Synchrotron computer tomographic (CT) scans complement traditional techniques in understanding the internal anatomy of permineralised *Fontainocarpa* (Crotonoideae, Euphorbiaceae) fruits from the Oligo-Miocene of eastern Australia

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Received xx: xx: 2016

Accepted xx.xx.2017

Available online xx.xx.2017

Abstract

The internal morphology and anatomy of silicified fruits of *Fontainocarpa* were studied using traditional thin sectioning techniques, SEM and synchrotron computed tomographic (CT) imaging and animations, to enable comparative analyses with extant, indehiscent-fruited genera in the Euphorbiaceae including *Fontainea*, *Aleurites* and *Hylandia* from Australia, and other non-Australian crotonoid genera. Thin sections and sectioning show that the fruits of *Fontainocarpa* are indehiscent, multicarpellate and usually 3- to 5-loculate, with axial placentation, a single ovule per carpel and the ovules

are anatropous and have antitropous curvature. A ventral vascular trace that supplies each ovule is embedded in the bitegmic seed coat. The internal anatomy is therefore consistent with the Euphorbiaceae. Additional characters, including indehiscent fruits, distinctive vascular channels (foramina) that penetrate through the fruit wall into the locule, and thin membranous seed coats are restricted to very few genera in the Euphorbiaceae, but occur together in extant *Fontainea*. The seed coat in extant *Fontainea* and fossil *Fontainocarpa* seeds is membranous, and appears to lack the palisadal exotegmen of most genera in the Euphorbiaceae. *Fontainocarpa* fruits were compared with those of extant *Fontainea* and the fossil has a combination of features unlike those of extant taxa. It shares with *Fontainea picrosperma* in having endocarps with convex intersutural surfaces lacking ornamentation and a similar number of locules and with *F. venosa* in having conspicuous foramina. This study therefore supports a close relationship between *Fontainea* and *Fontainocarpa* and is further evidence of the Crotonoideae in the fossil record in Australia, and is one of the few records of this subfamily worldwide. This study is one of the few, to date, using synchrotron CT imaging to reveal the internal morphology of silicified fruits and to utilize animations to examine the structure of these fruits.

Key words: *Fontainocarpa*; *Fontainea*; Euphorbiaceae; indehiscent fruits; Cenozoic; Australia

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1. Introduction

Seeds and fruits from a silicified flora from near Capella, Central Queensland was shown to consist of a diverse assemblage of rainforest taxa (Rozefelds, 1990). One of the taxa described as a new genus of Euphorbiaceae, *Fontainocarpa*, was compared to the extant genus *Fontainea* which is one of the few genera in this family from Australia with indehiscent fruits. The original, although somewhat preliminary study, focused on external fruit structure and overall appearance of the fruits highlighting characters, such as fruit shape, presence of foramina in the indehiscent fruit wall, and variable number of locules.

Since the original study was undertaken molecular-based systematics (Tokuoka, 2007; Wurdack et al., 2004, 2005) have provided greater clarity into relationships within the Euphorbiaceae. In addition other botanical studies particularly those on pollen (Erdtman, 1952; Punt, 1962; Köhler, 1965; Nowicke, 1994; Levin and Simpson, 1994; Simpson and Levin, 1994; Nowicke et al., 1998, 1999; Takahashi et al. 2000, Nowicke and Takahashi, 2002; Matamoro-Vidal et al., 2012) have contributed to a clearer understanding of relationships in the family (Webster, 2014) and also into others, including the Picrodendraceae, Putranjivaceae and Phyllanthaceae previously included in the Euphorbiaceae, but now recognized as distinct (Angiosperm Phylogeny Group IV, 2016).

There is also a scattered literature describing and illustrating ovule development, and fruit and seed morphology in the Euphorbiaceae (Wichmann, 1880; Gram, 1896; Mandl, 1926; Netoliztzy, 1926; Landes, 1946; Singh, 1954, 1968, 1970; Singh and Chopra, 1970; Wunderlich, 1967; Corner, 1976; Tokuoka and Tobe, 2003). More comprehensive and comparative studies on seed morphology have been completed on the Crotonoideae (Tokuoka and Tobe, 1998; *Jatropha*, Dehgan and Webster, 1979),

Euphorbioideae (Tokuoka and Tobe, 2002), and Picrodendraceae and Phyllanthaceae (Stuppy, 1996).

The fossil record of the Euphorbiaceae worldwide is limited and fossil records, particularly of fruits, e.g. Vaudois-Miéja (1986), were often in the past referred to the family in a general sense, i.e. including the Picrodendraceae and Phyllanthaceae, so opportunities exist to reassess the affinities of these specimens. The discovery of new fossils, such as the acalyphoid leaf, pollen and fruit from New Zealand (Lee et al., 2010; Nucete et al., 2012) has provided significant new insights into the history of some subfamilies. The discovery of an *Aleurites* seed from deposits in south eastern Queensland and an overview of the fossil pollen records assigned to the Euphorbiaceae, including Picrodendraceae and Phyllanthaceae, in Australia and New Zealand was recently completed by Rozefelds et al. (2017) who recognized that due to the paucity of records from Australia it was timely to re-examine in detail the affinities of the putative indehiscent-fruited, euphorbiaceous genus, *Fontainocarpa*.

Herein, the internal anatomy of *Fontainocarpa* fruits is described using thin sectioning, SEM and synchrotron imaging. These techniques collectively allow us to compare these fruits with extant *Fontainea*, *Hylandia* and *Aleurites* and other indehiscent fruited members of the Crotonoideae. The literature on fruit morphology in the crotonoids, albeit incomplete, was also assessed to interpret the variation in indehiscent fruits within the subfamily. The comparative study on extant fruits of *Fontainea* and *Hylandia* therefore provides new morphological data on their fruits and seeds, and also provides insights into the evolution of fruits in the Crotonoideae.

2. Geology and Preservation

The plant remains from near Capella, in central Queensland, are derived from silcrete blocks associated with the Paleogene basalts (Rozefelds, 1990; Cook and Rozefelds, 2015) that have been isotopically dated at 30-32 my B.P. (Sutherland et al., 1977). The plant remains, which includes wood, roots, fruits and leaves, have been replaced by cryptocrystalline quartz that has preserved their three-dimensional shape and internal anatomy, commonly in fine detail. The mass of different sized plant organs was originally interpreted as being accumulated under high energy conditions but the taphonomic factors operating at the site remains unclear (Rozefelds, 1990). The cellular structure of the fruits revealed in this paper, the fine roots and ectomycorrhiza on roots, uncoiling fern fronds (Rozefelds, 1990), and the rare preservation of the exocarp of some fleshy fruits (Rozefelds and Christophel, 2002) suggests that burial and preservation was rapid. The presence of growing roots indicates that the deposit was, in-part, a palaeosol with a plant litter horizon and decaying wood, and arthropod frass provides evidence of termites and other detritivores.

The associated flora was documented by Rozefelds (1990, 1991, 1992), Rozefelds and Christophel (1996, 2002), Dettmann and Clifford (2000, 2002) and Rozefelds et al. (2014) and has been interpreted as a complex rainforest community with emergent conifers and woody lianas of the Menispermaceae and Vitaceae (Cook and Rozefelds, 2015, Rozefelds and Pace, in prep.).

3. Methods

Complementary approaches were undertaken to understand and interpret the internal morphology of modern and silicified fossil fruits. The fossil specimens are from the Queensland Museum (QM) collection and were sectioned using standard petrological techniques. Modern fruits were sawn in half and polished using a range of emery

papers. The specimens, both herbarium and fossil, were photographed with a Canon DSLR camera, Zerene Stacker software (<http://www.zerenesystems.com/>) with a hydraulic hoist using 'portable imaging' software by Visionary Digital Photographic System. They were also imaged with a Nikon camera with a 105 mm macro lens, or with a Canon 100EOS 5D. The polished sections were photographed immersed in 70% alcohol.

Thin sections were prepared petrographically and were photographed with a Nikon Eclipse 80i microscope. Sections of the seed coat were examined, without coating, using a Zeiss SEM EOMA15 at the Smithsonian Museum of Natural History.

Synchrotron (CT) scans were produced at the Imaging and Medical Beamline (IMBL) at the Australian Synchrotron, in Melbourne, Australia. The smaller silicified specimens and extant fruits were wrapped in tissue and placed in a plastic tube for scanning with synchrotron radiation (high energy-rays). The larger specimens were placed directly on the platform. The experiment was conducted in enclosure 3B with the X-ray photon energy tuned to 40 keV. CT data acquisition for the samples consisted of 1800 projections over an arc of 180 degrees.

The images were recorded using the IMBL's Ruby detector (12 μm gallium (Ga)) scintillator that converts the X-rays into visual light, which are reflected upward by a silicon mirror and photographed by a *pco.edge sCMOS* camera equipped with a Nikon lens. The lens, scintillator and camera-to-detector distance were optimized for each sample. Depending on these parameters, the pixel size ranges between 6 μm and 40 μm which, if multiplied by the number of pixels in the camera (2560 wide x 2480 high), gives a view area range of approximately 15 mm wide x 13 mm high, to 100 mm wide x

90 mm high. However, at large pixel sizes, the maximum height of the image is limited by the beam height, as noted above.

The experimental setup optimized for the samples used the maximum pixel size (6 μm) and a measured resolution of 13.7 μm . Under these conditions the exposures were 100 ms per projection, and accumulated time taken to scan a single sample was approximately 20 minutes. The scans included 100 images of each background (no sample in the beam) and dark-field (beam is off) contrasts for (the further) processing. A sample-to-detector distance of 20 cm was used to ensure maximum propagation-based phase contrast, which has a higher sensitivity to the boundaries of different materials in specimens.

Post-processing of the scan data involves several steps, clean background and dark-field images were formed as the median of all 100 repeats, which were then applied to each of the 1800 sample images (sample – dark-field / background – dark-field). Light noise was suppressed and the resulting images were vertically stitched to form a full-sized sample. The stack of horizontal cross-sections were converted using a CT reconstruction algorithm, and this reconstruction included phase retrieval and ring artefact suppression filters which allowed 3D rendering and visualizations to be performed. The analysis used the MASSIVE (Multi-model Australian Sciences Imaging and Visualisation Environment) super-computer cluster based in Melbourne. The software used in the pipeline included CSIRO's XT for initial data processing, and the open source program DRISHTI for 3D rendering (Limaye, 2012).

While the synchrotron imaging allowed us to visualise the internal and external morphology of both extant and fossil material, we were also reliant upon standard sectioning techniques and the SEM to study the cellular structure of the seed coat.

Data for modern plant records is from the *Atlas of Living Australia* (ala.org.au), and the abbreviations, BRI and QRS, refer to herbarium collections held in the Queensland Herbarium (Brisbane) and Australian Tropical Herbarium (Cairns) respectively. Authorities to extant plant taxa are available at the International Plant Names index website: <http://www.ipni.org/>. Information on the ecology and distribution of modern *Fontainea*, from both the literature and records in the *Atlas of Living Australia*, <http://www.ala.org.au/>, are used to interpret the habitat in which the plant grew. Seed coat terminology and seed microstructure follows that of Schmid (1986) and Corner (1976) respectively. Description of mature fruit morphology of *Fontainea* is based largely upon the fruits of *F. venosa*, *F. picrosperma* and *F. pancheri*, with data on seed morphology from Tokuoka and Tobe (1998). Fruits of extant *Hylandia* are also described and illustrated herein.

4. Systematics

Since the fossil fruits are indehiscent, comparisons were made with indehiscent crotonoid genera in the Euphorbiaceae from the Australian Region (Webster, 2014), i.e., *Fontainea*, *Hylandia* and *Aleurites*. The focus was on the internal morphology of the poorly known genera *Hylandia* and *Fontainea*, while *Aleurites* is comparatively well known (Rozefelds et al., 2017). These studies were complimented by literature-based reviews of taxa in the Crotonoideae and Acalyphoideae with indehiscent-fruits.

Family Euphorbiaceae Jussieu

Crotonoideae Beilschmied

Fontainea Heckel

A genus of at least 10 species occurring in eastern Australia, New Guinea, New Caledonia, and Vanuatu (Heckel, 1870; Jessup and Guymmer, 1985; Forster, 1997; Forster and van Welzen, 1999) (Fig. 1).

Fruits of extant *Fontainea* (Plate I, II, IV)

Fruit a drupe, ovoid to broadly ovoid, subcircular in transverse section (Plate II, 1). Axis woody with vasculature branches to each locule. Ovary, 3- to 5-, rarely 6-loculate, oriented dorsiventrally. Exocarp consisting of a layer of parenchyma cells, variable in colour, yellow brown in *F. pancheri*, and pink red to red in *F. picrosperma*, *F. rostrata* and *F. australis*. Mesocarp composed of sclerenchyma, fibers and parenchyma forming a fleshy outer layer surrounding the fruit stone (endocarp) (Plate I, 1; II, 1, 2). In mature fruits (Plate I, II, IV) the endocarp consists of sclereids that are arranged into two zones, an outer layer of somewhat radially oriented cells (1–1.5 mm thick) and an inner zone of tangentially oriented cells, 1–2 mm thick, surrounding the placental region of the fruit (Plate II, 1-4). The endocarps are ovoid to broadly ovoid, the intersutural surfaces are concave to flat to convex, the outer surface of which in different species are smooth to rugose, with scattered or a single foramen in the form of a narrow longitudinal slit that marks the original position of the micropyle (Plate I, II, IV; Table 1). Carpel with one pendulous, anatropous ovule and ovule curvature is antitropous *sensu* Bachelier and Endress, 2009 (= epitropous). Seeds globose, in fruits with a single seed; but fruit shape is determined by the number of seeds that develop. A nucellar beak occurs in both *F. picrosperma* and *F. venosa*, a raphal ridge extends down the ventral side of seed, no

caruncle is present but a zone of tissue, ripped from the placental wall, is present around the hilum (Plate I, 3, 4). Testa membranous, with slightly thickened exotestal cells overlying exotegmen that consists of radially orientated parenchyma cells in *F. venosa* and *F. picrosperma* (Plate I 1, 7).

Remarks

The fruits, and particularly the woody endocarps (fruit stones) have a consistent internal morphology and structural plan but they exhibit considerable variation in their external appearance, which has been used to define and describe the extant species, differences are noted below (see also Table 1). Jessup and Guymer (1985) concluded that there was only a single seed per fruit at maturity. Heckel (1870), however, noted that in fertile fruits of *F. pancheri* there was usually a single seed, although fruits with two or three seeds also occurred. Similarly in *F. venosa* single seeded fruits are common, but fruits with two seeds also occur (Plates I, 3; IV, 1, 2). Seed shape is therefore determined by the number of seeds that develop within the fruit. The mature seed or seeds occupy the entire locular space and the developing seeds compress the adjacent locules (Plate I, 3).

Hylandia Airy Shaw (Plate III)

A monotypic genus restricted to north eastern Queensland (Airy Shaw, 1976)

Fruits of extant *Hylandia dockrillii* Airy Shaw

Dried fruit, indehiscent, bilobed, in transverse view, c. 3 cm wide, c. 2 cm long, with 2 carpels (Plate III, 1-4; Table 1). Fruit wall (dried and shriveled in herbarium voucher) 2.0 mm thick consisting of exocarp of small isodiametric cells, a mesocarp of loosely

arranged non-sclerified fibres with small vascular bundles (vb) at its inner edge, and a thin endocarp encloses the 2 locules (Plate III, 5). A dorsiventrally depressed zone exists between the two seeds, and conspicuous septicial sutures occur laterally (Plate III, 2). Indumentum of short trichomes occur over the fruit surface and larger trichomes, 1-2 mm long, occur along depressions in the fruit surface. Seeds semi-globose, ca. 14.2 mm long, 13.3 mm wide. Seed coat 1.6 mm thick, consisting of radially-arranged, thickened, columnar cells, and round scars shows position of seeds, which had aborted (Plate III, 3, 4, 6, 7). Ovules pendulous, anatropous and ovule curvature is antitropous with ventral vascular traces (Plate III, 3, 4). No caruncle present in the mature seed.

Remarks

In the Euphorbiaceae, the vascular trace occurs on the inner facing (ventral) side of the seed within the testa of the seed coat. These ventral carpel vascular traces in both *Hylandia* and *Fontainea* therefore occupy the same position as illustrated for *Aleurites* (Corner, 1976; p. 179, bottom left hand drawing).

The seeds are attached to the inside of the locular wall, near the top (distal end) of the fruit, and the vascular trace attaches to the chalaza forming a longitudinal ridge (raphe) along the ventral side of the seed (Plate I, 4). The seeds in *Fontainea picrosperma* and *F. venosa* both show a raphal scar below where the hilum attaches (Plate I, 4) and in this respect they resemble the seeds of many other genera in the family, and also those of the Picrodendraceae and Phyllanthaceae (Stuppy, 1996; Webster, 2014). In both *Aleurites* and *Hylandia* the raphal scar is not evident and there is no evidence of a caruncle in any of the genera.

The seed coat consists of radially-arranged, thickened, columnar cells in both *Aleurites* (Rozefelds et al. 2017, pl. 1, fig. 2) and *Hylandia*. These cells have been shown to be derived from the outer tegmen, which is a common feature in the fruits of many genera in the Euphorbiaceae (Wunderlich, 1968; Tokuoka and Tobe, 1998). The seed coat in these genera therefore forms a thickened resistant layer (Plate III, 3-5), which differs from that in *Fontainea* where the cells although radially oriented, are not enlarged or thickened (Plate II, 7), and the seed coat has been described as membranous (Heckel, 1870; Jessup and Guymer, 1985). While Tokuoka and Tobe (1998) did not illustrate the seed coat of *Fontainea pancheri* they did describe it as exotegmic, and therefore consistent with that in the other crotonoids. Our studies confirm Jessup and Guymer's (1985) observation that the seed coat is thin, at least in the Australian species that we examined (Table 1), and that there is no evidence of a layer of thickened sclereids. So the seed coat consists of radially arranged and slightly sclerified cells that could be derived from either the testa or the tegmen (Plate II, 5, 7). Thus, in *Fontainea* there is a transfer of function with the endocarp, not the seed coat, protecting the developing embryo. Webster (2014) noted that the seed coat in genera in the Euphorbiaceae with indehiscent fruits could be thin or rudimentary. As the radially-arranged exotegmic seed is likely to be plesiomorphic condition in the family, indehiscent-fruited species with thin (membranous) seed coats have evolved independently. While the thick-walled exotegmic structure of the seeds of *Hylandia* and *Aleurites* is plesiomorphic; they share a fleshy outer fruit layer and semi-globose seeds, features which are not common in the family.

Redescription of *Fontainocarpa* Rozefelds, emended Rozefelds, Dettmann et Clifford

Generic Diagnosis: Fossil fruit stones, obovoid, 4- to 5- locular, rarely more with longitudinal sutures corresponding to number of ovules, fruit stone consists of outer zone of dense, highly sclerotic, radially-arranged tissue and an inner zone of less dense, tangentially-arranged, sclerotic tissue; placentation axile, with seeds attached apically, seeds variable in shape (due to number developing), seed testa membranous in mature seeds, consisting of slightly thickened exotestal cells, lacking enlarged, thickened cells in the exotegmen, fruits indehiscent, although probably tardily dehiscent over time, splitting along the sutures.

Redescription of *Fontainocarpa foraminata* Rozefelds, emended Rozefelds, Dettmann et Clifford (Plate I, 6-10; IV, 3-6; V, 1-12, VI, 1-7)

Material examined: QMF58787-QMF58790, QMF16743

Repository; Geoscience Collections, Queensland Museum

Species diagnosis (emended). Endocarp (fruit stones) obovoid, equatorial diameter 12–23 mm, polar diameter, 21–39 mm, apex rounded, not beaked, base rounded, the intersutural faces convex and the sutural margins are extended into prominent longitudinal ridges in the fruits. Fruit wall consists of two layers, an outer layer consisting of heavily sclerotised, elongate, thick-walled cells that form a hard protective zone, the cells of which are aligned radially, and an inner layer of $\pm$ tangentially arranged thick-walled cells with obliquely oriented conspicuous pores (foramina); part of the vascular tissue, extends through the wall. Ovary, 4- to 5-locular, rarely more, solitary ovule per carpel. Carpel walls consisting of interdigitating fibers in younger fruits (Plate V, 5-7), i.e., the developing seeds don't fill the entire locular space (Plate IV, 5, 6). Ovules pendulous, anatropous and ovule curvature antitropous; Seeds, 1 to 3, ca.

10 mm long, 6–7 mm wide, globose to ellipsoid; seed coat, bitegmic. Seed coat thin-walled, consisting of multiplicative layers, with a ventral vascular trace (Plate VI, 4). Multiplicative layers consist of an outer layer of radially oriented sclereids and an inner zone of thick-walled parenchyma (fibre) cells interpreted as testa (plate VI, 4-7); with a second layer of radially oriented sclereids and parenchyma and fibers (Plate VI, 5-7) interpreted as tegmen. In older specimens these multiplicative layers appear to be reduced and compressed, and it is not clear whether they are exotestal or exotegmic in origin (Plate V, 10, 12)

Remarks

The fruit stone is indehiscent, highly sclerotized with the cells aligned somewhat radially in an outer zone and an inner zone of tangentially arranged fibres (Plate II, 1, 2). Sutures occur along the longitudinal ridges and dissect the endocarp into sectors, equal to the number of carpels in the ovary (Plate 1, 6, 7). The intersutural surfaces are concave and foramina extend through the wall often on an oblique trajectory connecting to the central vascular traces (Plate 1, 6-10, Video file). The foramina occur towards the top (distal end) of the fruit (Plate 1, 8-10, Video file).

As noted above, in the Euphorbiaceae, the vascular trace consistently occurs on the inner facing (ventral) side of the seed within the outer testa of the seed coat. The position of the ventral carpel vascular traces in *Fontainocarpa* therefore occupy the same position as illustrated for *Fontainea* and *Hylandia* (herein) and *Aleurites* (Corner, 1976; p. 179, fig. 220, bottom left hand drawing), *Jatropha curcas* (Corner, 1976; p. 192), other crotonoids and in the Euphorbiaceae more generally. The flower merosity in *Fontainea*, both in sepaline and petaline elements and numbers of locules suggests a 4-

to 5-merous fruit, although the number of seeds that develop is typically less in number. The ovules are anatropous and ovule curvature antitropous. In *Fontainea*, 1- , rarely 2- to 3- seeded fruits (Plate I, 1, 3; 11, 1) occur and similarly in *Fontainocarpa*, fruits with either 1- or 3- ovules per fruit have been observed (Plate I, 8-10: IV, 3-6, Video file). There is greater variation in the number of ovules than previously recognized. In extant *Fontainea*; the seed, or seeds, occupy the entire locule chamber of the fruit (Plate 1, 3). In the specimens of *Fontainocarpa* studied, as the ovules/seeds vary in size and don't occupy the entire locular chamber, and as there is variation in the thickness of their seed coats (Plate V, 5, 7, 10, 12; VI, 4-7), these observations collectively suggest that the fruits were immature.

The smaller ovules/seeds (developing seeds) in *Fontainocarpa* have multiple cell layers in the seed coat which are interpreted as the testa and tegmen (Plate V, 5, 7, 10-12; VI, 4-7). Larger seeds that occupy much of the internal locule have a thinner seed coat (Plate V, 4, 10), with an outer layer of thickened cells, and an inner layer of parenchyma cells which are thought to be derived from the testa; there is no evidence of the additional layering seen in the smaller ovules/seeds and younger fruits (Plate V, 5, 7; VI, 4-7).

The seeds of Euphorbiaceae are bitegmic, being derived from the outer and inner integument of the ovary and these two primary layers, as noted above, give rise to the testa and tegmen respectively (Corner, 1976; Webster, 1994). During development of the carpels, and then seeds, these two layers are multiplicative (Tokuoka and Tobe, 1998), i.e., the cells undergo periclinal and/or anticlinal divisions and both integuments typically consist of multiple layers of cells (Singh, 1954, 1968, 1970; Singh and Chopra, 1970; Corner, 1976; Tokuoka and Tobe, 1998). Studies on the development of seeds in

various genera in the Euphorbiaceae with capsular fruits show that as the seeds and fruits mature, the testa and tegmen, and thin-celled elements (e.g. parenchyma, of these two layers) are compressed together due to expansion of the growing seed, or seeds, resulting in the formation of the seed coat (Singh, 1954, 1968, 1970; Singh and Chopra, 1970; Tokuoka and Tobe, 1998). In many crotonoids the outer epidermal cells of the inner integument elongate anticlinally and become columnar and curved, and in the mature seed forms a radially arranged, impervious layer of sclereids in the seed coat (Singh, 1954; Singh and Chopra, 1970; Tokuoka and Tobe, 1998). This palisadal arrangement of cells has been shown to be derived from the tegmen and forms the protective layer around the embryo. In *Fontainocarpa*, the embryo is protected in an indehiscent fruit (endocarp) and the seed coat is derived from multiplicative layers from the tegmen and/or testa. In *Fontainea* (Plate II, 5, 7), the seed coat is membranous and it is unclear whether the radially arranged sclereids in the seed coat are derived from the testa or tegmen. Ontogenetic studies of ovule development in *Fontainea* could confirm an exotegmic origin for the seed coat.

5. Discussion

5.1. Assignment of Fontainocarpa to Euphorbiaceae and the Crotonoideae

Fontainocarpa fruits share with *Fontainea*, and many other genera in the Euphorbiaceae, in having ovules that are anatropous with antitropous ovule curvature; syncarpous ovary and axile placentation; a single ovule per carpel; equal numbers of locules to the number of sutures; ventral carpel traces embedded in testa; multilayered endotesta and exotegmen (Plate VI, 4-7); a tendency towards reduction in the number of seeds per fruit, to a single seeded fruit (Plate I, 3; IV, 5, 6); and septicidal dehiscence as splitting of the fruit occurs along the longitudinal sutures (Jessup and Guymer, 1985).

While many of these characters, e.g. anatropous ovules and antitropous ovule curvature, syncarpous ovary, axile placentation are common in the Malpighiales, the single ovule per locule would exclude the Picrodendraceae and Phyllanthaceae as they have two ovules per locule (Stuppy, 1996), although some taxa may abort an ovule during fruit development and could appear to be uniovulate. Being uniovulate, and having the multilayered cell wall derived from the testa and tegmen are both features of the Euphorbiaceae. Additional characters, including indehiscent fruits, distinctive vascular channels (foramina) that penetrate through the fruit wall into the locule, and thin membranous seed coats are taxonomically restricted features seen in very few genera in the Euphorbiaceae, but do occur together in extant *Fontainea*.

5.2. Aspects on fruit morphology and seed structure in the Crotonoideae and Euphorbiaceae

Most genera in the Euphorbiaceae have dehiscent capsular fruits and indehiscent fruits are rare within the family. Only a few genera in Australia have indehiscent fruits and they include *Hylandia*, *Aleurites* (Rozefelds et al., 2017) and *Fontainea*. *Fontainocarpa* differ from *Aleurites* in having a woody dry fruit stone and foramina in the fruit wall. In *Aleurites* and *Hylandia* the thick seed coat is formed from the exotegmen and the outer fruit walls are relatively fleshy, not woody, so protection of the embryo is provided by the seed coat not the fruit (Rozefelds et al., 2017). As their fruit morphology differs this also indicates that the indehiscent fruits of *Aleurites* and *Fontainea* have evolved independently. The combined *rbcL* and *trnL-F* sequence data from Wurdack et al. (2005) and Matamoro-Vidal et al. (2012) also shows that *Fontainea* belongs in a largely Australian clade of inaperturate crotonoids consisting of *Baloghia*, *Beyeria* and *Ricinocarpos* that have capsular fruits.

Non-Australian crotonoid genera with all, or some species, having indehiscent fruits include *Ricinodendron* (including *Schinziophyton*) (Africa), *Oligoceras* (south east Asia), *Deutzianthus* (south east Asia), *Pantadenia* (Madagascar/ south east Asia), and *Givotia* (Africa, Madagascar and Sri Lanka) and while generic limits for some genera are still unclear (compare Radcliffe-Smith 2001 with Webster, 2014), we have largely adopted the more recent treatment herein. *Ricinodendron rautanenii* was described as having a tough woody testa (Keegan, 1982) so it differs from *Fontainea* that has a membranous seed coat, but it shares with this genus foramina in the fruit wall (Peters, 1986). *Oligoceras* fruits are described as drupaceous, but information on seeds is not available (Webster, 2014). The fruit of *Deutzianthus* is described as a drupe, subglobose, indehiscent; epicarp crustaceous; endocarp woody but the structure of the seed coat is not described (www.efloras, Flora of China, FOC, vol. 11, p. 267, 15 July 2016). *Pantadenia gervaisii* from Madagascar, which has been placed in *Parapantadenia* by some authors, differs from *Fontainea* in having thinly fleshy indehiscent fruits and no endocarp (Rabevohitra and MacPherson, 2012), while *P. adenanthera* from south east Asia differs in having dehiscent fruits (Webster, 2014). *Givotia* has a bony testa (Indianbiodiversity.org/species/show/229803) and therefore also differs from *Fontainea*. While the descriptions and information on the fruit and seeds of some genera is limited or incompletely known, i.e. *Deutzianthus* and *Oligoceras*, all of these genera appear to differ, based upon the limited published descriptions, from *Fontainea* in fruit and/or seed morphology. Our literature-based review of the morphology of indehiscent Euphorbiaceae in the subfamily Acalyphoideae, such as *Podadenia*, *Ptychopyxis*, *Cleidocarpon*, *Mareyopsis* and some *Mallotus* and *Plukenetia* species with indehiscent fruits also showed that their fruits differ from those in *Fontainocarpa* in lacking foramina and/or in having fleshy fruits (Radcliffe-Smith, 2001; Webster, 2014).

In most crotonoids, and in most genera in the family, the dehiscent fruits are capsular and the outer layer of the tegmen forms the protective layer around the developing embryo in the seed (Tokuoka and Tobe, 1998), and the seeds have been described as exotegmic (Corner, 1976). Webster (2014) noted that in those genera with indehiscent fruits the seeds typically have a thin-walled seed coat, which suggests that the indehiscent walls of the fruit undertake the same function as the exotegmen in protecting the developing embryo.

The exotegmen layer is a conspicuous feature in most crotonoids, and the seed coat is thickened and protects the developing embryo. In *Fontainea* the seed coat is formed from both the testa and tegmen as is typical for the family but the tegmen fails to develop the characteristic palisade layer of thickened cells as seen in most other crotonoid genera. In *Fontainea* the seed coat is membranous and not thickened and it is not clear whether it is derived from the inner and outer integument, or both (Plate II, 5, 7). As the seed coat in *Fontainocarpa* is interpreted to be membranous this implies that these fruit and seed characters and fruit adaptations may have been in place since the end of the Oligocene. Although information on crotonoid seed and fruit morphology is limited, *Fontainea* can be distinguished from all other Australian Euphorbiaceae genera with indehiscent fruits. For example, fruits of some species of *Fontainea* have conspicuous foramina, a feature absent from other indehiscent genera in Australia but it is shared with the African species *Ricinodendron rautanenii*. The distribution and arrangement of foramina, however, differs from that seen in *Fontainea* and suggests that foramina have arisen independently in these genera.

5.3. Comparison with extant species of *Fontainea*

Fontainocarpa is closely comparable to *Fontainea* in having relatively large, indehiscent woody endocarps (fruit stones) and foramina in the fruit wall, which is an unusual character in the Euphorbiaceae. The variation in morphology between the different extant species of *Fontainea* includes fruit stone shape, number of carpels, presence and arrangement of foramina, ridging or otherwise, degree of ornamentation, and whether the intersutural surfaces are flat, convex or concave (Table 1).

The fruit stones in *Fontainocarpa* vary from being ovoid to broadly ovoid in shape while in *Fontainea* there is greater variation and some species are beaked (Rozeffelds, 1990; Jessup and Guymer, 1985; Forster, 1997; Table 1). The number of carpels varies both between and within the extant species from 3 to 5, sometimes 6, and *Fontainocarpa* shows similar variation with 4 to 5, rarely 7 locules (Rozeffelds, 1990), but this character is probably of limited value in determining relationships. In *Fontainocarpa* there is a series of foramina towards the midline of each intersutural surface, and they connect to the vascular tissue of the fruit as shown clearly in the attached video file (Video file). Scattered foramina occur in *F. venosa* and *F. pancheri*; in others, e.g., *F. australis*, *F. picrosperma*, *F. rostrata* and *F. oraria* only a single foramen occurs indicating the original position of the micropyle (Table 1). Most extant species have bluntly to sharply ridged fruits with the exception of *F. venosa* which lacks ridges (Table 1). *Fontainea* also shows variation as to whether the fruit wall is convex (*F. venosa*, *F. oraria*), or concave, like *F. picrosperma* which has concave intersutural surfaces similar to the fossil material (Table 1).

5.4. Phylogenetic relationships and fossil record of crotonoid Euphorbiaceae

A group of genera, including *Fontainea*, within the Crotonoideae has inaperturate pollen with crotonoid exine sculpture which consists of triangular – rounded structures in regular arrays (Nowicke, 1994; Tokuoka, 2007). This pollen type is a synapomorphy for this clade (Nowicke, 1994; Wurdack et al., 2005; Tokuoka, 2007; Matamoro-Vidal et al., 2012) and occurs in a number of tribes in the Euphorbiaceae including the Crotonae, Codiaeae, Ricinocarpeae, Ricinodendreae and Aleuritideae, all of which are represented by species in Australia or New Guinea (Webster, 2014). Combined analysis of *rbcL*, *atpB*, *matK*, and *18S rDNA* data by Tokuoka (2007) placed *Fontainea* in a clade with *Baloghia inophylla*, *Ricinocarpos pinifolius*, *Bertya sharpeana* (all from Australia), *Coccomerion minus* (New Caledonia) and *Neoboutonia manii* and *Ricinodendron rautanenii* (as *Schinziophyton rautanenii*) (which are both from Africa). Wurdack et al.'s (2005) more comprehensive analysis using plastid *rbcL* and *trnL-F* DNA sequences placed *Fontainea* sister to *Baloghia inophylla*, in an entirely Australian clade with species of *Beyeria* and *Ricinocarpos tuberculatus*. As the dataset used in Cheek et al.'s (2016) phylogenetic analysis and description of *Karima* was largely derived from Wurdack et al.'s (2005) earlier study, so the general pattern of relationships within this clade were reiterated.

Inaperturate, Euphorbiaceae pollen recorded from early Oligocene of Western Australia and from Late Miocene-Early Pliocene sites in the Murray Basin, southern Australia have been referred to several informal species of *Crotonipollis* (Truswell et al., 1985; Macphail and Truswell, 1993; Macphail, 1996; Macphail and Stone, 2004). Rozefelds et al. (2017) concluded that there was credible evidence for the crotonoids from the Oligocene onwards in Australia and described a fossil seed that they referred to *Aleurites* (Crotonoideae) from south eastern Queensland, for which they inferred a Miocene age. The fossil record of *Fontainocarpa* provides further evidence of the

Crotonoideae from Australia. The new data on *Fontainocarpa* is therefore a significant addition to knowledge of the Euphorbiaceae fossil record internationally and our studies on comparable modern genera has provided new insights into fruit evolution within the crotonoid euphorbs.

The only other Southern Hemisphere records known to the authors of possible crotonoids are fossil fruits from Peru that were named *Carpolithes jatrophaformis* Berry, and *Jatropha tertiaria* Berry from Bélen, Peru, South America and were compared with *Jatropha* (Berry 1929a, 1929b). The flora is considered to be Oligocene in age (Manchester et al., 2012). Berry's (1929a) original sketch of the holotype (by monotypy) of *Carpolithes jatrophaformis* shows a three carpellate, possibly capsular, fruit. He compared it with fruits of the Arecaceae, but also noted that the whole organization of the fruit are exceeding like those of *Jatropha*. The walls of the fruit are thin, and fibrous material adheres to some of the seeds, the ventral surface of which are convex, while the dorsal surface is flat to slightly curved. Manchester et al. (2012) have recently illustrated additional material of the same taxon, that they referred to as *Jatropha tertiaria*, and concluded was Euphorbiaceous, but not referable to *Jatropha*.

The holotype (by monotypy) of *Jatropha tertiaria* was re-examined in the UNSM collections by the senior author and it, and newly collected material from Bélen is currently being studied by Steven Manchester. Berry's (1929b) original illustration shows two seeds, and part of the fruit wall adhering to each seed. Berry (1929b) interpreted the seeds as having a very large caruncle, approximately seven mm long. Dehgan (2012) illustrated the seed morphology of a selection of American species in the genus. The largest caruncles in the genus are in the section *Peltatae* (Dehgan and Webster, 1979) which are to eight to ten mm in length.

5.5 Complementary research approaches and limitations

This study is one of the few to date to use synchrotron imaging to study permineralised (silicified) fossil angiosperm fruits, although Steart et al. (2014) have similarly used microtomography to study fossil conifer cones. Synchrotron imaging is a non-destructive method for visualising the entire fruit in 3D, the external appearance and provided an understanding of the internal morphology of fossil fruits (Video file), which provides evidence of the arrangement of ovules and the structure of foramina in the fruit wall. This ability to digitally construct the internal morphology of these fruits represents a significant advance on traditional approaches, like serial sectioning, that were used, in the past, to reconstruct the internal morphology of living and fossil fruits. Our studies of living material at the Australian Synchrotron provided insights into the morphology of extant fruits, allowing us to resolve the number of developing seeds, and visualise the seed coat, aspects of the fruit wall and foramina and the orientation of the ovule.

The limitations of the current synchrotron data are that it did not allow us to study the microstructure and microanatomy in detail, as microCT studies are currently not available at the Australian Synchrotron. These limitations are currently being addressed by the Australian Synchrotron through the development of a new micro CT beamline with these capabilities. To get around these limitations we used a combination of thin sectioning, SEM and synchrotron CT images which provide unique sets of complementary data that is useful in understanding, interpreting and describing the morphology of fossil and living fruits.

6. Conclusion

Rozefelds et al. (2017) and this study have illustrated the fruit morphology in indehiscent-fruited genera in the Crotonoideae from Australia and the closest relatives of *Fontainea* have schizocarpic/capsular fruits. These differences in fruit morphology, and current phylogenetic evidence (Wurdack et al. 2005), indicate that indehiscent fruits evolved multiple times in the Crotonoideae, and in the Euphorbiaceae more generally. Semantic discontinuities imposed by terms like 'dehiscent' and 'indehiscent' obscures the observation that fruit homologies will need to be found between capsular and indehiscent fruit types in the family; and not necessarily with other indehiscent-fruited genera. It is unclear what evolutionary pressures drive these morphological changes but as the indehiscent fruits in some species/genera are often fleshy, this suggests a transition from mechanical to animal-mediated dispersal.

Foramina are a distinctive feature in *Fontainocarpa*, but less so in some of the extant species of *Fontainea*, although all species have a subapical foramen (Table 1). Foramina are also present in *Ricinodendron* and it seems probable that they play a role in facilitating germination in those genera with hard, thick-walled fruits but not in fleshy-fruited taxa. Foramina are also seen in the hard, woody fruits of some genera in the Humiriaceae in the Malpighiales (Herrera et al., 2014).

While we examined too few genera to determine whether the Crotonoideae fruits could be differentiated from those in other clades in the family, we were able using the range of fruit and seed characters available to suggest close links to an extant genus and could exclude most other genera within the family. We were limited by the lack of systematic and comparative research on both the ontogeny and morphology of fruits of extant genera in the family, and also uncertainty in generic limits (Radcliffe-Smith, 2001; Webster, 2014). Euphorbiaceae seeds typically have thickened

exotegmen, and should preserve well in the fossil record, so more detailed systematic studies on the ontogeny and morphology of fruits from genera in the family might help in recognizing further fossil evidence of this poorly known family.

Acknowledgements

We thank Dr Gordon Guymer (Queensland Herbarium, BRI) and Prof. Darren Crayn for the loan of modern material of *Fontainea* and *Hylandia* respectively. Paul Forster provided a draft description of *Hylandia* for the Flora of Australia treatment of the family. We are grateful for the comments from one anonymous referee, in suggesting ways that the paper could be improved and strengthened. Peter Waddington and Geoff Thompson (Queensland Museum, QM) and Matthew Miller (Smithsonian Institution, SI) provided exquisite photographs of the fossil and modern material. We thank Terrence Ray and Peter La Black from Capella for allowing us to continue our research on this important flora from Central Queensland. Staff in both the SI and QM Library kindly tracked down the frequently obscure but relevant literature for this research. This research was undertaken while the senior author was on a Queensland Smithsonian Fellowship in the Palaeobotany Section at the Smithsonian Museum of Natural History in Washington DC in 2016 with Dr Scott Wing.

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Appendix A

Comparative material illustrated: BRIAQ 633445 *Fontainea venosa* L.W.Jessup 583 & G.P.Guymer, BRIAQ 349534 *Fontainea pancheri*, H.S.Mckee 40251. *Hylandia dockrillii* ATH, QRS500075, B.Hyland AFO2111.

Plate and fig Captions

Fig. 1. Map showing the distribution of extant species of *Fontainea* based upon the *Atlas of Living Australia* records, and the fossil site near Capella.

Plate I. 1. Volume render of extant *Fontainea pancheri* fruit showing the exocarp (Ex), mesocarp (Me), endocarp (En) and the walls of the endocarp which shows faint radial lines indicating the presence of foramina (F); there is a single developing seed (O) with a conspicuous seed coat (SC) and the position of the chalaza (C) is shown (BRIAQ 349534). 2-4. Extant *Fontainea venosa*, photographs of external appearance of fruit stone (endocarp), placement of seed in fruit and detail of surface of seed of *Fontainea venosa* endocarp (BRIAQ 633445). 2. Shows the ovoid shape of the endocarp, and conspicuous depressions of the foramina (F) in the endocarp wall. 3. The mature single seed is supplied by a ventrally placed vascular trace (VS) and the seed occupies a central position in the fruit and has expanded to fill the entire inner cavity of the fruit compressing the inner carpels walls, adjoining locules and soft tissues. 4. The seed

showing the hilum (H), conspicuous ventrally placed raphe (R), nucellar beak (NB) and placental tissue (S). 5. Extant *Fontainea picrosperma* showing the prominent ridges in the endocarp, apical beak and single foramen (F) at terminus of each carpel. 6-10. Synchrotron images of *Fontainocarpa foraminata* (QMF16743). 6-7. Volume render showing the external appearance, prominent longitudinal lateral ridges, sutures (S) aligned along the longitudinal ridges, and conspicuous longitudinal placement of foramina (F) along the mid line of the intersutural surfaces of the endocarp. 8-10. Internal volume render of whole specimen showing the internal morphology of the endocarps. 8.-9. Longitudinal view showing the arrangement of foramina (F) within the fruit wall, and two ovules (O). 10. Transverse view showing the placement of ovules within the fruit. Scale bar = 5 mm.

Plate II. Transverse section of *Fontainea venosa* fruit (BR1AQ 633445). 1. Section through fruit showing the fruit wall consisting of a light coloured layer of sclerieids (Sc) and internal layer of tangentially oriented fibers (Fi), foramina in the intersutural surface and sutures (S) of which there are four, indicating that the fruit was originally 4-locular, with two seeds (O) and the narrow cavities and the carpel walls (CW) are evidence of two aborted ovules. Scale bar = 5 mm. 2. Detail of fruit wall showing the inner zone of tangentially arranged fibers (Fi), and carpel wall (CW), and suture (S). Scale bar = 1.25 mm. 3. Detail of carpel walls (CW) surrounding the two seeds (O), note the narrow seed coat (SC). Scale bar = 1 mm. 4. Detail of outer sclereids (Sc) and inner fibres (Fi). Scale bar = 500 μ m. 5. SEM micrograph showing the external appearance, and outlines of the epidermal cells of the seed coat. Scale bar = 50 μ m, 6. SEM micrograph showing irregular arrangement of sclereids in the fruit wall. Scale bar = 200 μ m. 7. SEM micrograph of seed coat showing longitudinal section through the seed coat

and radial alignment of cells of the testa. Scale bar = 50 μ m. 8. Detail of 6, showing the regular pitting of the sclereids. Scale bar = 100 μ m.

Plate III. *Hylandia dockrillii* fruit (ATH QRS 500075) 1-2. Lateral and distal view of bilobed fruit showing the septicial lateral sutures (S). Scale bar = 1 cm. 3-4. Transverse section and line drawing of the fruit, showing exocarp (Ex), loosely arranged fibres in the mesocarp (Me) and vascular bundles (vb) at the base of the mesocarp, thin carpel walls (CW), ventral vascular traces (VVT) and thick seed coat (SC). Scale bar = 1 cm. 5. SEM of fruit wall showing the loosely arranged fibres of the mesocarp (Me) and the outer exocarp (Ex). Scale bar = 500 μ m. 6. Detail of 3, showing carpel wall (CW) and radially-arranged cells in seed coats and vascular bundles (vb) at the base of the fruit wall. Scale bar = 5 mm. 7. SEM of seed coat showing the radially-arranged, thickened columnar cells. Scale Bar = 50 μ m.

Plate IV. Transverse sections of fossil fruits of *Fontainocarpa* and modern *Fontainea*. 1.2. *Fontainea venosa* (BRIAQ 633445). Photograph and line drawing of transverse section through an originally 4-locular fruit, showing the woody fruit wall (FW) which consists of two layers, an outer layer consisting of radially oriented sclereids, and an inner layer of tangentially oriented fibers; conspicuous foramina (F) extend through the wall, two ovules have developed into seeds (O), while two aborted and have been compressed and are represented by narrow spaces between adjoining locules, carpel walls (CW) form two parallel layers in the centre of the fruit, the seeds are large consisting of endosperm and developing embryo (E), fill the entire inside of the fruit, and they have a thin membranous seed coat (SC) 3.-6. *Fontainocarpa foraminata*. 3.4. Line drawing and photograph of a partially mature, 5-locular fruit (QMF58787) highlighting the thick woody fruit wall (FW), conspicuous foramina (F) extend through

the wall, three ovules (O) which have developed, and two have aborted, and the locules have been compressed and are represented by hollow spaces (L), there is no evidence of carpel walls. The ovules (O) are conspicuous and the seed coat is clearly evident with ventral vascular traces (VVT) positioned on the inner (ventral) side of each seed and two of the seeds have a coarsely crystalline quartz core with adhering siliceous matrix (M) on the outside of the fruit. The sutures (S) are clearly evident as both external and internal features in the fruit, and the intersutural surface (IS) between the sutures is concave in appearance. 5. 6. Photograph and line drawing of uniovulate fruit (QMF58788), showing the thick woody fruit wall in an originally 5-merous fruit, with four sutures evident, and one ovule (O) has developed, and four have aborted, and the young seed (O) occupies a large proportion of the inside of the fruit. The ventral position of the ventral trace (VT) is consistent with it being a ventral vascular trace of one of the ovaries. Scale Bar = 5 mm.

Plate V. 1-4. Longitudinal sections through *Fontainocarpa foraminata* fruit.

(QMF58789). 1. Showing an anatropous ovule (O) with antitropous ovule curvature, the locules (L) are compressed on one side of the fruit and the curved white tubes on the right hand side of the endocarp wall are foramina (F), the seed coat (SC) shows the position of the ovule (O) which is quartz-infilled. Scale bar = 5 mm. 2. Detail of Fig. 1, showing the developing ovule, note the fine layering in the seed coat (SC) and the position of the chalaza (C). Scale bar = 2.5 mm. 3. Thin section through the same fruit, showing two ovules, the right hand ovule (O) is relatively large and occupies much of the locule, the seed coat of which is illustrated in Fig. 10, note the carpel wall (CW) and position of the foramina (F). Scale bar = 5 mm. 4. Detail showing the developing seed, seed coat (SC) and chalaza (C). Scale bar = 2.5 mm. 5. Arrangement of tissues in the fruit

shows the carpel wall (CW) next to the seed coat. The seed coat consists of multiple layers which are interpreted as testal in origin with thickened outer cells (TsS) and inner fibers (TsP). Scale bar = 1 mm. 6. Detail of the fibres that form the interlocking (braided) cellular arrangement in the carpel wall (CW). 7. Detail of seed coat showing the sclereids (Sc) forming the outer wall of the testa on the right, and the fibers of the carpel wall to the left. 8. 9. Detail of cellular arrangement of fibres, each fibre has thickened walls and conspicuous lumen. 10. Detail of partially preserved seed coat (SC) in large seed in Fig. 3, consisting of an outer zone of enlarged cells, and an internal zone of thin walled cells. 11. Detail of part of seed coat in the developing seed showing an oblique section through ovule wall. 12. Detail of seed coat showing the outer margin of the seed coat consisting of enlarged sclereids (Sc). Scale bar = 50 μ m. Scale bar in other figs = 100 μ m, unless otherwise stated.

Plate VI. Transverse section through *Fontainocarpa foraminata* fruit. (QMF58790). 1. Transverse section through a 5-locular fruit showing the sutures (S) and three developing ovules (O), two of which are partially filled with pink and grey mineral infillings and the other has been replaced by cryptocrystalline quartz and an abortive ovule (L). The ventral vascular traces (VVT) are oriented on the inside of the ovules towards the centre of the fruit. Scale bar = 5 mm. 2. Detail of a single seed, note the ventral vascular trace and layered nature of the seed coat (SC), and the mineral fillings in the inner part of the seed. Scale bar = 1.0 mm. 3. Thin section showing the arrangement of ovules (O) which are aligned along each suture, i.e. cavities in the fruit indicate the position of abortive ovules (L), and adhering siliceous matrix (M) is present on the margins of the fruit. Scale bar = 5 mm. 4. Detail of cellular structures around the ventral vascular trace (VVT), the outer layer of sclerified cells (TsS) forms the margin of

the seed coat (SC), a zone of thick walled fibers formed from parenchyma cells (TsP) surrounds the ventral vascular trace (VVT) and the black opaque masses in the vascular trace are precipitated mineral crystals. The tegmen consists of an internal layer of radially oriented cells (TgS) and a zone of tangentially oriented parenchyma cells (TgP) next to what would have been the endosperm (En) of the seed. 5. Detail of seed coat, shows a number of layers which are interpreted as a testa consisting of an outer layer of elongated radially oriented sclereids (TsS), with thickened cell walls and an inner rows of fibres consisting of thick-walled parenchyma cells (Pa) that are oriented tangentially; and inner rows of radially arranged slightly thickened cells (TgS) and parenchyma cells (TgP) which is evidence of the tegmen. 6. Details of parenchyma cells (TSP) showing the lumen in each fibre. 7. Detail of another part of the seed testa showing multiple layers of cells, with the angled cells of the carpel wall (CW), radially oriented testal sclereids (TsS), fibers consisting of thick walled parenchyma cells (TsP), radially oriented cells of the tegmen (TgS) and an inner layer of thickened parenchyma cells (fibers) (TgP). Scale bars = 100 μm , unless otherwise stated.

Table 1. Comparison of seed and fruit characters between extant species of *Fontainea*, *Aleurites* and *Hylandia* with fossil *Fontainocarpa foraminata*. Information on fruit characters for extant species is from Jessup and Guymer, (1985); Forster (1996), Forster and van Welzen (1997), Webster (2014), Rozefelds et al. (2017), and Paul Forster, pers. comm. 2016, and for *F. foraminata* (Rozefelds 1990; and herein).

Video file. ‘Unconcealedness’ an animation by Milroy, A.K., Rozefelds, A.C., Maksimenko, A., and Holmes, A., 2016. The animation reveals the internal structure of the fossil *Fontainocarpa foraminata*. Two young ovules are evident in the centre of the fruit and the foramina are connected through continuous tubes to the central vascular trace. The

staccato-like nature of the sound scape is seen as a metaphor for the punctuated (particle) theory of light that was used to study the fossil at the Australian Synchrotron.

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Species	Fruit Shape	Number of Carpels	Foramina Distribution	Ridges	Ornamentation	Intersutural faces	Distribution
<i>Fontainea australis</i>	Broadly ovoid, not beaked	3	Subapical foramen	Sharply ridged	Smooth	+/- flat/convex	Australia
<i>Fontainea borealis</i>	No fruits known						New Guinea
<i>Fontainea fugax</i>	Beaked	3,4	Absent or not mentioned	Bluntly ridged	Weakly rugose	+/-flat to convex	Australia
<i>Fontainea oraria</i>	Globose, not beaked	2,3	Subapical foramen	Sharply ridged	Rugose, longitudinally and medially grooved	convex	Australia
<i>Fontainea pancheri</i> spp complex	Broadly ovoid, beaked and non-beaked	4,5	Foramina present but variable	Ridged and non-ridged forms occur	Variable in different forms	Variable in different forms	New Caledonia
<i>Fontainea picrosperma</i>	Beaked	4,5	Subapical foramen	Bluntly ridged	Smooth	Concave	Australia
<i>Fontainea rostrata</i>	Beaked	3,4	Subapical foramen	Bluntly ridged	Strongly rugose	+/-flat to concave	Australia
<i>Fontainea subpapuana</i>	Beaked	3	Absent or not mentioned	Ridged	Smooth	+/-flat	New Guinea
<i>Fontainea venosa</i>	Broadly ovoid, globular, not beaked	3,4,5	Subapical foramen and scattered foramina	Not ridged	Smooth	Convex	Australia
<i>Fontainocarpa foraminata</i>	Broadly ovoid, not beaked	4,5,-7	Mid-lateral foramina and subapical foramen	Ridged	Smooth	Concave	Australia
<i>Hylandia dockrillii</i>	globose	2	none	Not ridged	Smooth	-	Australia

<i>Aleurites</i> spp	Semi-globose	2-3	none	Not ridged	Smooth	-	Australia/SE Asia
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