

## A RANUNCULALEAN LIANA STEM FROM THE CRETACEOUS OF BRITISH COLUMBIA, CANADA: *ATLI MORINII* GEN. ET SP. NOV.

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**Premise of research.** The lianoid habit is found in 125 extant plant families and is most diverse and abundant in structurally complex forests, such as tropical forests. A stem with lianoid anatomy is described from Cretaceous sediments of Hornby Island, British Columbia.

**Methodology.** The stem segment, 2.5 cm in diameter and 2.8 cm long, was studied using the cellulose acetate peel technique and SEM. Anatomy was documented and compared to fossil and modern taxa.

**Pivotal results.** The stem lacks distinct growth increments, and the fibrous wood is dissected by large (>10 cells wide) rays. Wood is diffuse porous with mostly solitary vessels, rarely in tangential multiples (2–4). Vessel elements have a mean tangential diameter of 198  $\mu\text{m}$  and mean length of 527  $\mu\text{m}$ , bearing medium to large, crowded, elliptical to flat-elliptical alternate pits. Axial parenchyma is diffuse and vessels are surrounded by vasicentric tracheids with alternate bordered pitting. Rays are homocellular and >2 cm tall. Phloem rays are dilated, protruding into the xylem rays; thick-walled ray cells contain prismatic crystals. Periderm is composed of thin-walled cells interspersed with sclerotic nests. Wood anatomy of the fossil shows the most similarity to that of lianas in the Menispermaceae, Lardizabalaceae, and Ranunculaceae.

**Conclusions.** The Hornby Island stem represents a new taxon, *Atli morinii* gen. et sp. nov. (Ranunculales). This liana specimen expands our knowledge of Cretaceous biodiversity and points to the presence of structurally complex forests on Hornby Island in the Campanian. Anatomy of *Atli* and other Cretaceous liana stems combines characteristics of several families in Ranunculales, documenting past anatomical diversity and possible stem lineage mosaicism. The most diverse lianoid lineages currently known from the Cretaceous and Paleogene are early-divergent eudicots, particularly Ranunculales and Vitales that account for more than 50% of described lianoid species during this key time period of angiosperm diversification.

**Keywords:** Campanian, Hornby Island, Menispermaceae, paleobotany, Ranunculales, wood.

**Online enhancement:** appendix table.

### Introduction

Lianas (woody climbers) play a fundamental role in structurally complex forests, competing with trees for light and water resources and playing an important part in succession and in the health of other forest species (Schnitzer and Bongers 2002). Under projected climate change scenarios, lianas' role in forest dynamics will become even more important, as they are predicted to increase in numbers due to forest fragmentation (Schnitzer and Bongers 2002). Some experiments have shown higher growth rates of lianas with increased CO<sub>2</sub> levels, while other experiments show no difference in growth rates of trees versus lianas (Zotz et al. 2006; Marvin et al. 2012). A better understanding of liana occurrence, diversity, and ecol-

ogy through geologic time should help us understand liana response to environmental change.

While lianas are present from midlatitude temperate deciduous forests to tropical forests, they have the highest density and species richness at lower latitudes (Gentry 1991). Lianas, along with epiphytes, are especially characteristic of warm-climate, high-humidity tropical forests. Surveys of tropical forests counting trees  $\geq 10$  cm dbh and vines  $\geq 1$  cm dbh consistently find that lianas contribute ca. 25% of the canopy diversity while they are only 5%–10% of total forest biomass (Gentry 1988; Schnitzer and Bongers 2002). In dry tropical forests, both canopy trees and lianas are deciduous.

The occurrence of lianas in structurally and compositionally complex tropical forests makes them useful in paleovegetation reconstruction. Climbers, as a functional group, are known from the Mississippian epoch ~335 million years ago (Burnham 2009). The climbing habit has evolved in ferns, extinct

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seed plants, Gnetales, and angiosperms, the latter currently the most common and diverse (125 families, 5000–10,000 species; Gentry 1991; Caballé 1993). Recognition of the climbing habit in fossil plants is based upon several characters (Burnham 2009), including taxonomic affinities to climbing taxa; direct observation of host-climber connections (e.g., lianoid stems within trunks of *Tempskya* Corda; Tidwell et al. 2010) and several anatomical and morphological characters, including climbing appendages (hooks, spines, tendrils, grappling structures; e.g., the pteridosperm *Karinopteris* Boersma; DiMichele et al. 1984), cambial variants (Carlquist 1991, 2007; Lopes et al. 2008; Burnham and Revilla-Minaya 2011), and biomechanical properties (e.g., seed ferns; Masselter et al. 2007; Wilson and Fischer 2011).

Here we describe a new taxon based on a single woody axis from the Cretaceous of Hornby Island, British Columbia, Canada, that shows diagnostic liana anatomy. While a diverse assemblage of marine organisms is known from this locality (Ludvigsen and Beard 1997), the terrestrial ecosystem is poorly characterized with only two previously described plants, *Cycadeoidea maccafferyi* (Rothwell and Stockey 2002) and *Cunninghamia hornbyensis* (Brink et al. 2009), and assorted wood known from the locality (Ludvigsen and Beard 1997). This fossil stem broadens our knowledge of the fossil record of Cretaceous angiosperm lianas.

### Material and Methods

A single incomplete woody angiosperm stem in a fractured nodule was recovered from Collishaw Point, Hornby Island, British Columbia. Carbonate concretions are preserved in silty mudstones, interpreted as being distal parts of submarine alluvial fan complexes deposited in marine waters and dated as Campanian (late Cretaceous; 77–74 million years; Ludvigsen and Beard 1997; Katnick and Mustard 2003). The Collishaw Point locality includes fossils of a variety of marine invertebrates and vertebrates, as well as anatomically preserved plants (Ludvigsen and Beard 1997; Rothwell and Stockey 2002; Morrisson et al. 2005; Brink et al. 2009; Arbor and Currie 2011; Dyke et al. 2011).

The specimen was sectioned both transversely and longitudinally, and serial peels were made using the cellulose acetate peel technique (Joy et al. 1956). Peels were mounted on slides using Eukitt (O. Kindler, Freiburg, Germany) xylene-soluble mounting medium. Photos were taken with a Leica DM2500 microscope and Leica DFC290 digital camera (Leica Microsystems, Buffalo Grove, IL). For SEM observations, the tangential face of the whole specimen was etched, adhered to an aluminum stub, and sputter-coated with gold using a Cressington 108 Auto Sputter-Coater. After the sample was sputter-coated for 60 s at 30 mA, it was examined with a JEOL JSM-5510 SEM at 5kV.

Order- and family-level taxonomy follows APG III (2009). Wood anatomy terminology follows Wheeler et al. (1989). Diversity of different angiosperm liana lineages was calculated using the Fossil Record of Climbers compilation from Burnham (2009; table 3; table A1, available in the online edition of the *International Journal of Plant Sciences*).

### Systematics

Order—*Ranunculales* Berchtold & J. Presl

Family—*incertae sedis*

Genus—*Atli* Smith, Little, Cooper, Burnham, et Stockey, gen. nov.

Type—*Atli morinii* Smith, Little, Cooper, Burnham, et Stockey, sp. nov.

**Generic diagnosis.** Stem with broad primary and secondary rays; fibrous wood composed of vessels, fibers, tracheids, and axial parenchyma; pith cells uniformly thin walled. Wood diffuse porous, lacking distinct growth increments and storied wood structure. Vessels large to very large in diameter; solitary or in rare tangential groups of 2–4; not of two distinct diameter classes; perforation plates simple; vessel pitting elongate, alternate; tyloses absent. Vasicentric tracheids, septate fibers present. Axial parenchyma scanty, paratracheal, and apotracheal diffuse; 2–6 cells per strand; strands short, fusiform. Rays multiseriate, tall (>2 cm), wide (7–35 seriate), homocellular (procumbent cells only); uniseriate rays absent; circular pits between ray cells present. Vessel-ray contact absent. Phloem rays protrude into xylem rays, with thin- and thick-walled cells. Prismatic crystals present in thick-walled phloem ray cells. Sclerotic phloem caps absent.

Species—*Atli morinii* Smith, Little, Cooper, Burnham, et Stockey, sp. nov. (Figs. 1–4)

**Holotype.** Here designated P16788, UAPC-ALTA.

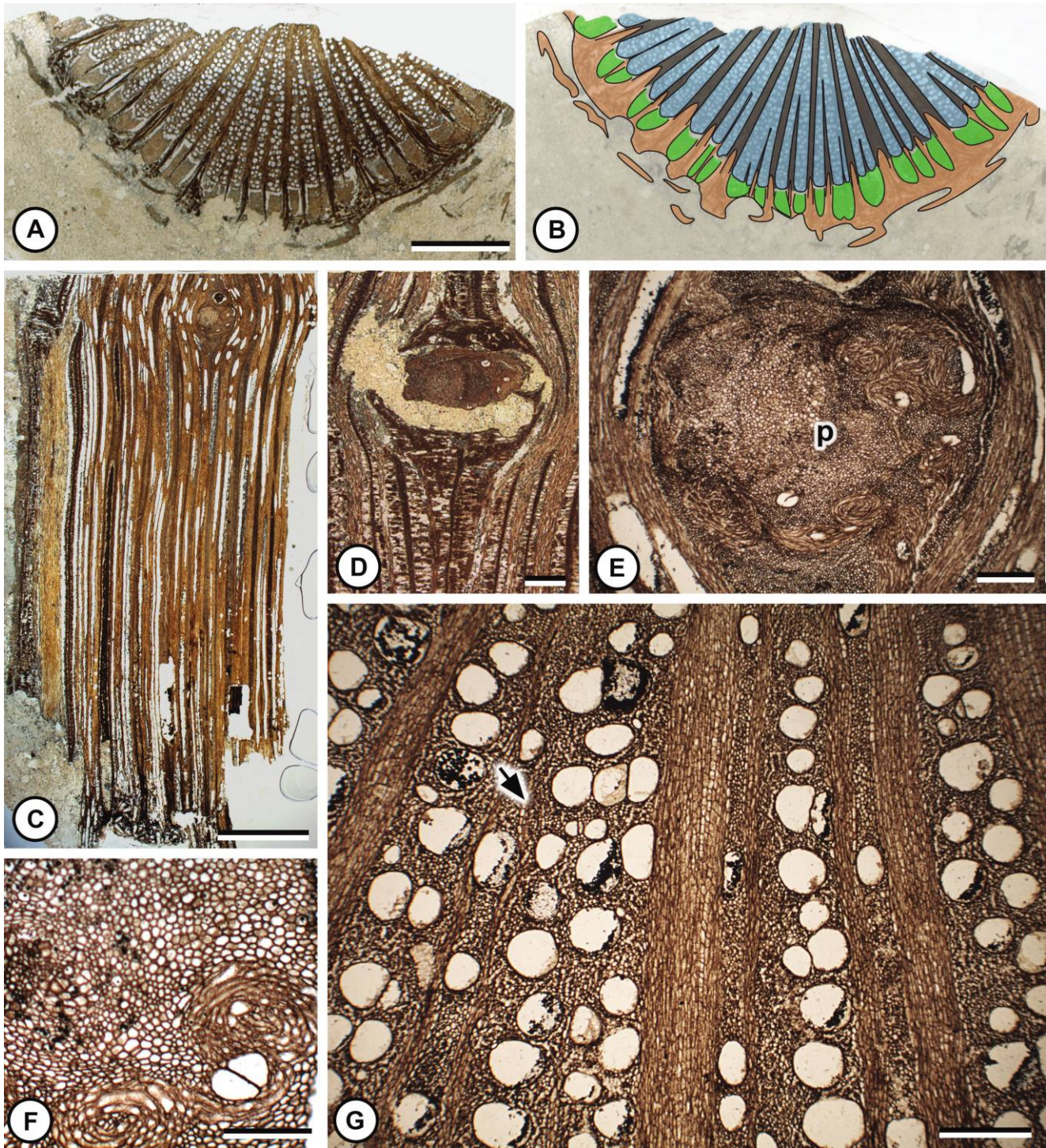
**Etymology.** The generic name *Atli* is derived from the Kwakwaka'wakw word for forest or woods; Kwakwaka'wakw is one of the languages spoken by the First Nations people in the Georgia Strait region. The specific epithet *morinii* is in honor of Joe Morin of Courtenay, British Columbia, who provided this and many other Vancouver Island–area fossils for scientific study.

**Type locality.** Collishaw Point, Hornby Island, British Columbia; Northumberland Formation, Nanaimo Group, Late Cretaceous (Campanian).

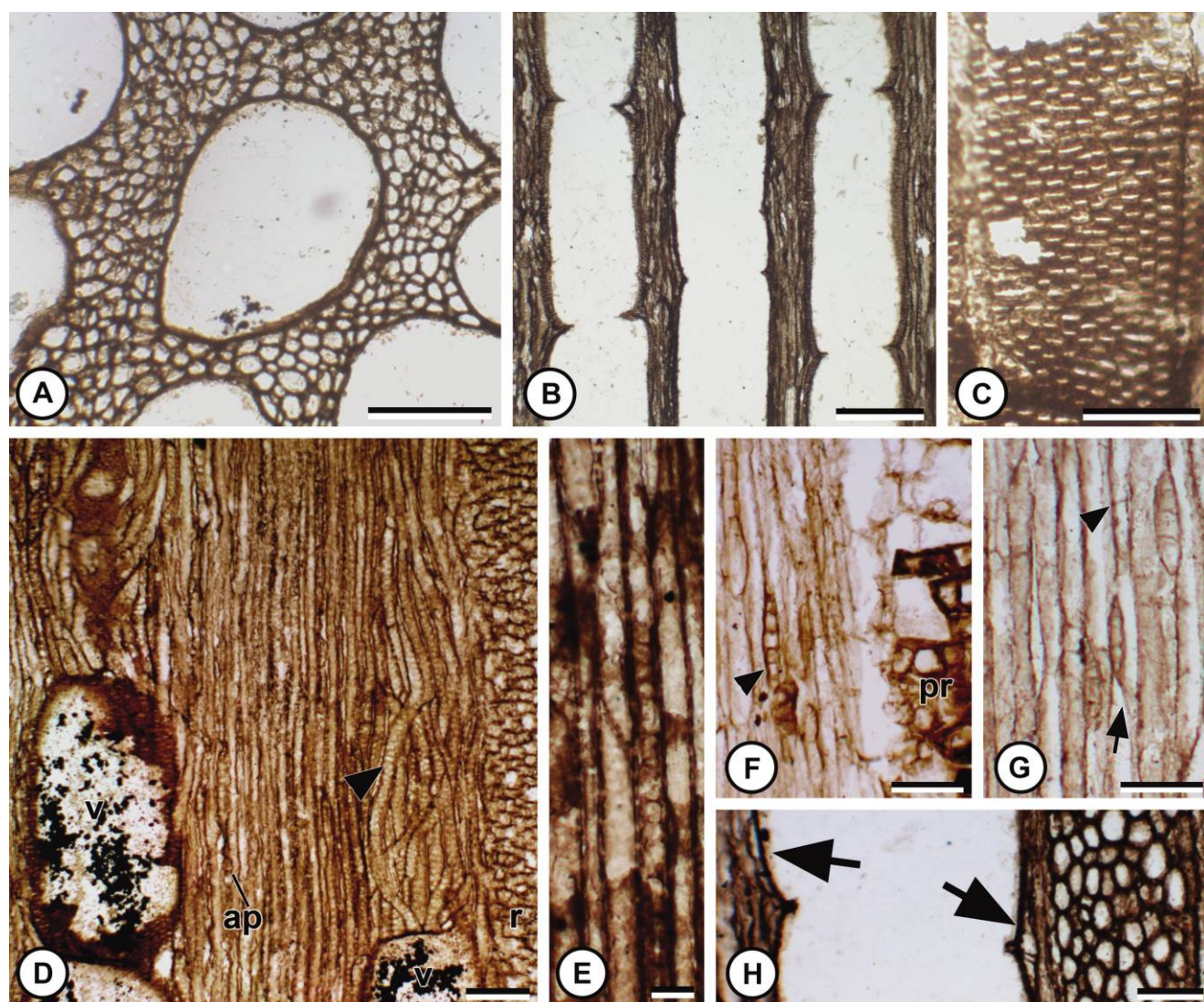
### Description

The single specimen is 2.5 cm in diameter and 2.8 cm long (fig. 1A, 1C). The stem is incomplete due to its recovery from a fractured nodule; the center of the axis is missing, and the peripheral tissues are incompletely preserved and appear to have been abraded prior to preservation (fig. 1A–1C). The internal portion of a branch is visible in tangential section (fig. 1C–1E). Pith is missing in the main axis but is present in the branch (fig. 1C–1E). Pith is uniformly composed of thin-walled isodiametric cells (fig. 1E, 1F). Tracheary elements surrounding the pith form a swirling cell pattern (fig. 1E, 1F), typical of the cellular patterns resulting from auxin flow disruption due to the presence of a lateral organ (e.g., Lev-Yadun 2000; Rothwell et al. 2008).

Distinct growth increments are not observed (fig. 1A, 1B,



**Fig. 1** *Atli morinii* gen. et sp. nov., UAPC-ALTA P16788. *A*, Transverse section (XS) of fractured specimen showing wide-diameter vessels, wide wood rays, phloem, and protruding phloem rays; periderm abraded on periphery of axis. Peel xs-27, scale bar = 5 mm. *B*, Tracing of *A* to show the tissue zones more clearly. Blue, “fibrous wedges”; gray, wood rays; green, phloem; orange, protruding phloem rays and periderm. *C*, Tangential longitudinal section (TLS) near stem margin; dark vertical lines are protruding phloem rays. Note branch base at upper right. Peel tls-98, scale bar = 5 mm. *D*, TLS of stem showing transverse section of branch base at top. Peel tls-58, scale bar = 1 mm. *E*, XS of branch base showing pith and tracheary elements in swirled pattern surrounding the pith. Peel xs-84, scale bar = 200  $\mu\text{m}$ . *F*, XS of branch pith with thin-walled, isodiametric cells; tracheary elements in swirled pattern (*bottom, right*). Peel tls-105, scale bar = 200  $\mu\text{m}$ . *G*, XS of stem showing fibrous wedges wood with large-diameter vessels, separated by wood rays. Rays originate both from pith (medullary rays) and within fibrous wood (e.g., arrow). Peel xs-41, scale bar = 200  $\mu\text{m}$ .

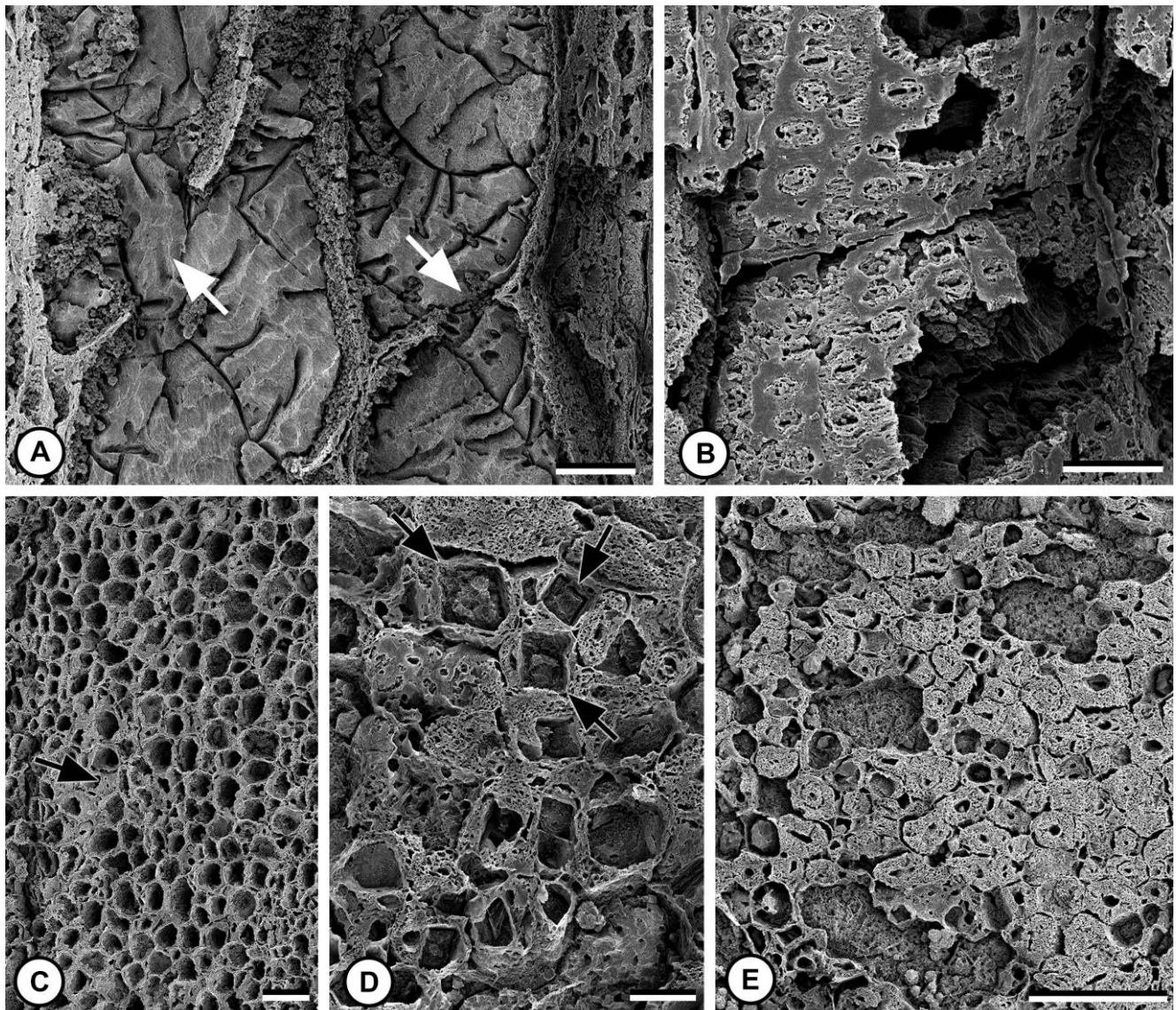


**Fig. 2** *Atli morinii* gen. et sp. nov., UAPC-ALTA P16788. **A**, Transverse section showing large-diameter vessel elements and thin-walled tracheids; axial parenchyma scanty. Peel xs-11, scale bar = 50  $\mu\text{m}$ . **B**, Radial longitudinal section (RLS) showing three vessels; vessel elements with simple perforation plates. Peel rls<sub>1</sub>-11, scale bar = 100  $\mu\text{m}$ . **C**, RLS showing side wall of vessel element bearing alternate crowded pits that are polygonal in outline. Peel rls<sub>1</sub>-11, scale bar = 25  $\mu\text{m}$ . **D**, RLS obliquely cutting through two vessels (v) and ray (r); files of sinuous vasicentric tracheids (e.g., arrowhead) bearing alternate, crowded pits with polygonal outlines visible above vessel element lumens; apotracheal axial parenchyma poorly preserved (e.g., ap). Peel rls<sub>2</sub>-7, scale bar = 100  $\mu\text{m}$ . **E**, RLS showing tracheids with tapered end walls, some bearing single file of large, circular pits. Peel tls-77, scale bar = 25  $\mu\text{m}$ . **F**, RLS showing edge of phloem ray (pr; note prismatic crystal outlines), tracheids, and short, fusiform chains of axial parenchyma (e.g., arrowhead). Peel rls<sub>1</sub>-16, scale bar = 50  $\mu\text{m}$ . **G**, RLS showing tracheids with tapered end walls (arrow) and septate fibers (arrowhead); three short, fusiform chains of apotracheal axial parenchyma, arrayed diagonally, also visible. Peel rls<sub>1</sub>-16, scale bar = 50  $\mu\text{m}$ . **H**, Tangential longitudinal section showing large vessel at center with adjacent short, fusiform chains of paratracheal axial parenchyma (arrows); ray at right. Peel tls-105, scale bar = 50  $\mu\text{m}$ .

1G). Wood is diffuse porous (figs. 1A, 1G, 4E, 4F). Vessels are predominantly solitary or in tangential clusters of 2 (rarely 3–4); there is no vessel arrangement pattern in transverse section (figs. 1A, 1G, 4E, 4F). Tracheids form the majority of the tissue surrounding the vessel elements in the fibrous wedges (figs. 1G, 2A, 2D, 4F). The axis does not bear any obvious secretory elements, although enlarged cells (idioblast-like but lacking preserved contents) are observed infrequently in rays

(fig. 4C). There is no evidence for any cambial variant, such as successive cambia or included phloem.

Vessels are large to very large in diameter, with circular to elliptical outlines in transverse sections; mean tangential diameter is  $198 \pm 43 \mu\text{m}$  (range: 98–317  $\mu\text{m}$ ), and diameters are of only a single size class (figs. 1G, 2A, 2B, 2H, 3A). Mean vessel density is  $11 \pm 1.17$  vessels per  $\text{mm}^2$ , with a range of 9.4 to 13.1 vessels per  $\text{mm}^2$  (fig. 1A, 1G). Vessel elements are



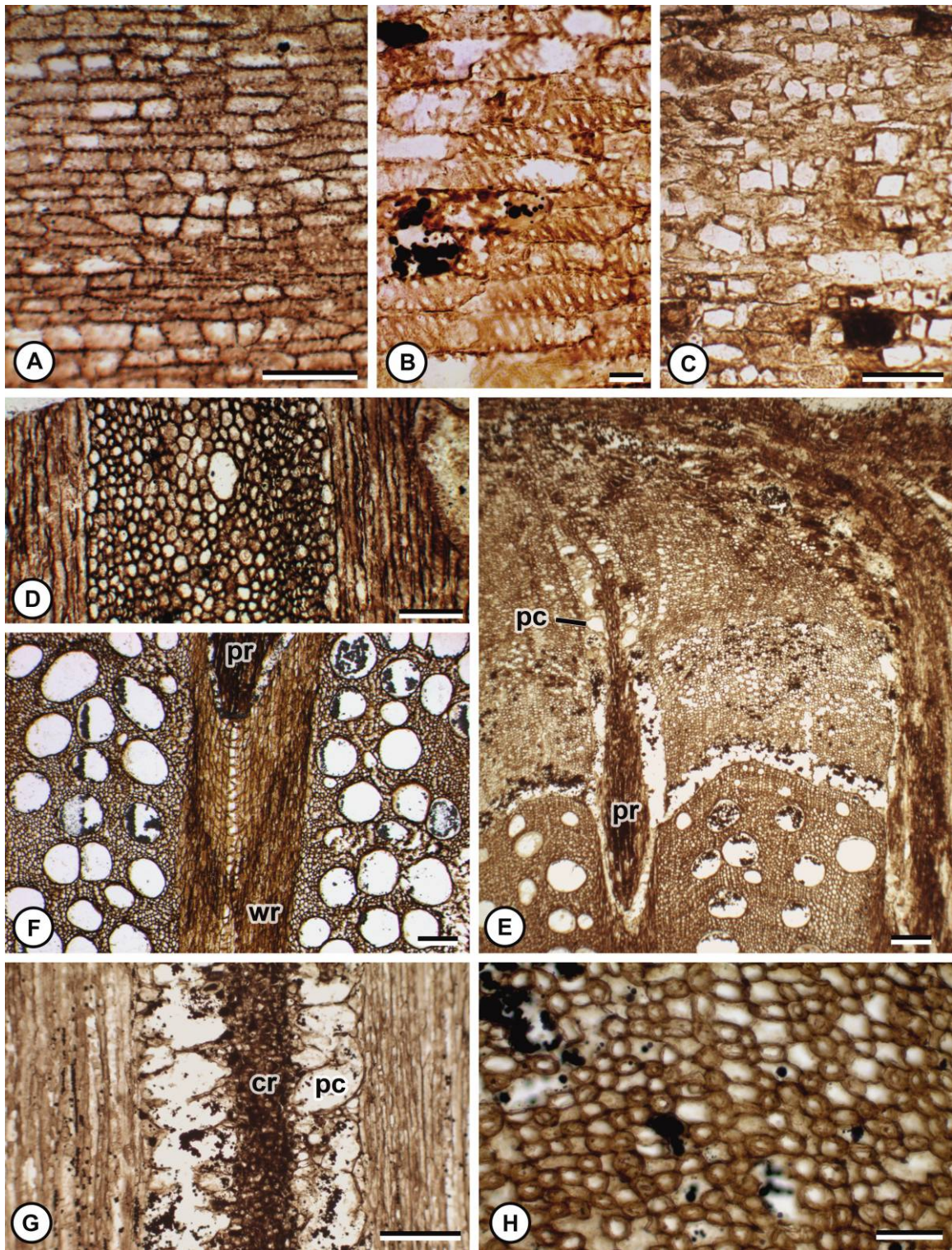
**Fig. 3** *Atli morinii* gen. et sp. nov., UAPC-ALTA P16788, SEMs of cut, etched tangential face. *A*, Two vessels with minerals filling lumen showing simple perforation plates (arrows). Scale bar = 50  $\mu\text{m}$ . *B*, Side walls of two vessel elements bearing alternate, crowded pits with elliptical to flat elliptical outlines; pit fields bearing some mineral residue from etching. Scale bar = 20  $\mu\text{m}$ . *C*, Large, multicellular ray with pitting visible on some obliquely exposed radial walls (e.g., arrow). Scale bar = 50  $\mu\text{m}$ . *D*, Cells of phloem ray, some with pitting; impressions of prismatic crystals inside several cells (e.g., arrows). Scale bar = 20  $\mu\text{m}$ . *E*, Sclerotic nest at stem periphery in region of secondary phloem and periderm. Scale bar = 100  $\mu\text{m}$ .

medium in length, mean  $527 \pm 88 \mu\text{m}$  (range: 294–764  $\mu\text{m}$ ; figs. 1C, 2B). Perforation plates are simple (figs. 2B, 2H, 3A). Intervessel and vessel-tracheid pitting is alternate, crowded, and nonvestured; individual pits are medium to large (7.8–13  $\mu\text{m}$ ) and elliptical–flat elliptical in shape (figs. 2C, 3B). Vessel-ray parenchyma pits are absent as no vessels are adjacent to rays; vascentric tracheids surround all vessels (fig. 2D). Helical thickenings and tyloses are absent.

The ground tissue in the “fibrous wedges” is composed of vascentric tracheids, tracheids, fibers (some septate), and rare axial parenchyma in short, fusiform strands. Tracheids have a mean length of  $206 \pm 65 \mu\text{m}$ , a mean width of  $24 \pm 5 \mu\text{m}$ ,

and uniseriate circular pits, and they lack helical thickenings (fig. 2D–2F). Vascentric tracheids have multiseriate, alternate, elliptical pitting (fig. 2D). Axial parenchyma is scanty paratracheal and diffuse apotracheal, often crushed or poorly preserved in the fibrous wedges (fig. 2B); however, where well preserved, it is composed of short fusiform chains of 2–6 cells (fig. 2F, 2G).

Wood rays are exclusively multiseriate and very prominent in both transverse and longitudinal sections (figs. 1A, 1C, 1G, 3C, 4D). Ray heights are  $>2 \text{ cm}$ , taking up the majority of the 2.8-cm-long fossil axis (fig. 1C). Rays are 7–35 cells wide (most  $>10$ ) and homocellular, composed of procumbent cells (fig. 4A,



**Fig. 4** *Atli morinii* gen. et sp. nov., UAPC-ALTA P16788. *A*, Radial longitudinal section (RLS) through homocellular multicellular ray showing some enlarged cells at ray margin (i.e., lower left). Peel rls<sub>1</sub>-16, scale bar = 100  $\mu$ m. *B*, RLS showing higher magnification of ray cell pitting. Peel rls<sub>2</sub>-7, scale bar = 10  $\mu$ m. *C*, RLS showing phloem ray; note outlines of prismatic crystals in cells. Peel rls<sub>2</sub>-7, scale bar = 25  $\mu$ m. *D*, Tangential longitudinal section (TLS) through ray; note larger cells at ray margin and central idioblast. Peel tls-105, scale bar = 100  $\mu$ m. *E*, Transverse section (XS) showing peripheral fibrous wood (*bottom*), secondary phloem, protruding phloem rays (pr) with enlarged peripheral cells (pc), and periderm with sclerotic nests (*top*). Peel xs-41, scale bar = 200  $\mu$ m. *F*, XS near periphery of stem showing edge of protruding phloem ray (pr) with small, thick-walled central cells and large, thin-walled peripheral cells; note central file of larger cells in wood ray (wr). Peel xs-28, scale bar = 200  $\mu$ m. *G*, TLS showing phloem ray with central, small thick-walled cells (cr) and large thin-walled peripheral cells (pc). Peel tls-74, scale bar = 100  $\mu$ m. *H*, Detail of secondary phloem in XS. Peel xs-28, scale bar = 25  $\mu$ m.

4B). Ray cells have abundant circular pitting (figs. 3C, 4A, 4B). Some marginal cells and rare central cells are enlarged (idioblast-like, but lacking contents) in longitudinal sections (fig. 4A, 4D). In transverse sections, a file of enlarged central ray cells regularly occurs (figs. 1G, 4E); this file is especially noticeable near the juncture with phloem rays (fig. 4E). Phloem rays protrude into wood rays and are dilated in the secondary phloem and periderm (figs. 1A, 1B, 4E, 4F). Thick-walled phloem ray tissue, with dark contents and prismatic crystals (figs. 3D, 4C, 4E–4G) is surrounded by a peripheral zone of large, thin-walled cells (fig. 4E–4G). Only molds of the crystals are left in the fossil material, so it is impossible to determine what type of crystals they were or to accurately describe their shape and size.

Secondary phloem tissue between the thick-walled phloem rays is composed of both thick- and thin-walled cells but lacks sclerotic nests or other features (fig. 4E, 4H). Enlarged thin-walled cells likely represent sieve tube elements and the thicker-walled cells are likely ground tissue parenchyma and/or companion cells (fig. 4G). The periderm, where preserved, is composed of thin-walled cells with scattered sclerotic nests (figs. 3E, 4E).

### Discussion

Lianas occur in multiple phylogenetic lineages but typically share syndromes of traits related to the lianoid lifestyle (Gentry 1991; Caballé 1993; Gianoli 2004; Isnard and Silk 2009). The presence of few, wide vessels, vessels in two diameter classes, anomalous growth, vascentric tracheids, and tall, wide multiseriate rays are typical of angiosperm liana wood anatomy (Carlquist 1975, 1991), and many of these features are observed in the Hornby fossil stem (anomalous growth and vessels in two diameter classes are lacking). In addition, the protruded phloem rays, fibrous wedges, and prismatic crystals in thick-walled phloem ray cells, as described here in *Atli morinii* gen. et sp. nov., are often seen in angiosperm lianas (Carlquist 1985, 1991). These features may represent convergences due to constraints of the lianoid habit, but the general combination of characters seen in the fossil is important in comparisons with wood of other taxa. Wood structure generally does not show synapomorphies but rather a combination of features are important for determining the taxonomic affinity of a sample (Wheeler et al. 1989).

#### Comparison with Modern Families

Our survey of the data included in Metcalfe and Chalk (1950), Miles (1978), Schweingruber (1990), and the InsideWood Database (2004–2013; Wheeler 2011) led us to focus comparison of the fossil liana on several extant families (tables 1, 2). The general appearance of the fossil stem, that is, lacking cambial variants, having wide rays (>10 cells wide), and wide-diameter vessels is found across a broad spectrum of angiosperm taxa: Annonaceae (*Artabotrys* R. Br.; Magnoliales); Aristolochiaceae (*Aristolochia* L.) and Piperaceae (Piperales); Celastraceae (e.g., *Hippocratea* L.; Celastrales); Dilleniaceae (Dilleniales); Rosaceae (Rosales); several asterid clade taxa (sensu APG III 2009) including Apiales, Ericales, Gesneriaceae, and Icacinaeae; ranunculalean families Lardi-

zabalaceae, Menispermaceae, and Ranunculaceae (*Clematis* L.); and Vitaceae (Vitales). However, when the presence of vascentric tracheids is also considered, all groups are excluded except Dilleniaceae, Vitaceae, and Ranunculales. Vitaceae and Dilleniaceae typically have scalariform vessel pitting and perforation plates (Dickison 1967; Wheeler and LaPasha 1994), unlike the exclusively simple perforation plates with alternate pitting seen in the fossil. In addition, Dilleniaceae typically have oil/mucilage cells in rays and included phloem (Dickison 1967), unlike this fossil. Vitaceae differ from the Hornby fossil in having frequent vessel multiples, vessels in two distinct diameter classes, and heterocellular rays (Wheeler and LaPasha 1994).

The combination of wood anatomical traits shown by *Atli*, specifically large solitary vessels, simple perforation plates, wide homocellular rays, and protruding phloem rays with prismatic crystals, are typical of lianoid Ranunculales. *Clematis*, the only woody climber in Ranunculaceae, has diffuse, axial parenchyma in short (2–6 cell), fusiform chains, and septate fibers (tables 1, 2) as seen in *Atli*. Maintaining the small size and shape of the cambium initial that produced an axial parenchyma strand results in this fusiform shape of the strand in longitudinal sections. However, *Clematis* differs from the fossil in having distinct growth boundaries in the wood (although little is known of specimens from more equable or aseasonal climates). In addition, woody stems in *Clematis* species differ from the fossil liana in having higher vessel densities, narrower vessel diameters, larger vessels per group, storied wood structure, and spiral thickenings in the tracheary elements (tables 1, 2; Grosser 1977; Sieber and Kučera 1980; Carlquist 1985, 1995; Fahn et al. 1986).

Lardizabalaceae are a family of vines/lianas including only one genus with a shrubby habit, *Decaisnea* Hook.f. & Thomson (Carlquist 1984). Seven species in six genera of climbing Lardizabalaceae were examined by Carlquist (1984) who found that the family had wood with narrow vessels (mean: 66.7  $\mu\text{m}$ , range of means: 46–116  $\mu\text{m}$ ; table 1), simple perforation plates (rarely scalariform in *Akebia* Decne.), and multiseriate rays (with uniseriate rays also present in *Sinofranchetia* Hemsl. and *Lardizabala* Ruiz & Pav.). Alternate, elliptical vessel pitting, simple perforation plates, and the presence of axial parenchyma in strands of 2–6 cells are found in Lardizabalaceae and in the fossil. When the extant species of Lardizabalaceae are compared in detail with the Hornby fossil liana, however, there are many differences. Pith in Lardizabalaceae is wholly or partially sclerotic, unlike the uniformly parenchymatous pith of *Atli*. Vessel elements are smaller in diameter (66.7  $\mu\text{m}$  diameter for Lardizabalaceae vs. 198  $\mu\text{m}$  for Hornby vine) and shorter (425  $\mu\text{m}$  in Lardizabalaceae vs. 527  $\mu\text{m}$  in the fossil) than in the fossil wood; and Lardizabalaceae have higher vessel densities (163 vs. 11 vessels per  $\text{mm}^2$  for Lardizabalaceae and *Atli*, respectively). In addition, genera of Lardizabalaceae tend to have two size classes of vessels (Carlquist 1984; Poole and Wilkinson 2000) and spiral thickenings typically found in smaller wood elements, neither of which is observed in the fossil wood. Rays tend to be wider in the fossil than in modern Lardizabalaceae, and the fossil wood does not show evidence of storied tissues that are typical of Lardizabalaceae liana wood (tables 1, 2; Carlquist 1984). Phloem, periderm, and pith all tend to be partially to wholly

Table 1

## Stem Anatomical Features of Extant Lianoid Families in Ranunculales and Cretaceous-Paleogene Extinct Lianoid Species: Vessels and Rays

Taxon	Group	Vessels						Rays							
		Two diameter classes	Tangential diameter (μm)	Element length (μm)	Density, vessel s/mm <sup>2</sup>	Perforation plates	Element pitting (μm)	Tyloses	Uniseriate rays <sup>a</sup>	Ray type	Ray height (mm)	Ray width (no. cells)	Intraray pitting <sup>b</sup>	Phloem rays protrude	Scl phloem ray cells
<i>Atli morini</i> gen. et sp. nov.	1–2 (3)	–	198 (98–317)	527 (294–764.4)	11 (9.4–13.1)	Simple	Elliptical, alt (7.8–10.4)	–	–	Homo	>20	21 (7–35)	+	+	+
Lardizabalaceae (lianas) <sup>1</sup>	1–2 (3)	+, –	67 (46–116)	425 (328–564)	163 (50–283)	Simple (rare scalar) <sup>c</sup>	Elliptical, alt (5–7)	–	– <sup>d</sup>	Hetero	>5	17 (10.5–22)	+, –	+, –	+
Menispermaceae (lianas) <sup>2,3</sup>	1–3 (4)	+, –	141 (43–282+)	301 (109–463)	22	Simple	Small, alt (4–10) <sup>e</sup>	+, –	+	Homo	>1	5–14 (2–27)	+, –	+	+
Ranunculaceae ( <i>Clematis</i> ) <sup>4–8</sup>	3–11–50+	+, –	12–97 (12–200+)	181–253	18–783	Simple, (scalar) <sup>f</sup>	Polygonal, alt (4–10+)	–	–?	Hetero	>1	4–10+	+, –	+, –	+
<i>Munzingoxylon delevoryasi</i> <sup>9</sup>	1(2–3)	–	95–115; 50–70 <sup>g</sup>	33–200	40–65	Simple, rare scalar	Round-scalar, (sub)opposite, (vestured) (5–7)	–	–	Hetero	?	11–33	–	–?	–
<i>Rodoxylon scheetzii</i> <sup>9</sup>	1(2–3)	–	70–112; 40–75 <sup>g</sup>	?	38	Simple	?	–	+	Hetero	?	Up to 30	–	–	–
“Javelina vine” <sup>10</sup>	1–10	+	72 (28–228)	?	8–20	Simple	?	–	–	Hetero	.3–.5	2–3	?	?	?
<i>Aristolochioxylon prakashii</i> <sup>11</sup>	1–2	+	108	?	12	?	Polygonal, alt	–	–	?	.03–.09	8–12	–?	–?	–
	1–3	+	225 (166–257); 75 (45–106) <sup>g</sup>	252–468	96 (51–198)	Simple	Polygonal, alt	–	+	Homo (hetero <sup>b</sup> )	?	8–16	–?	–?	–
<i>Anamirta pfeiffer</i> <sup>12</sup>	1	–	116 (58–156)	412 (237–588)	19 (12–29)	Simple	?	–	–	Hetero	>1	15+	–?	–?	–?
<i>Lardizabaloxylon cocculoides</i> <sup>13</sup>	1–3	–	100–163 (41–245)	435 (218–571)	34 (29–37)	Simple	Bordered, alt	+	–	Hetero	>1	7–18	+	+	+
<i>Lardizabaloxylon lardizabaloides</i> <sup>14</sup>	1	–	(36–172)	300–600	50–65	Simple	Alt (5–10)	–	–	Hetero	>10	~15	NP	NP	–?
<i>Menispermoxylon circumvallatum</i> <sup>15</sup>	1–3	–	246 (180–300)	300–400	10	Simple	Bordered, alt (5–7)	–	+	Homo	10	23–32	+	NP	–
<i>Ranunculodendron anzotegui</i> <sup>17</sup>	1–4	–	110.5 (55.5–166.6)	152.5 (55.4–277)	23	Simple	Bordered, alt	–	–	Hetero	1.7	2–4 cells	–?	–?	–?
<i>Vitaceoxylon</i> <sup>18</sup>	1–16	+	(50) 119–500	523 (120–757)	8–43	Simple	Oval, hexagonal, scalar, alt	+	+	Hetero	>5	Up to 15	+, –	–	–

Note. Abbreviations: alt = alternate; hetero = heterocellular; homo = homocellular; NP = not preserved; scalar = scalariform; scl = sclerenchyma; plus sign = present; minus sign = absent, question mark = uncertain. Numbers shown are means; ranges are in parentheses. InsideWood Database (2004–2013) was accessed for wood traits: superscript numbers indicate source of taxonomic data: 1 = Carlquist 1984; 2 = Carlquist 1995; 3 = Jacques and de Franceschi 2007; 4 = Fahn et al. 1986; 5 = Grosser 1977; 6 = Sieber and Kučera 1980; 7 = Carlquist 1985; 8 = Carlquist 1995; 9 = Cenomanian of United States, Tidwell et al. 2010; 10 = Maastrichtian of United States, Wheeler and Lehman 2000; 11 = Late Cretaceous of India, Kulkarni and Patil 1977; 12 = Late Cretaceous of India, Bonde 1997; 13 = Campanian of United States, Page 1970; 14 = age uncertain, Schönfeld 1954; 15 = Miocene of Thailand, Vozenin-Serra et al. 1989; 16 = Early Eocene of UK, Poole and Wilkinson 2000; 17 = Upper Miocene of Argentina, Lutz and Martínez 2007; 18 = Eocene and Miocene of United States, UK, and Europe, Wheeler and LaPasha 1994.

<sup>a</sup> All taxa have multiseriate rays, often medullary.

<sup>b</sup> As viewed in radial longitudinal sections.

<sup>c</sup> Rare scalariform perforations in *Akebia*.

<sup>d</sup> Uniseriate rays present in *Sinofranchetia* and *Lardizabala*.

<sup>e</sup> Enlarged pits near perforations in some.

<sup>f</sup> Some with reticulate to foraminiate perforations.

<sup>g</sup> Large vessels, small vessels.

<sup>h</sup> Heterocellular in uni-biseriate rays.



Table 2

## Stem Anatomical Features of Extant Lianoid Families in Ranunculales and Cretaceous-Paleogene Extinct Lianoid Species: General Characters and Wood

Taxon	General characters							Wood					
	Scl in pith	Fibers at 1° xylem	Scl in periderm	Scl caps over 2° phloem	Prismatic crystals	Anomalous growth	Distinct growth boundaries	Porosity	Storied structure	Vascular or vasicentric tracheids	Septate fibers	Axial parenchyma	Axial parenchyma, fusiform strand
<i>Atli morinii</i> gen. et sp. nov.	–	–	+ (nests)	–	+ , 2° phloem scl	–	–	Diffuse	–	+	+	Scanty paratracheal, diffuse apotracheal	+ (2–6 cells)
Lardizabalaceae (lianas)	+	–	– , + (nests)	+ , –	+ , scl	–	+ , –	Diffuse-(semi) ring porous	+ , obscure	+	+ , –	Vasicentric, (diffuse, in tangential lines)	– , + (2–7 cells)
Menispermaceae (lianas)	+	+	– , +	+	+ , –	+ , –	+ , –	Diffuse	+ , –	+	–	Tangential lines and/or diffuse	– (2–6 cells)
Ranunculaceae ( <i>Clematis</i> )	+ , –	+ , –	– , + (nests)	+ , –	?	+ , –	+ , –	Ring-semiring	+ , –	+ , –	+ , –	Scanty paratracheal, vasicentric	+
<i>Munzingoxylon delevoryasii</i>	+	–	–	–	–?	–	–	Diffuse	–	+	–	Scanty paratracheal (vasicentric)	–
<i>Rodoxylon scheetzii</i>	NP	NP	–	–	–?	–	–	Diffuse	–	+	–	Paratracheal, vasicentric and scanty	–
“Javelina vine”	?	?	?	?	?	?	–	Diffuse	–	–	–	Scanty paratracheal	?
<i>Aristolochioxylon prakashii</i>	–	–	NP	+	–?	–	–	Diffuse	–	–	–?	Paratracheal, vasicentric	–
<i>Anamirta pfeiffer</i>	–	–	NP	+	–?	+	+	Diffuse	–	+	–	Tangential lines, diffuse	–
<i>Lardizabaloxylon cocculoides</i>	+	+	NP	NP	+ , rays	–	–	Diffuse	–	+	–	Tangential lines and vasicentric	–?
<i>Lardizabaloxylon lardizabaloides</i>	–	–	+ (nests)	+	+ , pith and rays	–	+	Diffuse	–	+	–	Scanty paratracheal	–?
<i>Menispermoxylon circumvallatum</i>	NP	NP	NP	+	–?	+	+	Diffuse	–	–?	–?	Rare, apotracheal	–?
<i>Menispermoxylon</i> sp.	NP	NP	NP	?	–?	–	+	Diffuse	–	+	–	Rare, apotracheal	–
<i>Ranunculodendron anzoteguiiae</i>	NP <sup>a</sup>	NP <sup>a</sup>	NP	+	?	–	–	Diffuse	+	–?	–	Paratracheal (vasicentric and scanty)	–
<i>Vitaceoxylon</i>	?	?	+ , –	– <sup>b</sup>	– , + rays	–	+ , –	Diffuse	+	+ , –	+	Scanty paratracheal	+ , –

Note. Abbreviations as in table 1.

<sup>a</sup> Described as excentric and small (12.5 µm diam) with 4 protoxylem at periphery and internal metaxylem, suggestive of primary root anatomy.

<sup>b</sup> Series of fiber bundles throughout secondary phloem and periderm.

lignified in Lardizabalaceae with crystals present in sclerotic cells of these tissues (Carlquist 1984), whereas in the fossil, only scattered sclerotic nests are observed in the periderm, sclerotic fiber caps over the secondary phloem poles are lacking, and crystals are observed in the thick-walled cells of the protruding phloem rays only (table 2).

While most Menispermaceae lianas have woody stems with distinct growth boundaries and successive cambia, several genera lack both these features (i.e., *Borismene* Barneby, *Chasmanthera* Hochst., *Fibraurea* Lour., *Hypserpa* Miers, *Odontocarya* Miers, *Penianthus* Miers, *Stephania* Kuntze, *Syntriandrium* Engl. ex Diels, *Tinomiscium* Miers, *Tinospora* Miers; Jacques and de Franceschi 2007) and thus are more like the fossil liana, which has no evidence of successive cambia or growth boundaries. In addition, the menisperms listed above have prismatic crystals in ray-cells (although absent in *Penianthus*, *Stephania*, *Syntriandrium*, and *Tinomiscium*) and protruding phloem rays, similar to what is observed in the fossil liana. Wood in both Menispermaceae and in the fossil have simple perforation plates and vessels solitary or in multiples up to four (although multiples are uncommon in the fossil wood). Ray width and vessel tangential diameter in the fossil wood fall within the range of values reported in Menispermaceae (table 1; Carlquist 1996; Jacques and de Franceschi 2007). However, menisperm genera usually bear enlarged pits at the vessel element extremities (Carlquist 1996), which are not seen in *Atli*. Further, septate fibers (present in the fossil) have not been reported in menisperm liana species, and axial parenchyma tends to be grouped in tangential lines, unlike the diffuse and scanty axial parenchyma in the fossil wood. Short, fusiform axial parenchyma strands as in the fossil are not reported in extant Menispermaceae, and menisperm genera tend to have sclerotic fiber caps over secondary phloem poles, which do not occur in the fossil (table 2; Carlquist 1996; Jacques and de Franceschi 2007). Thus, while several anatomical features of the fossil wood are shared with taxa in Menispermaceae, *Atli morinii* does not fully conform to the family (tables 1, 2).

#### Comparison with Fossil Lianoid Stems

Fossilized woody stems of angiosperm lianas are known from the Cretaceous through Neogene and the majority of the taxa have been placed in Ranunculales or Vitaceae (tables 3, A1; Burnham 2009). Two lianoid taxa were described from stems growing inside *Tempyska* Corda trunks from the Cenomanian of Utah and New Mexico and were identified as Eudicots without being placed in any order or family (Tidwell et al. 2010). These two taxa, *Munzingoxylon* and *Rodoxylon*, are represented by much smaller stems than the Hornby liana and have higher vessel densities; heterocellular rays; and shorter, smaller-diameter vessels. In addition, *Rodoxylon* has both uni- and multiseriate rays, whereas the Hornby liana has only multiseriate rays. *Munzingoxylon* has abundant wood parenchyma and infrequent scalariform perforation plates (Tidwell et al. 2010), unlike the diffuse wood parenchyma and uniformly simple perforation plates observed in the Hornby liana.

Another Cretaceous (Maastrichtian) angiosperm stem with lianoid anatomy was described from Big Bend National Park

in Texas and informally called the “Javelina vine” (Wheeler and Lehman 2000; tables 1, 2). This axis has a vessel density (8–20 vessels per mm<sup>2</sup>) and rare scanty apotracheal parenchyma that are comparable to *Atli*, but other features (vessels in two diameter classes, vessels in radial multiples [up to 10 vessels], small vessel diameters [72 μm], and heterocellular multicellular [2–3 cells] rays) are unlike our Cretaceous stem and suggestive of Vitaceae. Although the presence of vessels in two diameter classes and in long radial multiples were interpreted as lianoid features, distinctive characters such as intervessel and ray-vessel pitting were not sufficiently preserved to allow confident placement in an angiosperm group (Wheeler and Lehman 2000).

*Vitaceoxylon* Wheeler and LaPasha, a genus established for fossil woods in Vitaceae, is currently composed of five species: two species from the Eocene Clarno Nut Beds (Wheeler and LaPasha 1994), one species from the Eocene London Clay (Poole and Wilson 2000), and two species from the Miocene of central Europe (Schönfeld 1930; Greguss 1969). Wheeler and LaPasha (1994) discuss additional fossil lianas that are not sufficiently well known to confidently place them within Vitaceae. Just as with extant Vitaceae, the Hornby stem can be excluded from *Vitaceoxylon* based on it having a single vessel diameter size class, a lack of frequent vessel clustering, a lack of storied elements, and heterocellular rays, all of which are found in *Vitaceoxylon* (tables 1, 2; Wheeler and LaPasha 1994).

*Ranunculodendron anzoteguiiae* Lutz et al., the only species currently in the genus, is based on a single small (4 mm diameter) axis from the Miocene of Argentina that is placed in Ranunculales (but not ascribed to any family; Lutz et al. 2007). This genus differs from the Hornby liana in being on a smaller axis and having narrower-diameter vessels, a higher vessel density, and wide heterocellular rays in addition to uniseriate rays (table 1). Therefore, the Hornby fossil cannot be placed in this genus.

*Anamirta pfeifferi* Bonde (Menispermaceae) represents an extinct species of the extant genus, based on a 17-mm-diameter stem from the Upper Cretaceous Deccan Intertrappean beds, Wardha district, Maharashtra, India (Bonde 1997). This taxon is distinct from the Hornby fossil in having successive cambia, axial parenchyma in short tangential lines (unlike the diffuse apotracheal axial parenchyma in *Atli*), vessels in two diameter size classes, uni- to biseriate rays, narrower and shorter vessel elements (even for the large diameter class), and a higher vessel density (table 1). This Cretaceous liana, although placed by the author in a modern menisperm genus, appears to have a vessel density that is higher than what is typical in Menispermaceae and that is more like that of Lardizabalaceae (our calculations from figs. 2, 3, and 5 of Bonde 1997; table 1; Carlquist 1984).

Two species of *Menispermoxylon* Vozenin-Sarra et al. have been described, a stem with successive cambia from the Miocene of Thailand (*Menispermoxylon circumvallatum*; Vozenin-Sarra et al. 1989; tables 1, 2) and a pyritized twig from the Eocene London Clay of the United Kingdom (Poole and Wilkinson 2000) that lacks successive cambia. *Menispermoxylon* is a form-genus placed in Menispermaceae, and the generic diagnosis of *Menispermoxylon* was modified and expanded by Poole and Wilkinson (2000) and now includes stems with suc-

**Table 3**  
**Angiosperm Fossil Liana Species Diversity by Lineage**

Taxon	Whole fossil record		Cretaceous-Paleogene records		Cretaceous-Paleogene wood only	
	No. species	% total species recorded	No. species	% total species recorded	No. species	% total species recorded
Vitales	159	37.3	122	40.7	7	28.0
Ranunculales	85	20.0	76	25.3	7	28.0
Rosids	65	15.3	26	8.7	4	16.0
Asterids	57	13.4	39	13.0	3	12.0
Monocots	34	8.0	23	7.7	0	.0
Basal angiosperms	12	2.8	7	2.3	1	4.0
Other eudicots	11	2.6	4	1.3	0	.0
Incertae sedis angiosperms	3	.7	3	1	3	12.0

Note. Data are modified from Burnham (2009).

cessive cambia that have tangential bands of parenchyma or wood without successive cambia. *Menispermoxyton* wood is further characterized by having simple perforation plates, alternate pitting, rays of two sizes, and either homocellular or heterocellular rays up to seven cells wide (Poole and Wilkinson 2000). The Hornby liana stem can be excluded from this genus because it lacks heterocellular rays as well as both multi- and uniseriate rays, and the rays in *Atli* are wider (>10 cells; table 1). Additional differences between the Hornby liana and *M. circumvallatum* are that the latter has distinctive growth rings and successive cambia (both absent in the fossil wood), exclusively solitary vessels, a higher vessel density (50–65 vessels per mm<sup>2</sup> in *M. circumvallatum* vs. 11 vessels per mm<sup>2</sup> in the Hornby liana), and heterocellular rays.

Poole and Wilkinson (2000) did not assign their specimen to a species within *Menispermoxyton*, but they greatly expanded the generic description to include their material in the genus. The London Clay sample differs in several ways from *M. circumvallatum* including the presence of homocellular (not heterocellular) rays, a lack of successive cambia, rays nearly twice the number of cells in width, the presence of rare uniseriate rays, and lower vessel density (10 vs. 50–65 vessels per mm<sup>2</sup> in *M. circumvallatum*). In many taxa that produce successive cambia, early stem growth has only a single xylem cylinder and only later in development produces successive cambia, although many taxa produce successive cambia early in development (Carlquist 1991). Further investigations of London Clay liana axes may reveal larger stems with successive cambia and higher vessels densities making these two species of *Menispermoxyton* more similar. However, *M. circumvallatum* has a much higher vessel density, making it appear less like modern Menispermaceae. In the future, this genus may need reevaluation both in its circumscription and in its affinities to Menispermaceae.

Two species are currently recognized for *Lardizabaloxyton* Schönfeld: one from Patagonia (stratigraphy and age uncertain; Schönfeld 1954) and one from California (Late Cretaceous [Campanian], Panoche Formation) of California (Page 1970). This genus has been compared most closely to Menispermaceae and Lardizabalaceae, and Page (1970) considered *Lardizabaloxyton cocculoides* to show features of both families. *Lardizabaloxyton lardizabaloides* Schönfeld was de-

scribed based on a 14-mm-diameter stem lacking both distinct growth boundaries and cambial variants and having diffuse porous wood, wide-diameter vessels, wide rays separating fibrous wedges, and protruding phloem rays, thus being similar in general appearance to the Hornby specimen. However, *L. lardizabaloides* differs from our fossil stem in having tyloses in vessels, a higher vessel density, spiral/helical thickenings in smaller wood elements such as fiber-tracheids, heterocellular rays, reticulate vessel pitting and vessel to ray parenchyma pitting, diffuse paratracheal parenchyma only (no apotracheal parenchyma), and crystals in pith cells (tables 1, 2; Schönfeld 1954).

*Lardizabaloxyton cocculoides* Page was described from a stem of 25-mm diameter that is also generally similar to our fossil but that differs in many features. *Lardizabaloxyton cocculoides* lacks tyloses, storied structure, and uniseriate rays and has protruded phloem rays, as in our specimen, but it differs in having only solitary vessels with a smaller mean diameter and length than those of *Atli*, heterocellular rays, and diffuse-in-aggregate axial parenchyma (tables 1, 2; Page 1970; InsideWood Database 2004–2013).

The Hornby fossil stem clearly does not conform to any previously described fossil taxon, and hence we name this fossil *Atli morinii* gen. et sp. nov. *Atli* shares the largest number of traits with *Lardizabaloxyton* but differs in several important characters. The Hornby stem shows a combination of features found in lianas of modern Ranunculaceae, Menispermaceae, and Lardizabalaceae (tables 1, 2).

#### *Climbers in the Cretaceous*

The angiospermous liana described here was recovered from sediments on Hornby Island, which is reconstructed as having a paleolatitude of 23.5°N during the Campanian (Ward et al. 1997), placing the locality within a tropical climate zone. The lack of distinct growth boundaries in the fossil stem points to an aseasonal or equable climate, consistent with the paleogeography. The paleogeographic location and the presence of a lianoid stem suggest that the terrestrial ecosystem of Hornby Island in the Campanian was an ecologically complex forest. Few plant fossils have been found from collections made at Collishaw Point. Two have been described so far: *Cycadeoidea*

*maccafferyi* (Rothwell and Stockey 2002), an extinct Mesozoic cycadeoid, and the cupressaceous conifer *Cunninghamia hornbyensis* (Brink et al. 2009). *Cunninghamia* today is found only in Southeast Asia. Gymnosperm wood with teredo borings, dicot wood, palm wood, and palm leaf bases have also been found here but have not been described (Ludvigsen and Beard 1997). This paucity of paleobotanical information is in stark contrast to the more diverse faunal assemblage, which includes cuttlefish, a crab, a spiny lobster, a starfish (family Goniasteridae), numerous species of bivalves, scaphopods, gastropods, a diverse assemblage of both heteromorph and planispiral ammonites, a weevil beetle, sharks, a pterosaur, mosasaurs, and several species of extinct birds (Ludvigsen and Beard 1997; Morrisson et al. 2005; Arbor and Currie 2011; Dyke et al. 2011).

Fossil angiosperm climbers from the Cretaceous have been assigned to Aristolochiaceae, Dioscoreaceae, Icacinaceae, Menispermaceae, Ranunculales, Smilacaceae, and Vitaceae, as well as some genera not assigned to family (Burnham 2009). While the majority of these are represented by leaves or seeds from Russia, Europe, and North America, woody stems are also known: *Munzingoxylon* and *Rodoxylon* (angiosperm, incertae sedis) from Utah and New Mexico (Tidwell et al. 2010), the Javelina vine (incertae sedis) from Texas (Wheeler and Lehman 2000), *Anamirta pfeiffer* (Menispermaceae) and *Aristolochioxylon* (Aristolochiaceae) from the Deccan Interrappean beds (Kulkarni and Patil 1977; Bonde 1997), and *Lardizabaloxylon cocculoides* (Ranunculales; Lardizabalaceae/Menispermaceae) from California (Page 1970). The presence of fossil lianas can be inferred from familial affinities of leaves or seeds, but without evidence of morpho-anatomical modifications for climbing, their certainty as lianas remains equivocal since families with lianoid species often also have species with other habits (i.e., trees, shrubs). In contrast, woody axes represent a reliable report for the presence of lianas in the fossil record because of the diagnostic syndromes of wood anatomical traits associated with the lianoid habit (Carlquist 1985, 1991).

While *Munzingoxylon*, *Rodoxylon*, and the Javelina vine are uncertain in their phylogenetic position, the other Cretaceous woody liana stems (*Lardizabaloxylon*, *Anamirta pfeifferi*, and *Atli morinii*) are all in Ranunculales. This differs from the nonwood fossil record for Cretaceous climbers, where leaves of Vitaceae and Menispermaceae represent the highest number of described liana species (data from Burnham 2009; table A1). *Atli* and *Lardizabaloxylon* are interesting because they both show a mosaic of features found in present-day ranunculalean lianas. *Atli* has the menispermaceous features of wide and mostly solitary vessels, low vessel density, lack of spiral thickenings on wood elements, homocellular rays, and diffuse axial parenchyma; however, the small fusiform shape of the axial parenchyma chains are more like *Clematis* and some Lardizabalaceae and have not been reported in Menispermaceae. *Atli* lacks sclerotic fiber caps over secondary phloem poles, which while typical of Menispermaceae, can be absent in *Clematis* and Lardizabalaceae. *Clematis* and Lardizabalaceae tend to have storied wood structure, which is not present in the Hornby fossil wood. *Lardizabaloxylon* was named for wood showing similarities to Lardizabalaceae, and characters such as spiral thickenings in the tracheary elements

of the wood and crystals in the pith affirm its affinities to Lardizabalaceae. However, *Lardizabaloxylon* has wide vessels with a low density and prismatic crystals in nonsclerotic cells, traits that are more menisperm-like (table 2). *Lardizabaloxylon cocculoides* also lacks spiral thickenings, which is more typical of menisperms. Thus, it seems that several early angiosperm lianas possessed traits that are now recognized in separate ranunculalean families, documenting past anatomical diversity within the group, and suggesting that these extinct taxa represent stem-lineage trait mosaicism in wood anatomical characters. These fossils are older than recent inferences about the timing of rapid diversification in Menispermaceae, inferred to peak at 60–70 million years ago (Wang et al. 2012). Cretaceous Ranunculales with mosaic traits are not limited to wood. For example, fossil flowers from the Early Cretaceous of Portugal were described as having characters typical of several different families in Ranunculales (von Balthazar et al. 2005).

Overall, woody axes of lianas are relatively uncommon in the fossil record. They are represented by taxa assigned to Ericales, Fabales, Malphigiales, Piperales, Ranunculales, Rosales, and Vitales (tables 3, A1; Burnham 2009 and references therein). We reexamined the data of Burnham (2009) to assess any taxonomic and evolutionary trends in early angiosperm lianas (tables 3, A1). We recognize that while some of these taxa may have to be reinterpreted on further study and that future fossil discoveries may change the conclusions reached here, our goal here is to provide a first examination of these data and stimulate others to reinvestigate the many less confidently assigned records and revisit this question.

For woody stems, Wheeler and LaPasha (1994) reexamined and revised putative taxa in Vitaceae, and thus woody stems can be assigned to this family with high confidence. For other taxa, reinvestigation will be necessary, either because of poor initial descriptions/illustrations (e.g., *Aristolochioxylon*; Kulkarni and Patil 1977) and/or because there has been much progress in recent years in our understanding of angiosperm phylogeny and anatomy. Reexaminations of nonvitaceous woods are needed, for example, *Anamirta pfeiffer* (Bonde 1997) and the expanded description of *Menispermoxylon* (Poole and Wilkinson 2000) fall outside of the range of features in modern Menispermaceae. Because combinations of characters are important in identifying wood to a family or genus, rather than single characters, continued refinement of databases such as InsideWood (Wheeler 2011) will provide the resources necessary for determining diagnostic suites of characters of these families. The Cretaceous and Paleogene wood record, in particular, would be worthy of further study in order to further examine and separate evolutionary and ecological patterns in wood structure (e.g., Wheeler et al. 2007; Carlquist 2009; Chave et al. 2009).

While wood is complex and can be difficult to identify, fruits and seeds can generally be more confidently assigned to family. Leaves can be diagnostic, but there is some convergence among forms that can make it difficult to place them in families (e.g., Piperaceae, Saururaceae, and Aristolochiaceae leaves) and much of the vein architecture work is recent (e.g., Ellis et al. 2009) so older (early-mid 1900s or before) descriptions may not be as reliable. Preservation also plays a role, as poorly preserved specimens will be less confidently assigned to a clade.

In the data set we analyzed, leaves account for ~45% of species, fruits/seeds for ~40% of species, pollen for ~9%, and wood for ~5.5%. Looking at just Cretaceous-Paleogene records, the numbers are similar: leaves comprise ~47%, fruits/seeds ~45%, wood ~4%, and pollen ~3% each of species in the database (modified from Burnham 2009). Consequently we have analyzed the record at a higher taxonomic level to try to minimize errors that might occur from misidentifications.

Interestingly, as with the Cretaceous record of climbers, when all species of fossil woody axes are considered (including *Atli*), Vitales and Ranunculales are equally represented and together account for 54% of all species. Because the Cretaceous and Paleogene were key periods of lineage diversification in angiosperms (e.g., Crepet and Niklas 2009; Magallón and Castillo 2009; Doyle 2012) we further analyzed liana diversity during this geological time period. The largest number of described species are Vitales (41% of all liana taxa) followed by Ranunculales (25%). Basal eudicots (in a broad sense) comprise 66.5% of the lianoid species described from the Cretaceous and Paleogene (with the inclusion of Sabiaceae and Dilleniaceae; table 3). This is in contrast to other angiosperm groups represented by fewer described species: monocots (7.7%), basal angiosperms (2.3%), asterids (13%), and rosids (8.7%; table 3). The pattern we observe from woody axes alone is congruent with that of the whole fossil record of lianas from the Cretaceous through Paleogene (table 3). Whole-plant

reconstructions of extinct taxa, revision of less confidently identified lianoid taxa, and further research into wood anatomy of early-divergent lineages of eudicots is needed to improve our ability to resolve possible trait mosaicism of ancient lineages. Such advances should shed light on this intriguing pattern of early-divergent eudicot liana diversity in the Cretaceous, a key period in the evolution of angiosperms (Crepet and Niklas 2009). Understanding these evolutionary patterns in the Cretaceous will be important to test hypotheses regarding how wood anatomical traits change with habit (e.g., Carlquist 1975, 1991, 1988) and how climbing angiosperms occupied different niches within tropical forests during this period of rapid evolution prior to the Cretaceous-Paleogene extinction.

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### Literature Cited

- APG III (Angiosperm Phylogeny Group III) 2009 An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot J Linn Soc* 161:105–121.
- Arbor VM, PJ Currie 2011 An istiodactylid pterosaur from the Upper Cretaceous Nanaimo Group, Hornby Island, British Columbia, Canada. *Can J Earth Sci* 48:63–69.
- Bonde SD 1997 Fossil dicotyledonous liana *Anamirta pfeifferi* sp. nov. (Menispermaceae) from the Deccan Intertrappean Beds of India. *Palaeobotanist* 46:89–94.
- Brink KS, RA Stockey, G Beard, WC Wehr 2009 *Cunninghamia hornbyensis* sp. nov.: permineralized twigs and leaves from the Upper Cretaceous of Hornby Island, British Columbia, Canada. *Rev Palaeobot Palynol* 155:89–98.
- Burnham RJ 2009 An overview of the fossil record of climbers: bejucos, sogas, trepadoras, lianas, cipós, and vines. *Rev Bras Paleontol* 12:149–160.
- Burnham RJ, C Revilla-Minaya 2011 Phylogenetic influence on twinning chirality in lianas from Amazonian Peru. *Ann Mo Bot Gard* 98:196–205.
- Caballé G 1993 Liana structure, function and selection: a comparative study of xylem cylinders of tropical rainforest species in Africa and America. *Bot J Linn Soc* 113:41–60.
- Carlquist S 1975 Ecological strategies of xylem evolution. University of California Press, Berkeley.
- 1984 Wood and stem anatomy of Lardizabalaceae, with comments on the vining habit, ecology and systematics. *Bot J Linn Soc* 88:257–277.
- 1985 Vasicentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions: review of vasicentric tracheids. *Aliso* 11:37–68.
- 1988 Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer, New York.
- 1991 Anatomy of vine and liana stems: a review and synthesis. Pages 53–72 in FE Putz, HA Mooney, eds. *The biology of vines*. Cambridge University Press, Cambridge.
- 1995 Wood and bark anatomy of Ranunculaceae (including *Hydrastis*) and Glaucidiaceae. *Aliso* 13:65–84.
- 1996 Wood and stem anatomy of Menispermaceae. *Aliso* 14:155–170.
- 2007 Successive cambia revisited: ontogeny, histology, diversity, and functional significance. *J Torrey Bot Soc* 134:301–332.
- 2009 Xylem heterochrony: an unappreciated key to angiosperm origin and diversifications. *Bot J Linn Soc* 161:26–65.
- Chave J, D Coomes, S Jansen, SL Lewis, NG Swenson, AE Zanne 2009 Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366.
- Crepet WL, KJ Niklas 2009 Darwin's second "abominable mystery": why are there so many angiosperm species? *Am J Bot* 96:366–381.
- Dickson WC 1967 Comparative morphological studies in Dilleniaceae. 1. Wood anatomy. *J Arnold Arbor* 48:1–29.
- DiMichele WA, MO Rischbieter, DL Eggert, RA Gastaldo 1984 Stem and leaf cuticle of *Karinopteris*: source of cuticles from the Indiana "paper" coal. *Am J Bot* 71:626–637.
- Doyle JA 2012 Molecular and fossil evidence on the origin of angiosperms. *Annu Rev Earth Planet Sci* 40:301–326.
- Dyke G, X Wang, G Kaiser 2011 Large fossil birds from a Late Cretaceous marine turbidite sequence on Hornby Island (British Columbia). *Can J Earth Sci* 48:1489–1496.
- Ellis B, DC Daly, LJ Hickey, JD Mitchell, KR Johnson, P Wilf, SL Wing 2009 *Manual of leaf architecture*. Cornell University Press, Ithaca, NY.
- Fahn A, E Werker, P Baas 1986 *Wood anatomy and identification of trees and shrubs from Israel and adjacent regions*. Israel Academy of Sciences and Humanities, Jerusalem.
- Gentry AH 1988 Changes in plant community diversity and floristic

- composition on environmental and geographical gradients. *Ann Mo Bot Gard* 75:1–34.
- 1991 The distribution and evolution of climbing plants. Pages 3–50 in FE Putz, HA Mooney, eds. *The biology of vines*. Cambridge University Press, Cambridge.
- Gianoli E 2004 Evolution of a climbing habit promotes diversification in flowering plants. *Proc R Soc B* 271:2011–2015.
- Greguss P 1969 Tertiary angiosperm woods in Hungary. Akadémiai Kiadó, Budapest.
- Grosser D 1977 Die Hölzer Mitteleuropas. Ein mikrophotographischer Lehratlas. Springer, Berlin.
- InsideWood Database. 2004–2013. Accessed June 14, 2012. <http://insidewood.lib.ncsu.edu/search>
- Insnard S, WK Silk 2009 Moving with climbing plants from Charles Darwin's time into the 21st century. *Am J Bot* 96:1205–1221.
- Jacques FMB, D De Franceschi 2007 Menispermaceae wood anatomy and cambial variants. *IAWA J* 28:139–172.
- Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose acetate peel technique in paleobotany. *Ann Bot, NS*, 20:635–637.
- Katnick DC, PS Mustard 2003 Geology of Denman and Hornby islands, British Columbia: implications for Nanaimo Basin evolution and formal definition of the Geoffrey and Spray formations, Upper Cretaceous Nanaimo Group. *Can J Earth Sci* 40:375–393.
- Kulkarni AR, KS Patil 1977 *Aristolochioxylon prakashii* from the Deccan Intertrappean Beds of Wardha district Maharashtra India. *Geophytology* 1:44–49.
- Lev-Yadun S 2000 Whirled grain in wood and topological defects. *J Theor Biol* 205:511–514.
- Lopes WAL, LA Souza, IM Moscheta, ALM Albiero, KSM Mourão 2008 A comparative anatomical study of climbing plants from forest remnants of Maringá, Brazil. *Gayana Bot* 65:28–38.
- Ludvigsen R, G Beard 1997 West Coast fossils, a guide to the ancient life of Vancouver Island (revised edition). Harbour, Madeira Park, British Columbia.
- Lutz AI, CA Martínez 2007 Nuevo género y especie de liana del Mioceno Superior (Formación Palo Pintado), provincia de Salta, Argentina. *Ameghiniana* 44:205–213.
- Magallón S, A Castillo 2009 Angiosperm diversification through time. *Am J Bot* 96:349–365.
- Marvin DC, K Winter, SA Schnitzer, RJ Burnham 2012 Tropical lianas and trees under elevated CO<sub>2</sub>: seasonal drought results in differing growth and physiological responses. Paper presented at 49th annual meeting of the Association for Tropical Biology, Bonito, Brazil, June 18–22.
- Masselter T, NP Rowe, T Speck 2007 Biomechanical reconstruction of the Carboniferous seed fern *Lyginopteris oldhamia*: implications for growth form reconstruction and habit. *Int J Plant Sci* 168:1177–1189.
- Metcalfe CR, L Chalk 1950 Anatomy of the Dicotyledons. Vol I. Clarendon, Oxford.
- Miles A 1978 Photomicrographs of world woods. HMSO Building Research Establishments, London.
- Morrison K, GJ Dyke, LM Chiappe 2005 Cretaceous fossil birds from Hornby Island (British Columbia). *Can J Earth Sci* 42:2097–2101.
- Page VM 1970 Angiosperm wood from the Upper Cretaceous of central California. III *Am J Bot* 57:1139–1144.
- Poole I, HP Wilkinson 2000 Two early Eocene vines from south-east England. *Bot J Linn Soc* 133:1–26.
- Rothwell GW, RA Stockey 2002 Anatomically preserved *Cycadoidea* (Cycadeoidaceae), with a reevaluation of systematic characters for the seed cones of Bennettitales. *Am J Bot* 89:1447–1458.
- Rothwell GW, HL Sanders, SE Wyatt, S Lev-Yadun. 2008 A fossil record for growth regulations: the role of auxin in wood evolution. *Ann Mo Bot Gard* 95:121–134.
- Schnitzer SA, F Bongers 2002 The ecology of lianas and their role in forests. *Trends Ecol Evol* 17:223–230.
- Schönfeld E 1930 Über zwei neue Laubhölzer aus dem Miozän. *Senckenbergiana* 12:111–126.
- Schönfeld E 1954 Über eine fossile Liane aus Patagonien mit einigen Bemerkungen über Beobachtungen an breiten Markstrahlen. *Palaeontogr Abt B* 97:23–35.
- Schweingruber FH 1990 Anatomy of European woods: an atlas for the identification of European trees, shrubs and dwarf shrubs. Haupt, Bern.
- Sieber M, LJ Kučera 1980 On the stem anatomy of *Clematis vitalba* L. *IAWA Bull, NS*, 1:49–54.
- Tidwell WD, SR Ash, BB Brooks 2010 Oldest known dicotyledonous lianas from the early Late Cretaceous of Utah and New Mexico, U.S.A. Pages 271–291 In CT Gee, ed. *Plants in Mesozoic time: morphological innovations, phylogeny, ecosystems*. Indiana University Press, Bloomington.
- von Balthazar M, K Raunsgaard Pedersen, EM Friis 2005 *Teixeiraea lusitanica*, a new fossil flower from the Early Cretaceous of Portugal with affinities to Ranunculales. *Pl Syst Evol* 255:55–75
- Vozenin-Serra, C, C Privé-Gill, L Ginsburg 1989 Bois Miocenes du Gisement de Pong, nord-ouest de la Thaïlande. *Rev Palaeobot Palynol* 58:333–355.
- Wang W, RDC Ortiz, FMB Jacques, X-G Xiang, H-L Li, L Lin, R-Q Li, et al. 2012. Menispermaceae and the diversification of tropical rainforests near the Cretaceous–Paleogene boundary. *New Phytologist* 195:470–478.
- Ward PD, JM Hurtado, JL Kirschvink, KL Verosub 1997 Measurements of the Cretaceous paleolatitude of Vancouver Island: consistent with the Baja–British Columbia hypothesis. *Science* 277:1642–1645.
- Wheeler EA 2011 InsideWood: a web resource for hardwood anatomy. *IAWA J* 32:199–211.
- Wheeler EA, CA LaPasha 1994 Woods of the Vitaceae: fossil and modern. *Rev Palaeobot Palynol* 80:175–207.
- Wheeler E, P Baas, PE Gasson 1989 IAWA list of microscopic features for hardwood identification. *IAWA Bull, NS*, 10:219–332.
- Wheeler EA, P Baas, S Rodgers 2007 Variations in dicot wood anatomy: a global analysis based on the InsideWood Database. *IAWA J* 28:229–258.
- Wilson JP, W Fischer 2011 Geochemical support for a climbing habit within the Paleozoic seed fern genus *Medullosa*. *Int J Plant Sci* 172: 586–598.
- Zotz G, N Cueni, C Körner 2006 In situ growth stimulation of a temperate zone liana *Hedera helix* in elevated CO<sub>2</sub>. *Funct Ecol* 20: 763–769.