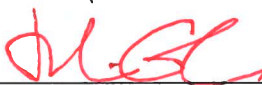1

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First confirmed occurrence of *Nothofagus* in the Cretaceous of western North America

submitted in partial fulfillment of the requirements for the degree
of **Master of Science in Earth and Environmental Sciences**
Department of Earth and Environmental Sciences
The University of
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Nothofagus Blume (southern beech; Family: Nothofagaceae, Order: Fagales) has a substantial fossil record across the Southern Hemisphere. Due to their extensive fossil record and southern distribution, *Nothofagus* remains an important group for understanding the evolution and biogeographical history of Gondwanan floras. While the reported fossil record of *Nothofagus* is restricted to Gondwanan landmasses, there are a number of *Nothofagus*-like fossils from North America. These fossils have been important for understanding the early evolution of Fagales, and the phylogenetic and morphological divergence between Nothofagaceae and other Fagales. Here we present a fagalean fossil fruit with closest similarities to *Nothofagus*. The specimen is a single trimerous fruit recovered from EV Henry Point, Sucia Island State Park, Washington (Cedar District Fm, early Campanian). The specimen was preserved in a calcareous concretion and studied using serial cellulose acetate peels, light microscopy and a 3D reconstruction, allowing the characterization of morphological and anatomical characteristics. The fruit is ~8.8 mm in cross sectional width with three longitudinally elongated wings and three glabrous locules separated by thin septa. The pericarp is differentiated into three layers: outer, middle, and inner. There are two ovules per locule, with axile placentation attached to an apical placental column. There is a single whorl of three persistent tepals at the apex of the fruit. This combination of characters is highly diagnostic of Fagales, especially Nothofagaceae. A number of *Nothofagus*-like fruit-containing cupules and isolated fruits have been previously described from the late Cretaceous of North America; however, these fossils differ from the extant genus in key characters such as the number of tepal whorls and the presence of trichomes lining the locules, which has precluded them from being assigned to Nothofagaceae. In contrast, the fossil described here has fruit characters diagnostic of *Nothofagus*, representing a new species, *Nothofagus suciaensis* sp. nov. However, important cupule characters are missing precluding confident assignment to a subgenus. This new occurrence of *Nothofagus* in the late Cretaceous of North America provides evidence for a wider distribution of the family than previously thought and supports a hypothesized biotic exchange between North America and Gondwana at this time.

Key Words: Cretaceous, Fagales, fruit fossil, Gondwana, morphological comparison, western North America

Introduction
Fagales Evolutionary History

The Cretaceous is notable for the rapid, extensive diversification of angiosperms (flowering plants), a group that now occupies almost every terrestrial environment excluding high-latitude regions (Friis et al., 2006; Magallon and Castillo, 2009; Benton et al., 2022). This bloom of diversity occurred during the early Cretaceous (ca. 140 Ma) at low to mid-latitudes and globally spread polewards during the late Cretaceous (ca. 90–100 Ma; Friis et al., 2011; Korasidis and Wagstaff, 2020). The origin and diversification of several modern, ecologically important angiosperm clades can be traced back to the Cretaceous but the patterns and causes of this evolution are still unclear (Xing et al., 2014).

The order Fagales is a morphologically and taxonomically diverse group with a substantial fossil record dating back to ~125 Ma, now dominating forests in mesic temperate to subtropical habitats of both the northern and southern hemisphere (Friis et al., 2006; Friis et al., 2011; Xing et al., 2014; Gandolfo et al., 2018). The order includes Casuarinaceae (she-oaks), Juglandaceae (walnuts), Myricaceae (waxberries), Ticodendraceae (duranzo de ardilla or squirrel peach), Betulaceae (birches), Fagaceae (oaks and beeches), and Nothofagaceae (southern beeches; APG, 2016). The remarkable fossil record of Fagales has made them the subject of

several phylogenetic studies (Chen et al., 1999; Jordan and Hill, 1999; Manos et al., 2001; Manos, 2002; Li et al., 2004; Manos et al., 2007; Sauquet et al., 2012; Xing et al., 2014; Larson-Johnson, 2015). Fagales had a notable contribution to the flora of the late Cretaceous evident with fossils of flowers, fruits, dispersed pollen, leaves, and woods (Friis et al., 2006; Larson-Johnson, 2015).

Within Fagales, the monogeneric family Nothofagaceae forms the earliest diverging lineage (Manos, 1997). Previously, *Nothofagus* Blume was placed in Fagaceae (Forman, 1966; Hutchinson, 1967; Abbe, 1974), reflecting its similar morphology, but Nixon (1989) recognized Nothofagaceae as a family separate from Fagaceae *sensu stricto* and sister to the rest of Fagales. The genus *Nothofagus*, with 42 species, is the only extant genus of Nothofagaceae, and today is restricted to the southern hemisphere (Vento et al., 2022). Differing from the traditional system, the Nixon classification differentiates between Fagaceae and Nothofagaceae based on flower, fruit, and pollen characteristics (Table 1; Herendeen et al., 1995). *Nothofagus* is separated into four subgenera based on deciduous and evergreen habit, cupule morphology, and leaf vernation: *Lophozonia, Fuscospora, Trisyngyne,* and *Nothofagus* (Heenan and Smissen, 2013). Due to their extensive fossil record and modern ecological importance, Nothofagaceae are a highly studied family in systematics (Riveros et al., 1995; Manos, 1997; Rozefelds and Drinnan, 2002; Sauquet et al., 2012; Torres et al., 2012), phylogenetic analysis (Hill and Jordan, 1993; Jordan and Hill, 1999; Fernandez et al, 2016; Vento et al., 2017), biogeography (Hill, 2001; Vento et al., 2022), and new species descriptions (Hill, 1994; Hill et al., 1996).

Today, *Nothofagus* is an important component of the biodiversity of New Zealand, South America, Australia, Tasmania, New Caledonia, and New Guinea (Hill, 2001). *Nothofagus* has been considered a "key genus" in the study of plant biogeography (Hill, 2001) and is of particular interest in biogeographic and diversity reconstructions due to its trans-Antarctic fossil distribution (Manos, 1997; Vento et al., 2022). The fossil record of *Nothofagus* dates back to the late Cretaceous in the Antarctic Peninsula, with evidence pointing to Gondwana serving as a center for the diversification of the genus as well as many other biota (Manos, 1997; Vento et al., 2022). Microfossil (pollen) records of *Nothofagus* are first documented in the early Campanian of Western Antarctica and the Campanian–Maastrichtian of southern South America (Dettman et al., 1990; Hill and Jordan, 1993; Vento et al., 2022). The earliest macrofossil (leaves) record of *Nothofagus* dates to the Campanian (~77–86 Ma) in the Antarctic Peninsula (Vento et al., 2022).

Nothofagus has thus far only been described across the southern hemisphere with fossils found from the Paleogene to early Pliocene of Tasmania (~66–3.8 Ma; Hill, 1984; Hill, 1991; Pole et al., 1993; Scriven and Hill, 1996; Jordan, 1999; Hill, 2001), the late Eocene to early Oligocene of South America (~44.6–34 Ma; Vento and Agrain, 2018), the Cretaceous to late Pliocene of Antarctica (~86–33.9 Ma; Hill et al., 1996; Hill, 2001), the Cretaceous to Oligocene of Australia (~72.1–20 Ma; Hill, 1988; Hill, 2004) and the Cretaceous to early Pliocene of New Zealand (~72.1–5.8 Ma; Pole, 1992; Pole, 1993b; Hill, 2001). In contrast, there are no fossils found in the northern hemisphere that are assigned to Nothofagaceae. There are a few taxa, however, that share some morphological features with *Nothofagus* but have been placed in the family Fagaceae, considered to be stem Fagales, or simply described as an unnamed taxa within Fagales, leaving in question the timing and nature of early evolution in Fagales. These *Nothofagus*-like fossils include staminate flowers, fruits, and cupules of *Protofagacea* Herendeen, Crane & Drinnan and *Antiquacupula* Sims, Herendeen, & Crane from the Campanian of Georgia, US (Herendeen et al. 1995; Sims et al. 1998), flowers and fruits of *Archaefagacea* Takahashi, Friis, Herendeen, & Crane from the early Coniacian of Japan

(Takahashi et al. 2008), unnamed Fagales flowers and fruits from the late Cretaceous of Massachusetts, US (Taylor et al., 2012), and *Soepadmoa* Nixon, Crepet, Gandolfo, & Grimaldi flowers of the Upper Cretaceous of New Jersey, US (Gandolfo et al., 2018). Nothofagaceae taxa will present features such as one cycle of tepals, lenticular or triangular fruits, glabrous locules, and unitegmic ovules (Table 1; Herendeen et al., 1995). Fagaceae taxa will demonstrate two cycles of tepals, triangular fruits, trichomes in the fruit locule, and bitegmic ovules (Table 1; Herendeen et al., 1995). These fossils demonstrated unique combinations of traits not found together in modern members of Nothofagaceae or Fagaceae, such as an enlarged, six-parted perianth on a bicarpellate central flower and subtending primary bracts (*Soepadmoa;* Gandolof et al., 2018), or glabrous fruit locules, dorsifixed anthers, and two cycles of tepals (*Antiquacupula;* Sims et al., 1998).

Together, these fossils provide evidence of distribution of early Fagales in the northern hemisphere; however, the question about timing of divergence between Nothofagaceae and other Fagales remains. The historical biogeography of *Nothofagus* remains unsatisfactory (Humphries, 1981a; 1981b; Manos, 1997) and characteristic differences in its fossils have proven to be ambiguous among extinct members (Gandolfo et al., 2018). Here I present a fruit fossil with features of *Nothofagus* to provide more insight into the early history of Nothofagaceae and their distribution in the northern hemisphere.

Material and Methods

The fossil specimen was recovered from a calcium carbonate concretion at EV Henry Point, Sucia Island State Park, Washington and is accessioned in the University of Kansas Paleobotanical Collections as KUPB-19240-Htop. The fossil was collected under Washington State Parks and Recreation Commission Scientific Research Permit #160401. Deposits at this locality belong to the Cedar District Formation of the Nanaimo Group and have been interpreted as shallow marine shelf facies (Peecook and Sidor, 2015). Through biostratigraphy, magnetostratigraphy and preliminary strontium isotopic data, the formation has been determined as lower middle Campanian (~80 Ma) in age (Ward et al., 2012). Other fossil specimens found from this formation include plant material, ammonites, terrestrial gastropods, bivalves, and a theropod femur (Ward, 1978; Roth, 2000; Ward et al., 2012; Peecook and Sidor, 2015; Atkinson, 2016; Tang et al., 2022, 2023).

The specimen KUPB-19240-Htop was prepared using the cellulose acetate peel technique of Joy et al. (1956) using 5% hydrochloric acid and an etching time of 25 seconds. Slides of each peel were made. The area of interest was cut out, demineralized in 5% hydrochloric acid for 30 seconds followed by a 30 second rinse in deionized water and dried flat. Sections were then immersed in xylene and mounted onto microscope slides using the mounting medium Eukitt (O. Kindler GmbH, Freiberg, Germany). Slides were photographed using a Nikon Eclipse LV100ND (Nikon, Tokyo, Japan) transmitted light microscope. A 3D reconstruction of KUPB-19240-Htop was made from the serial peels. Images of each peel were aligned manually after initial automatic alignment and then segmented, all using the imaging software AVIZO 9 LITE 3D (Thermo Fisher Scientific, Waltham, MA, USA). Segmentation of the fruit was separated into the following materials: wings, fruit wall, locule cavities, and ovules. Voxel dimensions were scaled to x=y=1 and z=7 to account for missing material during the preparation process.

Morphological Characters

A data matrix of morphological characters was compiled for comparison of KUPB-19240-Htop. This included 63 extant and extinct Fagales genera representing 96 species (Table

2; Hill, 1991; Herendeen et al., 1995; Rozefelds and Drinnan, 2002; Takahashi et al., 2008; Larson-Johnson, 2015) in addition to the new Sucia triangular fruit. Data from the literature were supplemented with microCT scans of 19 species of *Nothofagus (*subg. *Nothofagus, Lophozonia, Trisyngyne, Fuscospora), Fagus, Castanea,* and *Castanopsis* from the United States National Herbarium (Appendix 1; US) for the final matrix. A total of 21 characters were used, building on previous phylogenetic matrices from Hill and Jordan (1993), Herendeen et al. (1995), Manos et al. (2001), Rozefelds and Drinnan (2002), Takahashi et al. (2008), and Larson-Johnson (2015), and an anatomical study from Picca (1998). Several new characters were added (#4, 11, 19, 20, 21). The characters used are:

1. Style and stigma shape. Styles of *Nothofagus* can present as slender while those of *Fagus* are commonly slender with a decurrent stigma. *Castanea, Castanopsis* and *Chysolepis* typically have slender styles with a terminally positioned stigma. *Quercus* and *Trigonbalanus* will have a more flattened or stout style with terminal capitate or swollen stigmas (Herendeen et al., 1995).

>   0= Stout with capitate stigma
>   1= Slender with decurrent stigma
>   2= Slender, stigmatic distally
>   3= Slender with terminal pore

2. Fruit per cupule. The number of fruits per cupule is variable between species with the most common arrangement being three fruits per cupule; one dimerous central fruit and two trimerous lateral fruits. *Protofagacea* and *Nothofagus* present this arrangement. The exceptions of this arrangement in *Nothofagus* are *N. alessandri* with seven fruits per cupule and *N. pumilio* with only one trimerous fruit. Two fruits per cupule is an arrangement undocumented in *Nothofagus* and typical in *Fagus* species (Hill and Jordan, 1993).

>   0= 2 trimerous, 1 dimerous
>   1= 3 dimerous
>   2= 1 trimerous
>   3= 1 trimerous, 1 dimerous
>   4= 2 trimerous
>   5= 4–7

3. Fruit in cross-section. Fruit can present differently in shape between taxa. Fruit of *Nothofagus, Fagus, Protofagacea, Antiquacupula, Trignobalanus,* and *Chyrsolepis* can be triangular or lenticular in shape. Those of *Castanea* and *Castanopsis* will present a more rounded irregular appearance. *Quercus* typically demonstrates a rounded fruit in cross section (Herendeen et al., 1995; Sims et al., 1998).

>   0= Triangular or lenticular
>   1= Round
>   2= Irregular or lenticular
>   3= Square

4. Female flowers clustering. Flowers can present as either solitary or clustered along the infloresence. Flowers of the Fagales family Betulaceae demonstrate reduced to compact clusters of minute flowers (Kubitzki et al., 2013). Flowers of Fagaceae usually present as staminate flowers solitary or in dichasial clusters of 2–30 along the rachis, sessile, or pedicellate (Kubitzki et al., 2013). Species of Nothofagaceae such as *N. cunninghamii,* can present flower clusters surrounded by prominent bracts (Rozefelds and Drinnan, 2002).

>   0= Solitary

1= Clustered

5.   Flowers per cupule. Four-valved cupules of *Nothofagus* will often present a dichasium of three flowers consisting of two tricarpellate, lateral flowers and one bicarpellate, central flower (Manos, 1997). Species of *Fagus* are reported to have two-flowered, four-valved cupules (Manos, 2001). Two-valved cupules, found in the subgenus *Trisyngyne,* can subtend 1–3 bicarpellate flowers while those of the species *N. pumilio* of the subgenus *Nothofagus* will present a two-valved asymmetric cupules with a single tricarpellate flower (Manos, 1997).

        0= 1 flower
        1= 3 flowers
        2= 2 flowers
        3= greater than 3 flowers

6.   Number of tepal cycles. *Nothofagus* mature fruits present only one cycle of tepals. Those of both *Protofagacea* and Fagaecae *sensu stricto* have two cycles of tepals or two cycles of three tepals in the trigonous fruits (Herendeen et al., 1995).

        0= 0 cycles
        1= 1 cycle
        2= 2 cycles
        3= 3 or more cycles

7.   Tepal whorl persistence. Tepal whorls may either persist or dehisce after fruit maturation.
        0= Non-persistent
        1= Persistent

8.   Cupule lamella type. Lamellae are present on all cupules on the outside of the valves and will either be glandular or non-glandular with rare cases of intermediate conditions occurring (Hill and Jordan, 1993).

        0= Non-glandular
        1= Glandular and non-glandular
        2= Glandular

9.   Cupule peduncle type: Short or sessile peduncles are common in most cupules of *Nothofagus* species with few species presenting elongated peduncles. *Fagus* species often have very short or relatively sessile peduncles (Hill and Jordan, 1993). Taxa of *Castanea, Castanopsis, Chrysolepis, Quercus,* and *Trigonobalanus* present sessile peduncles (Herendeen et al., 1995).

        0= Sessile or with short peduncle
        1= Long peduncle

10.   Cupule appendages. Both *Nothofagus* and *Protofagacea* present cupular appendages in the form of lamellae. Taxa of *Fagus* and *Trigonobalanus* are reported to have scale-like appendages while those of *Castanea* and *Chrysolepis* have spine-like appendages. Species of *Castanopsis* can have both lamellae and spines and *Quercus* can have both lamellae and scales present (Herendeen et al., 1995).

        0= Lamellae
        1= Caducous
        2= Persistent
        3= Scales
        4= Spines

11.   Number of rows of cupular appendages. Cupular appendages (spines, scales, lamellae) in Fagaceae are regularly arranged on the outside of the cupule and reflect a condensation of a

dichasial flower system (van Steenis and Veldkamp, 1984). The number of rows of cupular appendages can vary between one and six. Row number will vary among species.

> 0= 1–2
> 1= 3–4
> 2= 4–5
> 3= 5–6

12.   Valve number. Hill and Jordan (1993) suggested that cupule morphologies indicate autapomorphies. Cupules of *Nothofagus* are typically four- or two-valved and bilaterally symmetrical. The exceptions of this case are the two-valved asymmetrical cupules of *N. pumilio* and the three-valved, asymmetrical *N. solandri*. However, *N. solandri* can also present four-valved symmetrical or two-valved symmetrical or asymmetrical cupules. Species of *Fagus* will commonly present bilaterally symmetrical, four valved cupules (Hill and Jordan, 1993). Due to the unusual structures of *N. pumilio* and *N. solandri* this character state can be more difficult to score. A two-state character was employed following the suggestion Hill and Jordan (1993).

> 0= 4 valves or 2 or 3 asymmetrical valves
> 1= 2 bilaterally symmetrical valves

13.   Cupule dehiscence. The cupule of a given specimen can present valvate dehiscence (or opening at maturity) or instead present hemispheric indehiscence. Species of Fagaceae can present valveless to irregularly dehiscent cupule (Manos et al., 2001)

> 0= Valvate
> 1= Hemispheric indehiscent

14.   Valve dehiscence. Valve dehiscence can appear as indehiscent, partial opening, or complete dehiscence.

> 0= None
> 1= Partial
> 2= Complete

15.   Number of locules. Fruits can be unilocular, bilocular, trilocular or have four or more locules.

> 0= 1 locule
> 1= 2 locules
> 2= 3 locules
> 3= greater than or equal to 4 locules

16.   Trichomes in locule. Fagaceae *sensu stricto* and *Protofagacea* both bear numerous trichomes on the locule surface. Species of *Nothofagus* lack this feature (Herendeen et al., 1995).

> 0= Absent
> 1= Present

17.   Number of ovules per locule. *Soepadmoa* has a characteristic trilocular ovary with only one seed present in each locule. This is unseen in any modern or fossil Fagales (Gandolfo et al., 2018).

> 0= 1 ovule
> 1= 2 ovule
> 2= greater than to equal to 3 ovules

18.   Number of integuments in the ovules. Ovules of *Nothofagus* have been documented to be unitegmic while those of Fagaceae *sensu stricto* are bitegmic (Herendeen et al., 1995).

> 0= Unitegmic
> 1= Bitegmic

19.   Wings. Only some species of *Nothofagus* will develop wings along the margins of the fruit including *N. antarctica* and *N. obliqua.* Reduced wings can develop on the trigonal nuts of some *Fagus* species as well as genera in Betulaceae including *Alnus* and *Betula* (Manchester and O'Leary, 2010).

        0= Absent
        1= Present

20.   Fruit wall thickness (µm). Fruit wall thickness showed ranges between 50 µm and >401 µm in the specimens used for morphological analysis.

        0= 50–100
        1= 101–200
        2= 201– 300
        3= 301–400
        4= greater than or equal to 401

21.   Number of layers in the fruit wall. The fruit wall pertains to the pericarp of the fruit and can be divided into multiple layers; outer, middle, and inner.

        0= 1 layer
        1= 2 layers
        2= 3 layers

Results
Systematic Paleobotany
Family: NOTHOFAGACEAE
Genus: *Nothofagus* Blume
Species: *Nothofagus suciaensis* Morrison, Atkinson & S.Y.Smith, sp. nov.
Etymology: The specific epithet was chosen for Sucia Island, Washington, USA, where the specimen was collected.
Holotype: University of Kansas Paleobotanical Collections, KUPB-19240-Htop
Locality: EV Henry Point, Sucia Island State Park, Washington
Stratigraphy: Cedar District Formation, Nanaimo Group
Age: Early to Middle Campanian (~80 Ma; based on biostratigraphy, magnetostratigraphy and preliminary strontium isotopic data; Ward et al., 2012)
Description
      The fruit is about 8.8 mm in cross sectional width (Fig. 1A). The height of the fruit estimated from 3D rendering is 7.4 mm with the basal portion missing (Fig. 2). It has three longitudinally elongated, apically extended wings up to 3.9 mm in cross sectional length (Fig. 1A, 1B). The pericarp, ca. 170 µm thick, is differentiated into outer, middle, and inner layers of the hypanthium derived from the perianth (Fig. 1C). The outer layer includes thick-walled cells and idioblasts (Fig. 1C). Cells of the outer layer have widths of 5.4–11.3 µm and heights of 6.2–14.8 µm and the idioblasts, present on the abraded epidermis, range from 12.6–21.1 µm in width and 12.6–24.1 µm in height. The middle layer comprises horizontally elongated fibers, 23.6–86.5 µm long and 8.8–25.9 µm wide (Fig. 1C). The inner layer comprises small, thick-walled sclereids with a width range of 16.6–58.9 µm and height range of 12.1–40.9 µm (Fig. 1D) but changes distal from apex to become more parenchymatous with cells ranging from 14.9–68.3 µm in width and of 14.9–68.3 µm in height (Fig. 1E). At the fruit corners, the middle and outer layer extend outward to form wings. The wings are parenchymatous with cell widths of 7.1–25.9 µm and lengths of 19.3–45 µm with scattered sclereids (Fig 1B). The wings of the fruit terminate

above the apex. Three glabrous locules are present and separated by thin septa (Fig. 1F). The septa appear ruptured as they approach the apical placental column. In the more basal part of the preserved portion, very thin-walled cells fill the locule cavities (Fig. 1). Two ovules per locule are present with axile placentation attached to an apical placental column (Fig. 1G). The ovules are unitegmic and are relatively similar in size up to 97.3 μm wide. There is a single whorl of three persistent tepals at the apex of the fruit (Fig 1H; 1I). A narrow style base and a faint capitate stigma are present at the apex of the fruit (Fig. 1I).

Discussion

The specimen KUPB-19240-Htop shares several defining features with families of the order Fagales including unitegmic ovules (Nothofagaceae, Betulaceae, Juglandaceae, Myricaceae, Ticodendraceae), a triangular shaped fruit in cross sectional view (Nothofagaceae, Fagaceae), trilocular fruit (Fagaceae and Nothofagaceae), winged fruit (Fagaceae, Betulaceae, Juglandaceae, Casuarinaceae, and Nothofagaceae), and one cycle of tepals (Nothofagaceae, Casuarinaceae; Table 1; Casper, 1992; Herendeen et al., 1995). KUPB-19240-Htop presented only one tepal cycle and thus can be excluded from Fagales families that present two or more cycles such as Juglandaceae and Fagaceae as well as families that present zero cycles such as Betulaceae, Ticodendraceae, and Myricaceae. Placement in the family Casuarinaceae was excluded because species of this family have rounded fruits and bitegmic ovules. The presence of winged trilocular fruits further excludes the Sucia triangular fruit from the families Betulaceae, Casuarinaceae, Juglandaceae, Myricaceae, and Ticodendraceae, which do not have such fruits. The new fossil was also excluded from Fagaceae due to its pericarp consisting of a middle layer of elongated sclereids. Fruit walls of Fagaceae species do not present this pericarp characteristic (Soepadmo, 1968). Thus, the only family that shared the same general fruit morphology is Nothofagaceae, with one tepal cycle, unitegmic ovules, triangular cross sectional shape, and its trilocular, winged fruit.

Within Nothofagaceae, the different subgenera are distinguished primarily based on habit (deciduous or evergreen), cupule morphology, and leaf vernation: *Lophozonia, Fuscospora, Trisyngyne* (formerly *Brassospora* but reclassified by Heenan and Smissen, 2013) and *Nothofagus* (Heenan and Smissen, 2013) — features not preserved in the fossil examined here. The trilocular fossil fruit shares characteristics to that of the subgenera *Fuscospora, Nothofagus* (which have one trimerous flower) and *Lophozonia* (one dimerous or two trimerous fruits per flower), but can be excluded from subgenus *Trisyngyne,* which only has dimerous fruits (Heenan and Smissen, 2013). As only one isolated trimerous fruit has been found so far, the presence or absence of dimerous fruits, and important cupule morphology, is unknown, thus a determination on subgenus was not made.

Nothofagus comprises 42 extant species (Vento et al., 2022). Of those 42, 15 species were able to be used in this study for gross morphological and anatomical comparison. Species were selected based on observation of material at the US National Herbarium and published comparative anatomical and morphological data (Hill, 1991; Herendeen et al., 1995; Picca, 1998; Rozefelds and Drinnan, 2002; Takahashi et al., 2008; Larson-Johnson, 2015). Lack of comprehensive anatomical and morphological data limits the number of species and observable traits available for this comparative study. Species of subgenus *Lophozonia* included in this study were *N. cunninghamii* (Hill, 2001)*, N. glauca* (Hill, 2001)*, N. nervosa* (Rozefelds and Drinnan, 2002)*, N. obliqua* (Appendix 2.1.I; Appendix 2.1.J)*,* and *N. alpina* (Appendix 2.1.K; Appendix 2.1.L)*.* Of this subgenus, *N. cunninghamii, N. glauca, N. obliqua,* and *N. alpina* all present

triangular fruits and glabrous locules. Fruits of *N. alpina, N. obliqua,* and *N. cunninghamii* were winged while those of *N. glauca* and *N. nervosa* presented no wings. *Nothofagus alpina, N. obliqua,* and *N. cunninghamii* also showed three distinct layers of pericarp. The pericarp of *N. glauca* and *N. nervosa* was not observed and thus not scored in this comparison. Species of the subgenus *Trisyngyne* examined here included *N. starkenborghiorum* (Appendix 2.2.G; Appendix 2.2.H)*, N. pullei* (Appendix 2.2.A; Appendix 2.2.B)*, N. rubra* (Appendix 2.2.C; Appendix 2.2.D)*,* and *N. grandis* (Appendix 2.2.E; Appendix 2.2.F)*.* All species included of this subgenus present irregular, lenticular shaped, winged fruits with three distinct layers of pericarp. Species of subgenus *Fuscospora* included in this comparison were *N. solandri* (Appendix 2.2.K; Appendix 2.2.L), *N. cliffortioides* (Appendix 2.3.A; Appendix 2.3.B), and *N. fusca* (Appendix 2.2.I; Appendix 2.2.J)*. Nothofagus solandri* presented rounded, bilocular fruits and wings are absent. *Nothofagus cliffortioides* and *N. fusca* both presented triangular, trilocular fruits with the presence of wings. All species of *Fuscospora* presented three distinct layers of the pericarp. Species of subgenus *Nothofagus* compared in this study include *N. antarctica* (Appendix 2.1.A; Appendix 2.1.B)*, N. betuloides* (Appendix 2.1.C; Appendix 2.1.D)*, N. pumilio* (Appendix 2.1.E; Appendix 2.1.F)*,* and *N. dombeyi* (Appendix 2.1.G; Appendix 2.1.H)*. Nothofagus pumilio* showed only one ovule per locule, unlike two ovules per locule in the fossil. *Nothofagus antarctica* had rounded, unilocular fruits with three pericarp layers. *Nothofagus betuloides, N. dombeyi,* and *N. pumilio* all presented triangular, trilocular fruits with only two layers of pericarp. All species of this subfamily presented winged fruits.

Of the fruits considered here, the extant species *N. obliqua* (Appendix 2.1.I; Appendix 2.1.J) and *N. alpina* (Appendix 2.1.K; Appendix 2.1.L) of the subgenus *Lophozonia* and *Nothofagus fusca* (Appendix 2.2.I; Appendix 2.2.J) of the subgenus *Fuscospora* matched closest in morphological characters to KUPB-19240-Htop (Table 2). 11 character states are shared with the fruit fossil: stout style with capitate stigma, triangular fruit shape in cross sectional view, one tepal cycle, persistent tepal cycle, three locule cavities, glabrous locules, two ovules per locule, unitegmic ovules, wings present, fruit wall thickness between 101–200 µm, and three layers present in fruit wall. However, all three of these extant species presented three nuts within each fruit. KUPB-19240-Htop was preserved as a single, isolated triangular nut, so this is not a trait we can use for comparison. The fossil fruit pericarp is moderately thick (~101–200 µm) and differentiated into distinct outer, middle, and inner layers, which is consistent with observations of the extant species *N. obliqua* (Appendix 2.1.I; Appendix 2.1.J), *N. alpina* (Appendix 2.1.K; Appendix 2.1.L), and *N. fusca* (Appendix 2.2.I; Appendix 2.2.J). Wings of the Sucia triangular fruit occur along the marginal angles of the fruit and are apically extended, developing from the ovary wall. Wings of the species *N. obliqua* develop along the marginal angles of the fruit (Manchester and O'Leary, 2010), much like those of the Sucia triangular fruit, *N. alpina*, and *N. fusca.* The fruit walls of *N. obliqua* appear smooth while those of *N. alpina* and *N. fusca* show glandular surfaces and the presence of idioblasts. Idioblasts are prominent on the Sucia fruit in the epidermis of the fruit wall (Fig. 1.C). In longitudinal section (LS), the fruits of *N. obliqua* (Appendix 2.1.I) appear more stout and rounded, similar to the LS view of the 3D reconstruction of the apex of the Sucia fruit (Fig. 2.C). *Nothofagus alpina* (Appendix 2.1.K) and *N. fusca* (Appendix 2.2.I) are more elongated in LS view. While all three of these species share the most similar scores as the Sucia fruit, none have idioblasts in the epidermis of the fruit wall, or a stout, rounded fruit apex in LS view. While the fruit structure is consistent with *Nothofagus*, due to lack of cupule data and a definite number of nuts per fruit present in this extinct taxon, the fossil was not assigned to any extant species or subgenus.

Comparison with fossil Nothofagus-*like fruits*

The staminate flowers with associated fruits and cupules of *Protofagacea,* from the Campanian (late Cretaceous) Buffalo Creek Member of the Gaillard Formation in central Georgia, U.S., shared similarities to cupules of several extant *Nothofagus* species (e.g., *Nothofagus antarctica, Nothofagus dombeyi*; Herendeen et al., 1995). Cupules in both genera have a lenticular, bicarpellate central fruit, tricarpellate lateral fruits, and horizontal lamellae on the outer surface of the cupule valves (Herendeen et al., 1995). However, *Protofagacea* shared more similarities to Fagaceae *sensu stricto,* with trichomes present on the fruit wall and bearing two cycles of tepals. *Nothofagus* fruits lack trichomes in the locules and have only one cycle of tepal (Herendeen et al., 1995). The fossil fruit was assigned *Protofagacea* by Herendeen et al. (1995) due to its inflorescence structure (i.e. bearing a laterally attached peduncle) and a unique combination of characters unknown to occur in any extant taxa.

From the same locality as *Protofagacea,* fossil staminate flowers and fruits were described by Sims et al. (1998). The authors concluded that the flowers, fruits and cupules were morphologically distinct from both *Protofagacea* and Fagaceae *sensu lato*. The fossil was assigned a new genus, *Antiquacupula,* and interpreted as demonstrating an early divergence in at least two lingeas within Fagaceae *sensu lato* by the late Santonian (late Cretaceous; Sims et al., 1998). *Antiquacupula* and Nothofagaceae share a pronounced extension of the connective and glabrous fruit locules (Sims et al., 1998). However, unlike Nothofagaceae*, Antiquacupula* has dorsifixed anthers and two cycles of tepals much like Fagaceae *sensu stricto* (Sims et al., 1998). The authors assigned *Antiquacupula* to Fagaceae *sensu lato* due to the fossils' cupule characteristics, but addressed the uncertainty in relationships among extant Fagaceae and Nothofagaceae in this assignment (Sims et al., 1998).

Fossil flowers and fruits from the Asamigawa Member of the Ashizawa Formation (early Coniacian) of the Futaba Group in northeastern Honshu, Japan were described by Takahashi et al. (2008) and assigned as *Archaefagacea futabensis*. The fossil was proposed as an early Fagaceae but lacked important features (i.e. no cupulate structures present) for assignment to either Fagaceae or *Nothofagus* (Takahashi et al., 2008; Gandolfo et al., 2018). Much like *Protofagacea* (Herendeen et al., 1995) and *Antiquacupula* (Sims et al., 1998), establishing relationships within Fagales for the fossil proved difficult due to a lack of phylogenetic framework (Takahashi et al., 2008).

Taylor et al. (2012) described fossil flowers from the late Cretaceous Raritan and Magothy Formations of Massachusetts. The fossil shared characteristics of Nothofagaceae such as a perianth in one cycle and 1–7 lenticular or triangular fruits (Taylor et al., 2012). The fossil also shared features with Fagaceae: a trigonous, nut-like fruit structure and bitegmic ovules (Taylor et al., 2012). However, the fossil flowers presented characteristics of bisexual, carpellate flowers that conflict with flower features (i.e. unisexual flowers) of the Fagales group and thus the fossil flowers remain unassigned (Taylor et al., 2012).

Soepadmoa fossil flowers preserved in amber from the early Upper Cretaceous of New Jersey were described by Gandolfo et al. (2018) as the oldest known flower structures in the early stem complex of Fagales present in the northern hemisphere. The fossils were suggested by the authors as intermediate forms between *Nothofagus* and other Fagales. *Soepadmoa* was described as "strikingly similar" to modern species of *Nothofagus* due to the shared features of a central bicarpellate flower and two lateral tricarpellate flowers (Gandolfo et al., 2018). However, *Soepadmoa* also presented an enlarged, six-parted perianth of the bicarpellate central flower and subtending primary bracts not found in any modern members of Nothofagaceae or Fagaceae

(Gandolfo et al., 2018). The authors suggested that the *Soepadmoa* fossils support the hypothesis of a proto-fagalean lineage distributed in both the northern and southern hemispheres (Gandolfo et al., 2018).

Thus these "*Nothofagus*-like"(Tanai, 1986; Gandolfo et al., 2018) fossils show a mosaic of features of Nothofaceae and Fagaceae, but are clearly not assignable to Nothofagaceae itself. KUPB-19240-Htop shares features of triangular fruits and a single cycle of persistent tepals with *Archaefagaceae futabensis* of Takahashi et al. (2008) and the unnamed Fagales flowers of Taylor et al. (2012). However, KUPB-19240-Htop does not present bitegmic ovules found in the Fagales flowers (Taylor et al., 2012) or trichomes present on the locule of fruit found in both the Fagales flowers (Taylor et al., 2012) or *Archaefagecea futabensis* (Takahashi et al., 2008). Trichomes present on fruit locules is a trait also shared by Fagaceae, *Antiquacupula sulcata* (Sims et al., 1998), and *Soepadmoa* (Gandolfo et al., 2018). KUPB-19240-Htop lacks two cycles of tepals, a trait found in Fagaceae, *Protofagacea allonensis* (Herendeen et al., 1995), *Antiquacupula sulcata* (Sims et al., 1998), and *Soepadmoa* (Gandolfo et al., 2018; Table 3). Instead, the fossil fruit examined here does not match previously described fagalean fossils but shows strong affinities to Nothofagaceae based on the combined presence of one cycle of tepals, glabrous fruit locules, and unitegmic ovules in a winged trilocular fruit. Thus the fruit fossil has been designated as *Nothofagus suciaensis* sp. nov. of the family Nothofagaceae. Features of *N. suciaensis* are not consistent with any extant *Nothofagus* and show to be of crown Nothofagaceae with no intermediate feature or other characteristics suggesting other Fagales families.

Biogeographical implications

The presence of this *Nothofagus* fossil in North America expands the biogeographical distribution of Nothofagaceae in the Cretaceous. *Nothofagus* fossils are first documented in the early Campanian of Western Antarctica and the Campanian-Maastrichtian of southern South America based on pollen records (Dettman et al., 1990; Hill and Jordan, 1993; Vento et al., 2022) and Campanian (~77–86 Ma) of the Antarctic Peninsula from macrofossil records (leaves; Vento et al., 2022). Subsequently, there is a global increase in *Nothofagus* species diversity from the late Eocene to the late Oligocene–early Miocene, but still restricted to the southern hemisphere (Hill, 2001; Cook and Crisp, 2005). The break-up of Gondwana hypothesis (Sanmartin and Ronquist, 2004) places the separation of Australia and New Zealand at around 80 Ma, and the separation of Australia and South America from Antarctica between 50 and 30 Ma (Cook and Crisp, 2005). Molecular modeling and the fossil record of Nothofagaceae suggests the family diverged from the other Fagales between 93–83.5 Ma, before the separation of Gondwana (late Jurassic–late Cretaceous; Cook and Crisp, 2005).

The *Nothofagus* crown group has an estimated node age, based on fossil calibration using *N. tasmania* (Hill, 2001), of 45 Ma. A long stem subtending the crown group represents the sole lineage of which all extant *Nothofagus* species are derived (Cook and Crisp, 2005). The stem base as well as the crown of sister group of *Nothofagus,* or all other living Fagales were inferred to have node ages of 84 Ma based on evidence from multiple fossils (Cook and Crisp, 2005). Larson-Johnson (2015) suggested a calibrated age for stem *Nothofagus* of 83.5–70.6 Ma, derived from the first appearance of fossil *Nothofagidites senectus* (Dettmann, 1994). Phylogenetic analysis incorporating the *Nothofagus suciaensis* is planned for a future study. If this new taxon is found to be in the crown group, which is possible based on the suite of characters it shares with extant *Nothofagus*, this would push the age of the crown group back to the late Cretaceous, extending the crown group age by 35 million years. *Nothofagus suciaensis*, dated to be early middle Campanian (~80 Ma), suggests a close land-based biogeographic relationship between

the North American landmass and Gondwana existed by the late Cretaceous. Subgenera *Lophozonia, Trisyngyne,* and *Fuscospora* have shown a distribution pattern moving eastward between Antarctica to Australia and New Zealand between the late Cretaceous (~77.3 Ma) and the Oligocene (23 Ma; Vento et al., 2022). Subgenus *Nothofagus* and *Fuscospora* have shown an westward distribution between Antarctica and South America during this time range as well (Vento et al., 2022). The addition of *N. suciaensis* to the extensive fossil record of *Nothofagus* combined with the hypothesized calibration ages of Cook and Crisp (2005) and Larson-Johnson (2015) supports the hypothesis that Gondwana served as a central hub of diversification for Nothofagaceae during the Cretaceous (Manos, 1997; Vento et al., 2022).

Widespread distribution of all four subgenera of *Nothofagus* before the break-up of the supercontinent is required for vicariance, or land-dispersed, hypotheses (Linder and Crisp, 1995; Cook and Crisp, 2005). However, conflicting cladistic-biogeographical analyses have suggests that the subgenera *Lophozonia* and *Fuscospora* do not follow the pattern expected by a vicariance hypothesis and thus the mode of dispersal and distribution among *Nothofagus* subgenera pre-Gondwana breakup remains in question (Linder and Crisp, 1995; Swenson et al., 2001b; Sanmartin and Ronquist, 2004; Cook and Crisp, 2005). An all-vicariance scenario has been rejected as the radiation of the crown group of *Nothofagus* was estimated to be too recent (Cook and Crisp, 2005). However, if *N. suciaensis* is found to be in the crown group, thus extending the age range for the group, a reevaluation of an all-vicariance scenario will be needed to fully understand biotic exchange at the time of the separation of Australia and New Zealand at around 80 Ma. Pollen fossils of all four extant subgenera of Nothofagaceae indicate the presence of the family at the eastern Gondwana break-up with the fossil record also suggesting multiple extinctions with loss of entire subgenera in Australia, New Zealand, South America, and Antarctica (Hill, 2001; Cook and Crisp, 2005).

The mode of dispersal of *Nothofagus* to explain observed biogeographic patterns remains in question. Divergence between Australasian and South American taxa in *Lophozonia* and *Fuscospora* as well as between *Nothofagus* and *Trisyngyne* are in conjunction with the rifting events of Australia, Antarctic, and South America (~50–30 Ma; Cook and Crisp, 2005). This divergence timing also suggests that *Nothofagus* was not vicariant across the Tasman Sea, as the divergence of *Lophonzonia* and *Fuscospora* is found to be more than 30 Ma after the opening of this sea, and thus non-vicariant modes of dispersal would have been used by *Nothofagus* (Cook and Crisp, 2005). Long distance dispersal events of *Nothofagus* taxa are also hypothesized to have occurred in the Cenozoic between Australia and New Zealand (Sanmartin and Ronquist, 2004). Other scenarios for dispersal among *Nothofagus* taxa include wind dispersal (Cook and Crisp, 2005). Molecular dating for the divergence of *Nothofagus* between Australian and New Zealand suggested west wind drift as a mode of dispersal that is in conjunction with the Antarctic Circumpolar Current after the separation of Australia and South America from Antarctica (~31 Ma; Cook and Crisp, 2005). Wind dispersal is common among modern *Nothofagus* species and thus is a plausible form of ancient dispersal modes for long-distance distribution (Bustamante and Castor, 1998). In contrast, previous experimental evidence suggests that the fruit of *Nothofagus* are unable to adequately cross seaways, however, authors have concluded that the long-distance dispersal across the Tasman Sea evident in the Cenozoic was achieved via wind-blown (Rodway, 1914; Preest, 1963; Hill and Jordan, 1993). This would restrict dispersal of *Nothofagus* to only terrestrial modes of distribution. Terrestrial dispersion has been explained by the assumption of land connections or close proximity of past land masses of South America, Antarctic Peninsula and Australasia at one point in time (Vento et al., 2022). Biographical land

bridges between North and South America were hypothesized by Vinola-Lopez et al. (2022), who suggested that during the Cretaceous, volcanic island-arcs most likely lead to a land bridge between North and South America. This bridge could have facilitated a direct biotic exchange after the drift of Laurasia and Gondwana.

This is not the first time a Gondwanan lineage has been found in ancient North America. Cunoniaceae (red alder or butterspoon trees) fruits, another group previously thought to be restricted to the southern hemisphere, were also collected from EV Henry Point of Sucia Island, Washington, USA (~82–80 Ma; Tang et al., 2022). Much like Nothofagaceae, Cunoniaceae are thought to have been widely distributed in the southern hemisphere before the breakup of Gondwana. The dramatic expansion of geographic range in Cunoniaceae was found to be consistent with the hypothesis of a North American-South American-Antarctic (NA-SA-A) biotic exchange (Tang et al., 2022) similar to the biotic exchange between North and South America described in Vinola-Lopez et al. (2022). Together, these fossil fruits provide evidence for a direct biotic exchange between Laurasia and Gondwana during the Cretaceous and after divergence of the Nothofagaceae.

Conclusion

The fossil *Nothofagus suciaensis* sp. nov. represents the earliest and only confirmed *Nothofagus* fossil discovered in the northern hemisphere. Dating of this *Nothofagus* fossil (~80 Ma) suggests a much earlier and broader distribution of Nothofagaceae than previously thought. The fossil record proves as an important tool in understanding the evolutionary history of Fagales. The addition of *N. suciaensis* to the record of *Nothofagus* broadens the view of Fagales dispersal and floral evolution in the Cretaceous. *Nothofagus suciaensis* demonstrates the importance of studying biodiversity within the fossil record and its ability to provide impactful data to investigate the evolutionary and biogeographic history of major groups.

Land Acknowledgement for San Juan Islands

The San Juan Islands have a Indigenous history reaching back almost 11,000 years. The Islands and coastal mainland areas have been home to members of six Central Coast Salish Tribes who spoke the Northern Straits language: Sooke, Saanich, Songhee, Lummi, Samish and Semiahmoo. Coastal Salish families were deeply impacted by diseases brought to the archipelago by Europeans during the late 1700's. Villages residing on the resource-rich shores were scattered and displaced due to continued colonization from both European and Spanish groups. The Lummi Nation, the third largest tribe of Washington State, now lives on the Northwest coast of Washington. The Lummi seek to restore traditional reef netting methods and sustain their way of life that has been passed down for thousands of years.

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Tables

Table 1: Comparison of features in extant Nothofagaceae and Fagaceae (Herendeen et al., 1995; Takahashi et al., 2008), fossil fruit KUPB-19240-Htop, and the fossils *Protofaceae allonensis* (Herendeen et al., 1995), *Antiquacupula sulcata* (Sims et al., 1998), *Soepadmoa* (Gandolfo et al., 2018), *Archaefageceae futabensis* (Takahashi et al., 2008), and unnamed Fagales flowers (Taylor et al., 2012).

	Tepal cycles	**Fruit in cross section**	**Trichomes in fruit locule**	**Ovules**	**Number of carpels**	**Pollen exine**
KUPB-19240-Htop	**1**	**Triangular**	**Absent**	**Unitegmic**	**3**	**?**
Nothofagaceae	**1**	**Lenticular or triangular**	**Absent**	**Unitegmic**	**2 or 3 (lateral); 3 (central)**	Granular
Fagaceae	2	**Triangular**	Present	Bitegmic	**3**	Columellate
Betulaceae	0	Rounded	?	**Unitegmic or bitegmic**	**2-3**	Scabrate to rugulate
Casuarinaceae	**1-2**	Rounded	?	Bitegmic	2	Rugulate
Juglandaceae	2	Rounded	?	**Unitegmic**	**3-4**	Tectate-granular; columellae
Myricaceae	0	Rounded	Present	**Unitegmic**	2	Rugulate
Ticodendraceae	0	Rounded	Present	**Unitegmic**	2	Granular
Protofagacea	2	**Triangular**	**Absent**	**Unitegmic**	**3**	?
Antiquacupula	2	**Triangular**	Present	?	**3**	?
Soepadmoa	2	**Triangular**	Present	?	1	?
Archaefagacea	**1**	**Triangular**	Present	?	1	?
Fagales flowers	**1**	**Triangular**	Present	Bitegmic	1	?

Table 2: Morphological character matrix of extinct and extant taxa of Fagales, modified from Hill and Jordan (1993), Herendeen et al. (1995), Manos et al. (2001), Rozefelds and Drinnan (2002), Takahashi et al. (2008), and Larson-Johnson (2015). Fossil taxa indicated with (†).

											Character Number										
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Nothofagus suciaensis†	0	2	0	?	?	1	1	?	?	?	?	?	?	?	2	0	1	0	1	1	2

Taxon																					
Alfaroa guanacastensis	0	?	1	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	?	?	?
Allocasuarina verticillata	?	?	2	?	?	0	?	?	?	?	?	?	?	?	1	?	1	1	?	?	?
Alnus incana	?	?	3	?	?	2	?	?	?	?	?	?	?	?	1	?	1	0	1	?	?
Antiquacupula sulcata†	?	6	0	0	?	2	0	2	?	?	?	0	?	?	2	1	1	?	?	?	?
Antiquocarya verruculosa†	?	?	2	?	?	1	?	?	?	?	?	?	?	?	0	?	1	?	?	?	?
Archaefagacea futabensis†	?	?	0	0	1	1	1	?	?	?	?	0	?	?	2	1	1	?	?	1	?
Asterocarpinus perplexans†	?	?	2	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Beardia vancouverensis†	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Betula pendula	?	?	3	?	?	2	?	?	?	?	?	?	?	?	1	?	1	0	1	?	?
Budvaricarpus serialis†	?	?	2	?	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Castanea pumlia	0	2	1	0	0	2	0	2	0	0	1	1	1	0	3	1	1	1	0	2	2
Calathiocarpus minimus†	?	?	2	?	?	1	?	?	?	?	?	?	?	?	0	?	1	?	?	?	?
Canacomyrica monticola	?	?	?	?	?	2	?	?	?	?	?	?	?	?	0	?	0	1	?	?	?
Carpinus betulus	?	?	2	?	?	1	?	?	?	?	?	?	?	?	1	?	1	0	0	?	?
Carya ovata	?	?	1	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	?	?	?
Caryanthus knoblochii†	?	?	2	?	?	0	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?
Cascadiacarpa spinosa†	?	?	1	?	?	?	?	?	1	4	?	?	?	?	1	0	?	?	0	?	?
Casholdia microptera†	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Castanea henryi	0	2	1	0	0	3	0	0	0	4	1	1	1	0	3	1	?	?	0	4	2
Castanea seguinii	?	?	1	?	?	0	?	?	1	4	?	?	?	?	1	1	1	1	0	?	?
Castanopsis carlesii	0	2	1	0	0	1	1	0	0	4	2	1	1	0	2	1	1	1	0	4	2
Castanopsis tibetana	?	?	1	?	?	0	?	?	1	4	?	?	?	?	1	1	1	1	0	?	?
Castanopsoidea columbiana†	?	?	?	?	?	?	?	?	?	3	?	?	?	?	?	?	?	?	0	?	?
Casuarina equisetifolia	?	?	2	?	?	1	?	?	?	?	?	?	?	?	1	?	1	1	?	?	?
Ceuthostoma terminale	?	?	2	?	?	2	?	?	?	?	?	?	?	?	1	?	1	1	?	?	?

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Chrysolepis sempervirens	?	?	0	?	?	0	?	?	0	4	?	?	?	?	1	1	1	1	0	?	?
Colombobalanus excelsa	0	?	0	?	?	0	?	?	0	3	?	?	?	?	1	1	1	1	0	?	?
Comptonia peregrina	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	?	0	0	?	?	?
Contracuparius huntsvillensis†	?	?	0	?	?	?	?	?	0	3	?	?	?	?	?	?	?	?	0	?	?
Corylus avellana	?	?	1	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	0	?	?
Cranea wyomingensis†	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Cruciptera simpsonii†	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Cyclocarya paliurus	1	?	1	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	1	?	?
Dahlgrenianthus suecicus†	?	?	0	?	?	1	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?
Endressianthus miraensis†	?	?	2	?	?	1	?	?	?	?	?	?	?	?	1	?	1	?	?	?	?
Engelhardia roxburghiana	?	?	?	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	1	?	?
Fagus orientalis	1	4	0	1	2	2	0	2	1	1	1	0	0	2	2	0	1	1	1	2	2
Fagus sylvatica	1	4	0	1	2	2	0	2	1	0	1	0	0	2	2	1	1	1	1	3	2
Fagales flowers†	0	0	0	0	1	1	1	2	?	?	?	?	?	?	?	2	1	1	1	?	?
Fagopsis longifolia†	?	?	1	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?
Fagus crenata	1	4	0	1	2	2	0	1	1	1	1	0	0	2	2	1	?	?	1	1	2
Fagus sylvatica	1	?	0	?	?	0	?	?	1	4	?	?	?	?	1	1	1	1	0	?	?
Ferrignocarpus bivalvis†	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?
Formanodendron doichangensis	0	?	0	?	?	0	?	?	0	3	?	?	?	?	1	1	1	1	0	?	?
Gymnostoma nobile	?	?	2	?	?	2	?	?	?	?	?	?	?	?	1	?	1	1	?	?	?
Hamamelis japonica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	?	?	?
Hooleya lata†	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Juglans mandshurica	1	?	1	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	?	?	?
Lithocarpus henryi	?	?	1	?	?	?	?	?	0	3	?	?	?	?	1	1	1	1	0	?	?
Manningia crassa†	?	?	2	?	?	1	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?

Morella cerifera	?	?	?	?	?	2	?	?	?	?	?	?	?	?	0	?	0	0	?	?	?
Myrica gale	?	?	?	?	?	2	?	?	?	?	?	?	?	?	0	?	0	0	?	?	?
Nothofagus alpina	0	0	0	0	1	1	1	2	0	0	1	0	0	0	2	0	1	0	1	1	2
Nothofagus betuloides	1	3	0	0	0	1	1	2	1	0	1	0	0	1	2	0	1	0	1	0	1
Nothofagus bulbosa†	?	0	?	?	?	?	?	0	0	?	?	0	0	?	?	?	?	?	?	?	?
Nothofagus cliffortioides	0	0	0	1	1	1	1	0	0	3	1	0	0	1	2	0	1	0	1	1	2
Nothofagus cooksoni†	?	3	?	?	?	?	?	?	0	0	?	1	1	2	?	?	?	?	?	?	?
Nothofagus cunninghamii	0	0	?	?	1	?	?	?	?	1	2	0	?	?	?	?	?	?	?	?	?
Nothofagus cunninghamii	1	?	0	?	1	?	?	?	1	3	?	0	2	?	2	0	1	0	1	?	?
Nothofagus dombeyi	0	0	0	0	1	0	?	2	0	0	0	0	1	1	2	0	1	0	1	1	1
Nothofagus fusca	0	0	0	1	1	1	1	2	0	0	2	0	0	1	2	0	1	0	1	1	2
Nothofagus glandularis†	?	0	?	?	?	?	?	2	0	?	?	0	0	?	?	?	?	?	?	?	?
Nothofagus glauca	0	0	?	?	1	?	?	?	?	2	1	0	?	?	?	?	?	?	?	?	?
Nothofagus grandis	0	2	2	0	0	1	1	1	0	2	1	1	1	0	1	0	1	0	1	1	2
Nothofagus menszesii	0	0	?	?	1	?	?	?	?	1	2	0	?	?	?	?	?	?	?	?	?
Nothofagus moorei	0	0	?	?	1	?	?	?	?	1	3	0	?	?	?	?	?	?	?	?	?
Nothofagus nervosa	0	0	?	?	1	?	?	?	?	1	3	0	?	?	?	?	?	?	?	?	?
Nothofagus obliqua	0	0	0	0	1	1	1	1	0	0	1	0	0	0	2	0	1	0	1	1	2
Nothofagus peduncularis†	?	?	?	?	?	?	?	2	0	0	?	1	?	?	?	?	?	?	?	?	?
Nothofagus pullei	0	2	2	0	0	1	1	0	0	2	0	1	1	0	1	0	1	0	1	1	1
Nothofagus pumilio	0	2	0	0	0	1	1	0	0	?	?	1	0	0	2	0	0	0	1	2	1
Nothofagus rubra	1	2	2	0	0	1	1	0	1	3	1	1	1	0	1	0	1	0	1	1	2
Nothofagus solandri	0	2	1	0	0	1	1	0	1	0	1	1	1	1	1	0	2	0	0	1	1
Nothofagus starkenborghiorum	1	4	2	0	0	1	1	0	1	3	1	1	1	0	?	?	?	?	1	2	2
Normanthus miraensis†	?	?	2	?	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?

Nothofagus antarctica	0	0	1	0	1	1	1	2	0	0	1	0	0	0	0	0	0	0	1	3	2
Nothofagus cunninghamii	1	?	0	?	?	1	?	?	1	3	?	?	?	?	1	0	1	0	1	?	?
Notholithocarpus densiflorus	?	?	1	?	?	?	?	?	0	3	?	?	?	?	1	1	1	1	0	?	?
Oreomunnea mexicana	0	?	1	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	1	?	?
Ostrya carpinifolia	?	?	2	?	?	1	?	?	?	?	?	?	?	?	1	?	1	0	0	?	?
Ostryopsis davidana	?	?	2	?	?	1	?	?	?	?	?	?	?	?	1	?	1	0	0	?	?
Palaeocarpinus dakotensis†	?	?	2	?	?	1	?	?	?	?	?	?	?	?	1	?	1	?	0	?	?
Palaeocarya clarnensis†	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Palaeooreomunnea stoneana†	?	?	?	?	?	1	?	?	?	?	?	?	?	?	0	?	?	?	1	?	?
Palaeoplatycarya wingii†	0	?	?	?	?	1	?	?	?	?	?	?	?	?	0	?	?	?	1	?	?
Paraengelhardtia eocenica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Platycarya strobilacea	0	?	3	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	1	?	?
Polyptera manningii†	0	?	?	?	?	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Protofagacea allonensis†	?	0	0	?	3	2	0	?	0	?	?	0	?	?	?	1	?	?	1	1	?
Pseudofagus idahoensis†	?	?	0	?	?	?	?	?	1	3	?	?	?	?	?	?	?	?	0	?	?
Pterocarya stenoptera	1	?	1	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	1	?	?
Quercus rubra	?	?	1	?	?	?	?	?	0	3	?	?	?	?	1	1	1	1	0	?	?
Rhoiptelea chiliantha	0	?	3	?	?	1	?	?	?	?	?	?	?	?	0	?	1	1	?	?	?
Soepadmoa†	?	0	0	0	1	2	0	?	0	0	?	0	?	?	?	1	?	?	?	?	?
Ticodendron incognitum	1	?	2	?	?	1	?	?	?	?	?	?	?	?	0	?	1	0	?	?	?
Trigonobalanoidea americana†	1	?	0	?	?	?	?	?	0	4	?	?	?	?	?	?	?	?	0	?	?
Trigonobalanus verticillata	0	?	0	?	?	?	?	?	0	3	?	?	?	?	1	1	1	1	0	?	?

Figures

Figure 1: *Nothofagus suciaensis* sp. nov. fruit from the Cretaceous of Washington. KUPB-19240-Htop. A) Cross section of fruit toward the base of the preserved portion. Peel #1. Scale bar 50 µm. B) Junction of wing and fruit body showing parenchymatous wing forming from the outer and middle layer.. Peel #17. Scale bar 200 µm. C) Longitudinal section of pericarp showing distinct layers (outer, middle, inner). Idioblast on the outer layer indicated by blue arrow. Peel #1. Scale bar 50 µm. F) glabrous locules separated by thin septa. Septa indicated by blue arrows. Peel #10. Scale bar 250 µm. D) Inner layer with small, thick-walled sclereids. Peel #92 µm. Scale bar 200 µm. E) Inner layer shows more parenchyma above apex. Inner layer layer indicated by blue arrow. Peel # 51. Scale bar 250 µm. G) View of six ovules (two ovules per locule) with axile placentation attached to an apical placental column. Peel #92. Scale bar 200 µm. H) Appearance of a single whorl of three persistent tepals at the apex of the fruit. Peel #113. Scale bar 250 µm. I) Style base. Tepals indicated by blue arrows. Peel #131. Scale bar 250 µm.
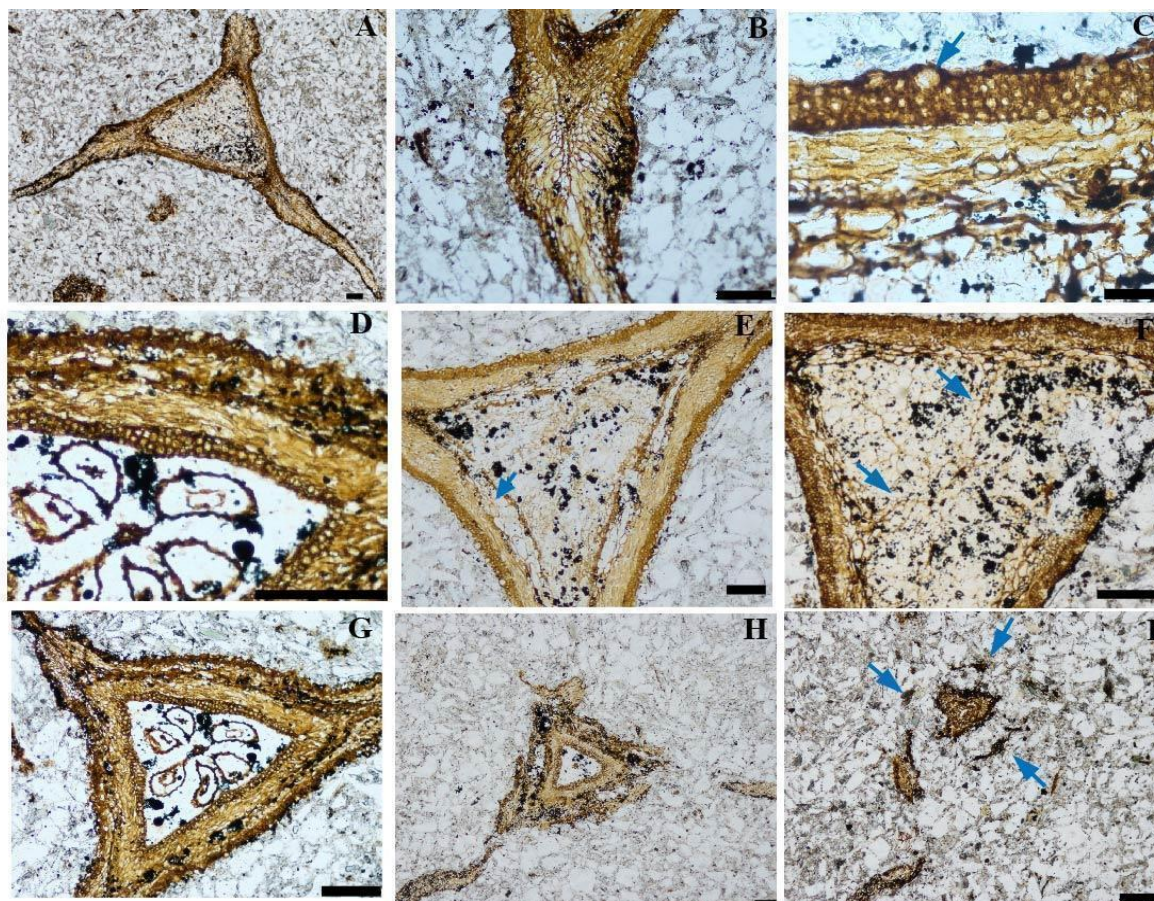
Figure 2: 3D reconstruction of KUPB-19240 Htop. A) Full view of the preserved portion of the specimen. Scale bar 1 mm. B) Wing material of fruit viewed from apex. Arrows indicating tepal placement. Scale bar. 1 mm C) Side view of fruit. Arrow indicating tepal placement. Scale bar 1 mm. D) Base view of ovule placement in locule cavities. Scale bar 1 mm. E) View from apex of six ovules with arrows indicating each ovule; horizontal lines are artifacts from deriving model from peels. Scale bar 1 mm. F) Side view ovule placement in locules. Scale bar 1 mm.
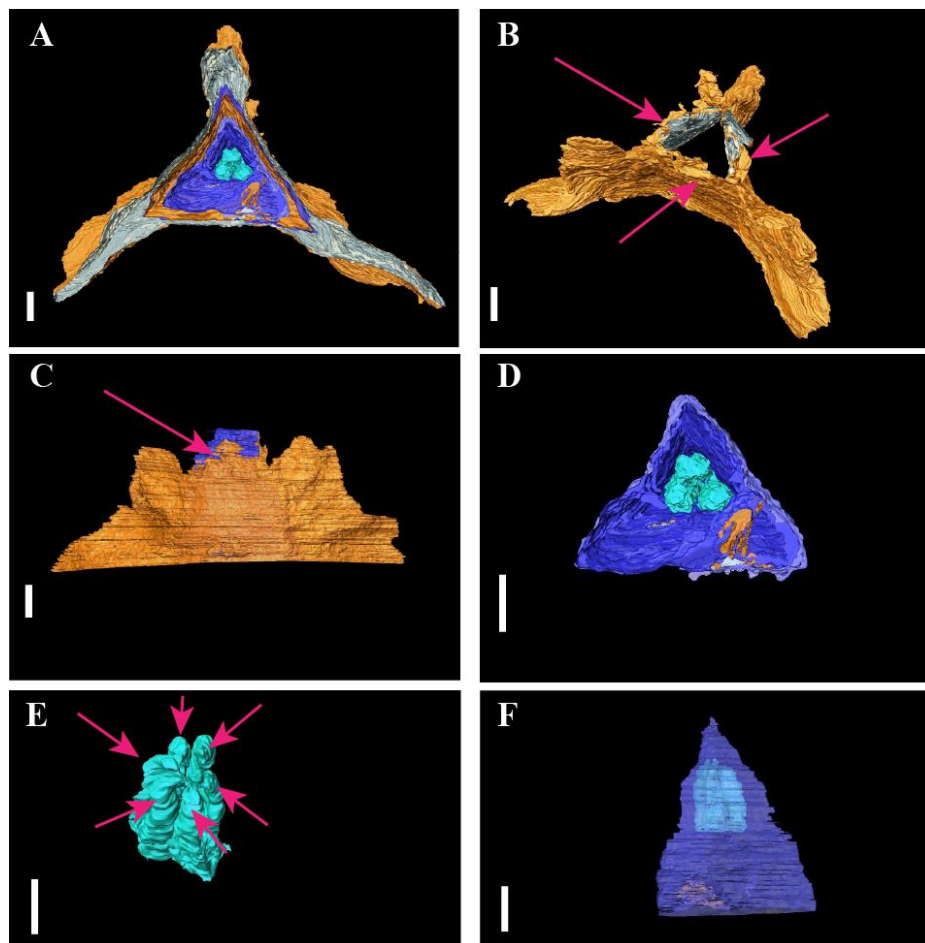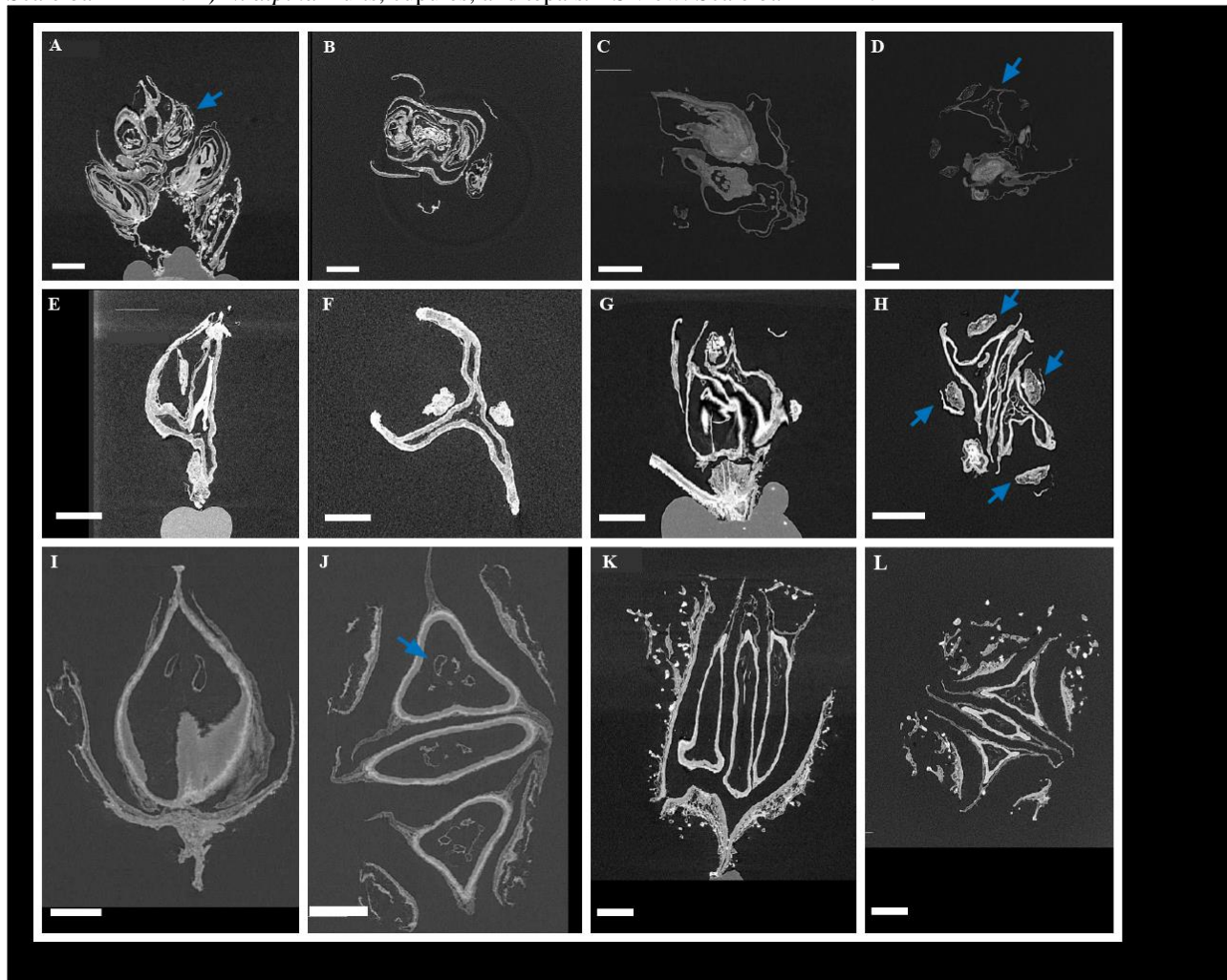
Appendix
Appendix 1: Table showing samples collected from the United States National Herbarium (US).

Family	Species	Collector	Collector Number	Location	Barcode
Nothofagaceae	*N. antarctica*	Burkart, A.E.	26469	Argentina	2595226
Nothofagaceae	*N. betuloides*	Goodall, N.	990	Argentina	2617408
Nothofagaceae	*N. pumilio*	Laegaard, S.	13111	Argentina	3736220
Nothofagaceae	*N. dombeyi*	Pederson, T.M.	212	Argentina	2122302
Nothofagaceae	*N. obliqua*	West, J.	4842	Chile	1692271
Nothofagaceae	*N. alpina*	Bernath, E.	607	Chile	3204349
Nothofagaceae	*N. pullei*	Pullen, R.	5400	Papua New Guinea	3454112
Nothofagaceae	*N. rubra*	Womersley, J.S.	LAE55324	Papua New Guinea	2929615
Nothofagaceae	*N. grandis*	Brass, L.J.	23356	Papua New Guinea	2374250
Nothofagaceae	*N. starkenborghiorum*	Clunie, N.M.u.	LAE63022	Papua New Guinea	2906392
Nothofagaceae	*N. fusca*	Walker. E.H.	4988	New Zealand	1994244
Nothofagaceae	*N. solandri*				
Nothofagaceae	*N. cliffortioides*	Matthews, H.J.	s.n.	New Zealand	6150000
Fagaceae	*F. crenata*	Suzuki, S.	SI-24	Japan	2214911
Fagaceae	*F. sylvatica*	Chater, A.O.	s.n.	Spain	2877109
Fagaceae	*F. orientalis*	Solomon, J.C. (MO)	20783	Georgia	3732759
Fagaceae	*C. henryi*	Wan, P.P. and K.S. Chow	79023	China	3400688
Fagaceae	*C. pumlio*	Cleve, Astrid Maria	s.n.	United States	1565295
Fagaceae	*C. carlesii*	Kanehira, R.	2935	Taiwan	1657007

Appendix 2: CT imaging of Nothofagaceae and Fagaceae fruits collected from United States National Herbarium (US). LS=Longitudinal section. TS=Transverse section.

Appendix 2.1: A) *Nothofagus antarctica* flowers and cupule appendages. Glandular cupule lamella indicated by blue arrow. LS view. Scale bar= 1 mm. B) *N. antarctica* fruits, cupules, and tepals. TS view. Scale bar= 1 mm. C) *N. betuloides* flowers and cupule appendages. LS view. Scale bar= 1 mm. D) *N. betuloides* fruist and cupules. Triangular fruit indicated by blue arrow. TS view. Scale bar= 1 mm. E) *N. pumilio* flower. LS view. Scale bar= 1 mm. F) *N. pumilio*. TS view. Scale bar= 1 mm. G) *N. dombeyi* flowers. LS view. Scale bar= 1 mm. H) *N. dombeyi* fruits and cupules. 4 cupule valves indicated by blue arrows. TS view. Scale bar= 1 mm. I) *N. obliqua* flower and cupule appendages. LS view. Scale bar= 1 mm. J) *N. obliqua* fruits, cupules, and tepals. TS view. Unitegmic ovule of triangular fruit indicated by blue arrow. Scale bar= 1 mm. K) *N. alpina* flowers and cupule appendages. LS view. Scale bar= 1 mm. L) *N. alpina* fruits, cupules, and tepals. TS view. Scale bar= 1 mm.

Appendix 2.2: A) *Nothofagus pullei* flower and cupule appendages. LS view. Scale bar= 1 mm. B) *N. pullei* fruit and cupules. Lenticular fruit with two locules and one ovary per locule indicated by blue arrow. TS view. Scale bar= 1 mm. C) *N. rubra* flower and cupule appendages. Slender style indicated by blue arrow. LS view. Scale bar= 1 mm. D) *N. rubra* fruit and cupules. TS view. Scale bar= 1 mm. E) *N. grandis* flowers and cupule appendages. One persistent cycle of tepals attached to peduncle indicated by blue arrow. LS view. Scale bar= 1 mm. F) *N. grandis* fruit and cupules. TS view. Scale bar= 1 mm. G) *N. starkenborghiorum* flower and cupule appendages. LS view. Scale bar= 1 mm. H) *N. starkenborghiorum* fruit and cupules. TS view. Scale bar= 1 mm. I) *N. fusca* flowers and cupule appendages. LS view. Scale bar= 1 mm. J) *N. fusca* fruit, cupules, and tepal cycles. TS view. Scale bar= 1 mm. K) *N. solandri* flower. LS view. Scale bar= 1 mm. L) *N. solandri* fruits. TS view. Scale bar= 1 mm.

Appendix 2.3: A) *Nothofagus cliffortioides* flowers. Cupule appendages indicated by blue arrows. LS view. Scale bar= 1 mm. B) *N. cliffortioides* fruits and cupules. TS view. Scale bar= 1 mm. C) *Fagus crenata* flowers. LS view. Scale bar= 1 mm. D) *F. crenata* fruits and cupules. TS view. Scale bar= 1 mm. E) *F. sylvatica* flower. LS view. Scale bar= 1 mm. F) *F. sylvatica* fruits and cupules. TS view. Scale bar= 1 mm. G) *F. orientalis* flowers. LS view. Scale bar= 1 mm. H) *F. orientalis* fruits and cupules. TS view. Scale bar= 1 mm. I) *Castanea henryi* flower. LS view. Scale bar= 1 mm. J) *C. henryi* fruit, cupule, and tepals. TS view. Scale bar= 1 mm. K) *C. pumlia* flower. LS view. Scale bar= 1 mm. L) *C. pumlia* fruit, cupule, and tepals. TS view. Scale bar= 1 mm.
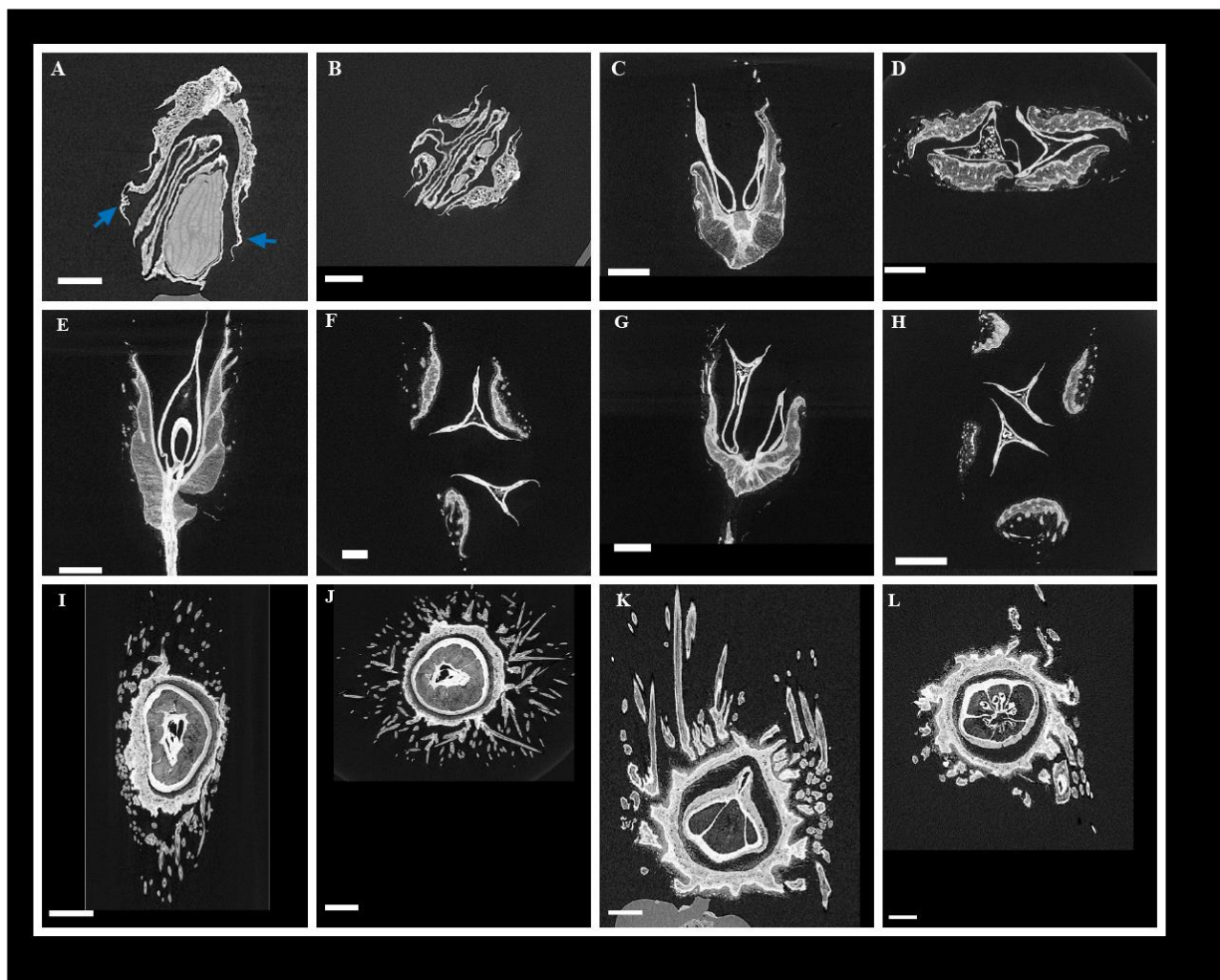
Appendix 2.4: A) *Castanopsis carlesii*. One rounded fruit. LS view. Scale bar= 1 mm. B) *C. carlesii*. Bilocular, rounded fruit. TS view. Scale bar= 1 mm.