Chanderbali et al. 2001; Renner 2005). Surprisingly, there are relatively few flowers of Lauraceae described from Cenozoic sediments, thus hindering our understanding of post-Cretaceous lauraceous evolution. Fossil flowers such as those of *Tinaflora beardiae* do provide important evidence supporting an Eocene radiation of Lauraceae.

With available data from previously described extinct species, comparisons of fossil flowers reveal that the most variable character in Cretaceous species is the number of pollen sacs per anther (von Balthazar et al. 2007; table 2), whereas this character seems to be more stable in Cenozoic fossil taxa (table 2). Furthermore, there is relatively more variation in stamen and androecial whorl numbers among Cenozoic lineages than in Cretaceous species (table 2). Characters such as the presence of staminodes and their morphology seem to be quite variable through time, while pollen sac arrangement appears to be more static. It is also noteworthy that dimery does not appear until the Eocene (Little 2006).

Tinaflora beardiae represents a new genus and species of Eocene Lauraceae that expands the diversity of the family during this important time of evolutionary radiation. Interestingly, flowers and the pollen morphology of *T. beardiae* share strong similarities with those of *Neusenia tetrasporangiata* and *Neocinnamomum*, suggesting possible affinities with these taxa. As additional fossils are recovered from Cretaceous and Cenozoic sediments, the patterns of evolutionary diversification within Lauraceae may become more clearly understood, thereby providing crucial information for further elucidating the evolutionary patterns within this important magnoliid lineage.

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