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Fruits of *Anacardiaceae* from the Paleogene of the Paris Basin, France

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Running title: DEL RIO et al. –Paleogene Anacardiaceae of the Paris Basin

Abstract

Premise of research. The Anacardiaceae family is distributed throughout the vegetated continents. The fossil record indicates extensive diversification of the family during the Paleogene and, in particular, during the Eocene. Despite the abundant fossil record of this period, there are only a few reliable anacardiaceous fossils in the Paris Basin. Here, we aim to document newly recognized fossils of Anacardiaceae from the Paris Basin, understand their paleoecology, and discuss their biogeographic history.

Methodology. Thirty-three lignite fruits were examined from two sites, one pre- and one post-the Paleocene-Eocene boundary, i.e., Petit Pâtis (Rivecourt) and Le Quesnoy (Houdancourt). The specimens were photographed and anatomy was studied using computed tomography and histological sections. Comparative analyses were undertaken using available descriptions of fossil and modern fruits of Anacardiaceae.

Pivotal results. A new species is described, *Cyrtocarpa biapertura* sp. nov., based on a unilocular fruit with two prominent apertures present on the ventral side of the endocarp, protruding into two lacunae surrounding the locule. Taphonomic analysis indicates that this plant grew close to river banks. Furthermore, a new record of “*Lannea*” *europaea* (Reid and Chandler) Chandler is reported from for the Eocene site.

Conclusions. The occurrence of *Cyrtocarpa* in both the Paleocene and Eocene floras in the Paris Basin suggests similar vegetation during both time intervals. It is likely that both floras grew under similar subtropical climates. Moreover, it appears that the early Eocene shows an enrichment of the paleodiversity of Anacardiaceae and other plant families in the Paris Basin. The presence of *Cyrtocarpa* documents a rarely reported disjunction between the Paleogene of Europe and the recent tropical flora of South America.

Key Words Cenozoic, Biogeography, Taphonomy, *Cyrtocarpa*, Sapindales.

Introduction

The family Anacardiaceae R. Br. contains 79 genera and about 870 species of trees, shrubs, and lianas (Pell et al. 2010; POWO 2022). This family occurs today in tropical, subtropical and temperate environments, particularly in the Americas, Africa, southern Europe, Asia, Australia, and most of the Pacific islands (Pell et al. 2010). It is an economically important family because of the consumption of fruits of *Anacardium* L. (cashews), *Mangifera* L. (mangos) and *Pistacia* L. (pistachios) as well as for timber of trees and diverse horticultural and medicinal uses (Pell et al. 2010).

Anacardiaceae is a well-defined family forming a sister group to the Burseraceae within the Sapindales supported by molecular phylogeny studies (Gadek et al. 1996; Pell 2004; Weeks et al. 2014; APG 2016; Muellner-Riehl et al. 2016) as well as morphology (Marchand 1869; Metcalfe and Chalk 1950). This family has been traditionally recognized as having a single ovule per locule with the ovule curved in the same direction as the carpel (syntropous) (Bachelier and Endress 2009). The infrafamilial classification is still under debate, but there has been improved understanding recently. It is generally inferred that Anacardiaceae can be divided into two subfamilies i.e., Spondioideae and Anacardioideae (Mitchell et al. 2006; Weeks et al. 2014; Rossini et al. 2021). However, neither of these groups appear monophyletic and the family was recently divided into six clades, two of which correspond to Spondioideae and four to Anacardioideae (Weeks et al. 2014). Nevertheless, the remarkable diversity of the fruit and key morphological and anatomical features facilitate the recognition of many genera within the family (Wannan and Quinn 1990; Bachelier and Endress 2009). For instance, the two clades of Spondioideae display drupe-like fruits containing similar sclerified endocarp structures (Herrera et al. 2018). They can be distinguished by the number of locules, the presence or absence of specialized germination

structures, the shape and symmetry of the fruit, and the presence and position of lacunae and apertures (Herrera et al. 2018).

The estimated crown age of Anacardiaceae varies depending on the calibration parameter used from early (ca. 129 Ma) to late (ca. 75 Ma) Cretaceous (Weeks et al. 2014; Muellner-Riehl et al. 2016). Phylogeny and niche modeling studies hypothesized the origin of Anacardiaceae within Southeast Asian tropical wet environments (Weeks et al. 2014), although the fossil record suggests a Laurasian origin for the family (Vassiljev 1976; Wilf 2000; Hofmann et al. 2011; Smith et al. 2014). There are no unambiguous fossils from the Cretaceous to our knowledge, but fossils attest that the group was already distributed in North America, Europe, and Central Asia during the late Paleocene to the early Eocene (Reid and Chandler 1933; Chandler 1961; Vassiljev 1976; Wilf 2000; Hofmann et al. 2011; Smith et al. 2014). Numerous fossils, especially of fruits, are found in Eocene deposits from North America (Manchester 1994; Manchester and Judd 2022a, b; Tiffney and Manchester 2022), Europe (Reid and Chandler 1933; Chandler 1961; Manchester et al. 2007; Collinson et al. 2012) and Asia (He and Tao 1997; Manchester et al. 2005; Jin 2017). These occurrences could indicate a rapid and early diversification of the family during the Paleogene, but this scenario needs further analyses. A similar trend occurs in South and Central America, where fossil endocarps and wood show unexpected paleogeographic scenarios (Herrera et al. 2012; Woodcock et al. 2017; Herrera et al. 2019; Barreda et al. 2020; Rodríguez-Reyes et al. 2020; Rodríguez-Reyes et al. 2021). The diversity of endocarps and the multiple inferred long-distance dispersal events of Anacardiaceae and other tropical plants may have been linked to the multiple warming events during the early Paleogene (Zachos et al. 2008; Westerhold et al. 2020).

The Paris Basin is the largest sedimentary basin in France. This basin shows an almost continuous record from Triassic to Pliocene deposits (Perrodon and Zabek 1991). In

particular, the early Paleogene is well represented and includes numerous paleontological sites (Mégnyien 1980; Aubry et al. 2005). Plants macrofossils (mostly leaves) and palynomorphs suggest a subtropical climate during the Paleocene and Eocene (e.g., Watelet 1866; Saporta 1868; Furon and Soyer 1947; Koeniguer 1987; Cavagnetto 2000; Tanrattana et al. 2020). Despite the numerous field campaigns and detailed taxonomic studies on the Paris Basin plant remains, very few fossil specimens of Anacardiaceae have been found and described. The family is represented in the Paris Basin Paleogene deposits by pollen and fruits. From the pollen record, two genera with suggested affinity to *Bouea* Meisn. and *Rhus* L. are recognized from the early Eocene of Le Quesnoy, Oise (Cavagnetto 2000), and pollen with affinity to *Lannea* A. Rich. from the Eocene of the Paris Basin, but without details of the specific site (Gruas-Cavagnetto 1987). Furthermore, a solitary fruit assigned to cf. *Lannea* was recorded from the Paleocene of Rivecourt, Oise (Smith et al. 2014). Here, with the aim of improving knowledge of European Anacardiaceae diversity in the early Paleogene, we revise and describe the fruits belonging to aff. *Lannea* s.p. from Rivecourt (Smith et al. 2014) and describe new fruits belonging to Anacardiaceae from Le Quesnoy (Nel et al. 1999). We aim to establish their systematic affinities and paleoecology and discuss their biogeographical history.

Material and Methods

Geological setting

The fossils studied here were collected from two paleontological sites in the Paris Basin on either side of the Paleocene-Eocene boundary, i.e., Petit Pâtis (Rivecourt, Oise, France) and Le Quesnoy (Houdancourt, Oise, France). Both sites are located about 200 km north of Paris

and approximately 7 km from each other (Fig. 1) (Nel et al. 1999; Smith et al. 2014). These sites are no longer accessible because they were flooded with water when mining activity ceased.

The upper Paleocene-lower Eocene succession of the Paris Basin is divided into four lithostratigraphic groups. From the bottom to the top these are the Vigny Group, Vesles Group, Mont Bernon Group and Montagne de Laon Group. The Vesles Group contains the Rivecourt site which is also known in the literature as Petit Pâtis, Oise (Smith et al. 2014). This group is further divided into several formations. The upper part of the Bracheux Formation is represented by continental and brackish clays, limestones, sands and lignites. The lignite beds are rich in vertebrates and plant remains, i.e., wood fragments, palynomorphs as well as seeds and fruits, some of which are studied here (Aubry et al. 2005). These beds are part of sedimentary successions composed of coarse sandstones with erosive bases followed by sandstones with planar cross bedding covered by lignite interpreted as deposited in a fluvio-estuarine environment (Smith et al. 2014). The paleontological material from this bed is significant for the paleoenvironmental and biostratigraphic understanding of the Paris Basin. For instance, a preliminary analysis shows a high diversity of fruit taxa among the most represented families, which include Icacinaceae, Menispermaceae, Vitaceae, and Betulaceae (Smith et al. 2014; Del Rio et al. 2019b). Furthermore, these beds also contain vertebrates belonging to mammals, fish, amphibians, and squamates (Smith et al. 2014; Solé et al. 2016). The biostratigraphic studies based on vertebrates and palynology indicate a late Paleocene age, i.e., MP6b, ca. 57-56 Ma (Smith et al. 2014).

The Mont Bernon Group that overlies the sands of the Vesles Group contains the Le Quesnoy site (Houdancourt, Oise). The beds studied here are characterized by sedimentary successions of alternating medium and fine-grained sands, clays and lignites (Nel et al. 1999). This successions is similar to that observed in Rivecourt and the fruits studied here come from

the topmost of two river channels i.e., QNY1 and QNY2. This succession corresponds to a fluvial to swamp environment (Nel et al. 1999). Associated with the fruits, palynomorphs (Cavagnetto 2000), wood fragments, flowers, amber with bioinclusions, vertebrates and insects were also found (Nel et al. 1999). The paleobotanical material is diverse including families such as the Fabaceae (De Franceschi and De Ploëg 2003), Menispermaceae (Jacques and De Franceschi 2005) and Icacinaceae (Del Rio et al. 2017; Del Rio et al. 2019a). A larger number of plant taxa recognized from palynological studies indicate a tropical to subtropical paleoenvironment (Cavagnetto 2000). Biostratigraphic studies based on vertebrate and palynomorph assemblages as well as studies on amber indicate an age of early Eocene (early Ypresian) for the Le Quesnoy paleobotanical site (MP7, Nel et al. 1999; Cavagnetto 2000; De Franceschi and De Ploëg 2003). The relative preservation from the different sites is considered, based on the inferred taphonomic processes, in the discussion section.

Fossils, comparative material and methods

The material examined here consists of eleven endocarp specimens from Rivecourt and twenty-two fruits from Le Quesnoy. These specimens show three-dimensional lignitic preservation (Smith et al. 2014). Specimens were identified and studied using a stereomicroscope (Wild M3Z) and photographed with a Canon EOS 5D Mark III coupled to a Canon MP-E 65 macro lens. A polarizing filter was used to decrease the brightness of the lignite and associated minerals (e.g., quartz or pyrite). The photographs and figures were edited using the software Affinity Photo and Designer (v. 1.10). Measurements were taken using ImageJ Software (Rasband 2016). CT-scan via the AST-RX platform of the Museum national d'Histoire naturelle (Paris, France, MNHN) was used for the Rivecourt specimen Riv-PPB 17 to reconstruct a 3D model, and gain access to the internal organization, the reconstruction was made using the software Mimics Innovation Suite. The CT scan 3D

reconstruction and raw data are available in the DRYAD repository <https://doi.org/10.5061/dryad.2rbnzs7s8>. A specimen from Le Quesnoy, MNHN.F.50217 was embedded in polyester resin and cut using a wire saw of 0.3 mm width after three days of polymerization. The specimen was glued on a slide and polished in order to study the anatomy of the fruit. The slide was studied and imaged using the numerical microscope Hirox rh-2000.

The description follows the proposed terminology used in the most recent morphological and anatomical review of spondioid Anacardiaceae fruits (Herrera et al. 2018). The climatic terminology “subtropical” refers to the Ca (subtropical) in the paleoclimate classification made by Zhang et al. (2016), and reconstructed for the Paris Basin during the Paleocene and Eocene by Tanrattana et al. (2020). The new species described here have been registered in the Plant Fossil Names Registry (<http://www.plantfossilnames.org>, (Kvaček 2020). Specimens from Le Quesnoy are housed in the MNHN (under the numbers: MNHN. F. 50201.—50222.) while those from Rivecourt are temporarily housed in the MNHN for study and will be permanently stored at the Musée Antoine Vivenel in Compiègne (Oise, France) under the numbers: Riv. PPB. 17, Riv. PPB 199-207. Three taphonomic features have been analyzed for paleoecological purposes, i.e., presence, completeness, and degree of tearing of the mesocarp, epicarp, and endocarp.

Results

Family – Anacardiaceae R. Br.

Genus – Cyrtocarpa Kunth

Species – *Cyrtocarpa biapertura* C. Del Rio, E. Kara & D. De Franceschi sp. nov. (Figs. 2-4)

Diagnosis. Drupe, endocarp compressed laterally, single-loculed, two prominent apertures present on the ventral side, protruding into two lacunae surrounding the locule. Endocarp surface fibrous and reticulately ribbed. Distal pore with likely recessed bilabiate germination.

Holotype. Riv-PPB 17, specimen from Rivecourt site, Musée Antoine Vivenel in Compiègne (Oise, France). Registry for species name: PFN003018.

Paratypes. MNHN.F.50201.—50221., specimens from Le Quesnoy, Riv.PPB 199—207, specimens from Rivecourt site.

Age range. Late Paleocene (ca. 57-56 Ma, MP6B) to early Eocene (56-53 Ma, MP7)

Localities. Rivecourt and Le Quesnoy sites, Oise, France

Description. Thirty-two specimens. Drupe, oblong to obovoid (Figs. 3A-C, 3E-G-G), Drupe surface smooth. Endocarp compressed laterally, unilocular, elliptical in outline. Endocarp base truncate or rounded and slightly asymmetrical (Figs. 2E, F), with a circular basal attachment 0.6–0.8 mm of diameter (Fig. 3D). Endocarp length 5.4–12.8 mm (mean = 9.0 mm; n = 29), width 3.8–7.9 mm (mean = 5.3 mm; n = 29) and thickness 2.7–4.5 mm (mean = 3.5 mm; n = 29). Endocarp lateral surfaces fibrous, reticulately ribbed with 2–7 depressions (Fig. 2). Two prominent apertures present on the ventral side (Fig. 2B), forming two lacunae around the locule (Fig. 4). In transverse view, mesocarp fibrous, ca. 0.4 mm thick (MNHN.F.50217), and composed of broad parenchymatous cells (Fig. 4), the external endocarp wall ca. 0.6 mm thick (Fig. 4D), internally ca. 0.3 mm thick (Fig. 4DE), and is composed of small isodiametric cells ca. 20 µm of diameter (Fig. 4 DE). Locule elliptical in transverse section, 2.0–2.8 mm in breadth, 0.8–1.3 mm in height (Fig. 4D). The distal end of the endocarp displays a prominent apical pore, more or less curved (as seen in lateral view), elliptical in outline, and extending up to ~1/3 of the total length in the ventral view. Remnants

of the locular envelope preserved inside the apical pore suggest a recessed bilabiate germination (Figs. 2B, G, I).

Affinity. The fruits correspond to drupes mainly characterized by a fibrous mesocarp with ventral apertures and depressions and a prominent apical pore with likely recessed bilabiate germination. Some of these characters are distinctive of spondioid Anacardiaceae (Herrera et al. 2018). The fossils are unilocular with two lacunae and show an apical pore with likely recessed bilabiate germination (Fig. 4). Sixteen spondioid genera show unilocular fruits, but *Attilaea* E. Martinez & Ramos and *Cyrtocarpa* type 3 have two lacunae (seen as ventral apertures) surrounding the locule (Herrera et al. 2018). *Attilaea* endocarps, however, show less prominent apical pores and distal-ventral apertures. *Cyrtocarpa* endocarps of type 1 and 2 of Herrera et al. (2018) differ from the new fossil species by the presence of a simple plug-like operculum near the apex. Based on these comparisons and the abundant fossil material, *Cyrtocarpa biapertura* best resembles endocarps of extant *Cyrtocarpa* type 3 (Fig. 5). Particularly, the fossils appear similar to *Cyrtocarpa caatingae* J.D. Mitch. & Daly, the only living species of *Cyrtocarpa* type 3 (Fig. 5). In addition, the species *C. caatingae* has a striking resemblance to our fossil, both in the external morphology (Figs. 5A-E) and the internal morphology and anatomy (Figs. 5F-H). In the absence of molecular data from *C. caatingae*, it is difficult to decide whether *C. caatingae*, which has a particular fruit shape, corresponds to the genus *Cyrtocarpa*, or if it should be assigned to a new genus (Herrera et al. 2018). However, we consider the taxonomic identification to *Cyrtocarpa* which was made on the basis of several morphological characters including leaves and flowers, as valid (Mitchell and Daly 1991) and we assign the fossil specimens to the genus *Cyrtocarpa*, likely close to the species *C. caatingae* (see also discussion).

Some Cenozoic species are close to, or can be related to *Cyrtocarpa* but have been assigned to other genera i.e., *Lansea*, *Colombicarpum*, and *Odinia*. In Europe, *Lansea*

hessenensis Collinson, Manchester & Wilde closely resembles our fossil in size, shape, outer endocarp covered by fibres, enclosing depressions, and an apical pore (Collinson et al. 2012), but differs in having no prominent apertures on the ventral side. Within the same genus, another species – *Lannea jenkinsi* (Reid and Chandler) Chandler from the London Clay flora, is also similar to our fossils with the exception of the prominent ventral apertures (Reid and Chandler 1933; Chandler 1961). *L. jenkinsi* illustrated by Chandler (1961) has a stopper like plug, which is more similar to what is found in *Cyrtocarpa*, but this character is obviously different from what we observe in the specimens of Rivecourt and Le Quesnoy. From the London Clay flora as well as from Geiseltal, *L. europaea* (Reid and Chandler) Chandler has two locules and is small compared to the specimens described here (Reid and Chandler 1933; Chandler 1961; Mai 1976). *Colombicarpum biloculare* Reid, is a poorly studied fossil from the Pacific coast, Western Cordillera of Colombia, likely of Pliocene age (Reid 1933; Aubert De La Rüe 1933). The endocarp shows several characters shared with *Cyrtocarpa*, such as the probable occurrence of 1-2 locules and the presence of a large aperture closed by a plug (Reid 1933). However, that fossil differs from our specimens by lacking ventral apertures and two pores. “*Odinia*” *miocenica* Chesters, described from the Miocene of Rusinga Island, Kenya, shows several similarities with our specimens, including the presence of an apical curved pore, but ventral apertures are missing. Finally, a specimen of Anacardiaceae from the late Eocene John Day Formation, USA, may have affinities with our specimens, but the apical part is broken making it difficult to compare (Manchester and McIntosh 2007). Thus, the specimens from Rivecourt and Le Quesnoy belong to a new species, namely, *Cyrtocarpa biapertura* C. Del Rio, E. Kara & D. De Franceschi sp. nov., which appears closely related to the modern species *C. caatingae* (*Cyrtocarpa* type 3).

Genus –?

Species – “*Lannea*” *europaea* (Reid and Chandler) Chandler (Fig. 6)

Specimen examined. MNHN.F.50222. housed in the MNHN collection.

Age range. Early Eocene (56-53 Ma, MP7)

Locality. Le Quesnoy; Oise, France.

Description. One specimen. Endocarp sub-ovoid in lateral outline, bilateral, length 4.5 mm, width 3.3 mm, height 3.1 mm. Two elliptical apical openings are visible at the distal end, one preserving a simple plug-like stopper (Figs. 6A, D), 1.6 mm in length, 0.8 mm in width, externally separated by a prominent keel. Endocarp surface fibrous (Fig. 6) with one lateral elongate aperture on each lateral face (Fig. 6C), length 1 mm, width 0.2 mm. Endocarp wall thickness ca. 0.3 mm. Basal attachment apparently circular. Seeds absent.

Affinity. This specimen is characterized by a small sub-ovoid fibrous endocarp with two germinal pores, each closed by a simple operculum. These characters point to spondioid Anacardiaceae (Herrera et al. 2018). The simple operculum mechanism is present in 10 genera. Of those, only *Poupartia* and *Sclerocarya* have two locules but neither of them shows lateral elongate apertures, as found in our specimen. The delicacy of the endocarp in the single specimen make it unsuitable for the preparation needed to study the anatomy. Given the available characters, we cannot assign this specimen at generic level. This specimen may represent a new fossil genus, but more specimens are needed to confirm this hypothesis.

This specimen is very similar to *Lannea europaea* from the middle Eocene of Geiseltal (Germany) and the lower Eocene from the London Clay Formation, UK (Reid and Chandler 1933; Chandler 1961; Mai 1976). This species has been assigned to *Lannea*, but this genus contains only one locule (Herrera et al. 2018) making this generic identification doubtful. Our specimen is smaller than the previous records, especially those from the London Clay [6.6 mm long from Sheppey (Reid and Chandler 1933); 6 mm long from Bognor (Chandler

1961)]. Such size differences could be explained by natural variation (especially as there is only one specimen from Le Quesnoy and two from each of the London Clay sites). Comparisons between Menispermaceae from Le Quesnoy and the London Clay revealed a smaller fruit size in Le Quesnoy which may reflect a tendency of fruit size to increase over time, as Le Quesnoy is older than London Clay (Jacques and De Franceschi 2005). Alternatively, the size differences could be due to preservation differences as the London Clay specimens are permineralized by iron pyrites and the Le Quesnoy specimens are preserved in lignite which tends to reduce in size during the fossilization process. This specimen is considered to be related to or included in the fossil-species “*Lannea*” *europaea* (Reid and Chandler) Chandler, regardless of the generic name.

Discussion

*Taphonomy and paleoecology of *Cyrtocarpa biapertura* sp. nov.*

The taphonomic analysis of the fruits from the two fossil plant localities from the Paris Basin pre-and post the PETM allows for evaluating the autochthony, parautochthony, or allochthony of these fruits.

The fruits of *Cyrtocarpa biapertura* sp. nov. from Le Quesnoy were collected from two plant beds i.e., QNY1 and QNY2. The fruits from the QNY1 have the best preservation (Table 1) and preserve whole endocarps (Figs. 3A-G). Eighty percent of the specimens also display the mesocarp, while ten specimens have a preserved epicarp and mesocarp (Table 1). Among these specimens, more than half have preserved the epicarp. Different features are observed at the QNY2 where the specimens are more degraded than at QNY1. 11 specimens from QNY2 show the epicarp and mesocarp remains, whereas two specimens are partially degraded and only 18% have a complete preservation (Figs. 3H-K). A higher degree of

degradation is observed in the Rivecourt fossil plant locality where 11 specimens have lost their epicarp and mesocarp (Fig. 2), four specimens are broken and one specimen is torn.

Only a few empirical taphonomic studies about fruit and seed taphonomy have been conducted, and most of them focus on the buoyancy of these generative plant organs (Gee 2005; Vassio and Martinetto 2012). Much more is known about the biostratinomic processes that affect other plant remains and this knowledge can be extrapolated to carpology (Spicer 1981; Ferguson 1985; Gastaldo 1988; Ferguson 1995). Usually, soft tissues such as epicarp are rarely preserved. The fact that most of the specimens from QNY1 still preserve the epicarp suggests that the fruits fell directly to the river channel where they were buried. Probably the fruits from QNY2 were transported a short distance before their burial since the fruits are slightly damaged and only the mesocarp is preserved. In both cases, the fruits of *Cyrtocarpa biapertura* indicate parautochthony. In contrast, the specimens from Rivecourt represent a parautochthonous-allochthonous assemblage because the specimens show significant degradation and a few of them are broken, indicating that the fruits fell to the river and were subsequently transported by fluvial flows with the suspended sediment for a prolonged period before deposition. That is in accordance with other observations regarding the sedimentary context and deposits at each site (Nel et al. 1999, Smith et al. 2014). The taphonomic features of the three studied plant beds indicate that *Cyrtocarpa biapertura* sp. nov. grew close to the river banks, likely as an element of the riparian community.

Plant paleodiversity across the PETM in the Paris Basin

The presence of *Cyrtocarpa biapertura* in Rivecourt at the end of the Paleocene and in Le Quesnoy at the beginning of the earliest Eocene shows that there were no local disturbances for this species before and after the PETM. This continuity of flora at the local

and species level has also been shown for the family Icacinaceae with at least three species of *Iodes* in common between the Thanetian and Ypresian in the Paris Basin (Del Rio and De Franceschi 2020). It is possible that the floras pre and post PETM were relatively similar but that the flora during the PETM was different in response to the short-living and rapid warming, as shown in USA (Wing et al. 2005). However, studies recording the flora at the PETM event in France (Garel et al. 2014), England (Collinson et al. 2009) and Austria (Hofmann et al. 2011) indicate no major turnover in the paleovegetation even though the composition changes.

Although different flora, the preliminary studies of the floras of Rivecourt and Le Quesnoy show relatively similar subtropical floras corresponding to subtropical environments (Nel et al. 1999; Smith et al. 2014). The pollen assemblage in the Paris Basin suggests a similar situation indicating persistence of the subtropical floras during the early Eocene (Gruas-Cavagnetto 1987; Cavagnetto 2000).

The pollen analysis of Le Quesnoy also documents a greater diversification of the flora for this Eocene site (Koeniguer 1987; Cavagnetto 2000). This diversification has been suggested for the fruits of Icacinaceae with new morphotypes appearing during the early Eocene and could be added to here by the appearance of another fruit morphotype of Anacardiaceae in Le Quesnoy as well as new occurrences in the pollen of this site (Cavagnetto 2000; Del Rio and De Franceschi 2020). The relative stability of the flora beyond the PETM contrasts with the drastic shift in vertebrate composition possibly due to migrations event from Asia (Nel et al. 1999; Smith et al. 2014; Hooker 2015; Solé et al. 2018).

The new occurrence of the genus *Cyrtocarpa* in the Paris Basin during the Paleogene is confirmed by our study and adds to the generic list of Anacardiaceae in the basin i.e., *Bouea*, *Rhus* and *Lannea* based on the pollen assemblage (Gruas-Cavagnetto 1987; Cavagnetto 2000). We also add a new morphotype for the Paris Basin, tentatively named “*Lannea*” *europaea* here, that probably corresponds to an undescribed fossil genus that occurred during the Eocene.

Cyrtocarpa biapertura sp. nov. has no direct equivalents elsewhere in early Paleogene floras of the Northern Hemisphere. However, it shows certain resemblance to a specimen from the London Clay *Lannea jenkinsi*, but a detailed study of the specimens is needed to confirm if they correspond to the same genus. *Cyrtocarpa biapertura* sp. nov. is similar to the modern species *Cyrtocarpa caatingae*, which is endemic to South America. It appears that during the Paleocene *Cyrtocarpa* was distributed in Europe which might be where the genus originated, even though it is later extirpated from this area. This biogeographical disjunction between Paleogene European flora and neotropical modern tropical flora has been little documented (Manchester et al. 2007). Examples of similar pattern include *Tetrapterys* Cav. (Hably and Manchester 2000) and *Dodonaeites descaisnei* Saporta, possibly a representative of *Fissicalyx* Benth. (Manchester and O’Leary 2010). Among the Anacardiaceae the fossil cashew nuts (*Anacardium germanicum* Manchester, Wilde & Collinson) from the middle Eocene Messel formation (Germany), show a strikingly similar phylogeographic history (Manchester et al. 2007). A common hypothesis to explain this pattern would be a shared flora between Europe and North America during the early-middle Eocene linked via the North Atlantic land bridge, followed by a regression of tropical flora during the late Eocene-Oligocene cooling event (Tiffney and Manchester 2001). The fossil endocarp of Anacardiaceae from the late Eocene John Day Formation, USA, could make this biogeographic link between the two areas, but the specimen is too fragmented to confirm this

hypothesis (Manchester and McIntosh 2007). As for *Anacardium*, *Cyrtocarpa* is a sister group of an African clade and the disjunction between these two clades is dated to the late Eocene (Weeks et al. 2014). With the discovery of *Cyrtocarpa biapertura* sp. nov. in the Paleocene and Eocene of France, this disjunction can be explained by two or more subsequent dispersals from Europe to Africa and South America. *Colombicarpum biloculare* from the Pliocene of Colombia could correspond to the only known occurrence in the South American area and may attest to the presence of the genus in the Neotropics during the Neogene, however, this specimen needs revision. At the present day, *Cyrtocarpa caatingae* grows in the seasonally dry tropical forest of Brazilian Caatinga (Mitchell and Daly 1991). This particular area is affected by recent aridification, and most species originate from recent and local ecological adaptations (Fernandes et al. 2022). *Cyrtocarpa caatingae* is the only one to possess all the characters found in our fossil, and has been considered separately from other *Cyrtocarpa* in recent fruit review (Herrera et al. 2018). It is possible that this species is the last representation of a larger, more diverse group that was living in a tropical environment during the Paleogene, with the Caatinga dry tropical forest acting as a recent ecological refugium for its last member.

During the early Eocene, the presence of *Lannea europaea* in northern France, Germany, and southern UK shows that these areas may have shared a similar flora. A study on global fossil vegetation in Europe defined several bioprovinces during the early and middle Eocene (Kvaček 2010). The three sites that contain *Lannea europaea* appear to belong to the same biogeographical range. This flora could correspond to what Kvaček (2010) called “paratropical forests” that dominated western Europe during the Early and middle Eocene, and declined from the end of Eocene onwards due to climate cooling (Kvaček 2010; Tanrattana 2020).

Conclusions

The study of the Anacardiaceae fruits from two fossil plant sites in the Paris Basin on both sides of the Paleocene-Eocene boundary, i.e., Paleocene of Rivecourt and the Eocene of Le Quesnoy, Oise, revealed a new species, *Cyrtocarpa biapertura*, and the new occurrence of “*Lannea*” *europaea* only in Le Quesnoy. The taphonomic features of the fruits of *Cyrtocarpa biapertura*, combined with the sedimentological setting of the fossil sites, indicate that they were transported by fluvial flows and that *Cyrtocarpa biapertura* grew close to the riverbanks representing a riparian element.

Cyrtocarpa biapertura occurs in both Paleocene and Eocene floras, which remained in the same subtropical climatic type. Combined with pollen data the record indicates an enrichment of the anacardiaceous floras during the Eocene. The presence of *Cyrtocarpa* in Europe documents a rarely reported disjunction between the European Paleogene and the current neotropics. The relative species is currently confined to a tropical dry forest in Brazil (Caatinga) – an ecological zone that could act as a refugium for this group.

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Table 1.

Taphonomic features of *Cyrtocarpa biapertura* C. Del Rio, E. Kara & D. De Franceschi

Specimen number	Presence Mesocarp	Presence Epicarp	Endocarp completeness
QNY1			
MNHN.F.50211	++	++	100%
MNHN.F.50212	++	+	100%
MNHN.F.50213	-	-	100%
MNHN.F.50214	++	++	100%
MNHN.F.50215	++	++	100%
MNHN.F.50216	+	+	100%
MNHN.F.50218	++	+	100%
MNHN.F.50219	++	++	100%
MNHN.F.50220	++	++	100%
MNHN.F.50221	++	++	100%
QNY1 + & ++	90%	90%	100%
QNY1 ++	80%	60%	100%
QNY2			
MNHN.F.50201	+	-	100%
MNHN.F.50202	+	-	100%
MNHN.F.50203	+	-	100%
MNHN.F.50204	+	-	100%
MNHN.F.50205	+	-	100%
MNHN.F.50206	+	-	100%
MNHN.F.50207	+	+	100%
MNHN.F.50208	+	+	100%

MNHN.F.50209	++	++	100%
MNHN.F.50210	-	-	50%
MNHN.F.50217	++	++	75%
QNY2 + & ++	91%	36%	81%
QNY2 ++	18%	18%	81%

Rivecourt

Riv.PPB 198	-	-	100%
Riv.PPB 199	-	-	25%
Riv.PPB 200	-	-	50%
Riv.PPB 201	-	-	100%
Riv.PPB 202	-	-	50%
Riv.PPB 17	-	-	100%
Riv.PPB 203	-	-	100%
Riv.PPB 204	-	-	100%
Riv.PPB 205	-	-	100%
Riv.PPB 206	-	-	75%
Riv.PPB 207	-	-	100%
Riv + & ++	0%	0%	63%

Note: - (not present), + (present less than 50% covering), ++ (present more than 50% covering)

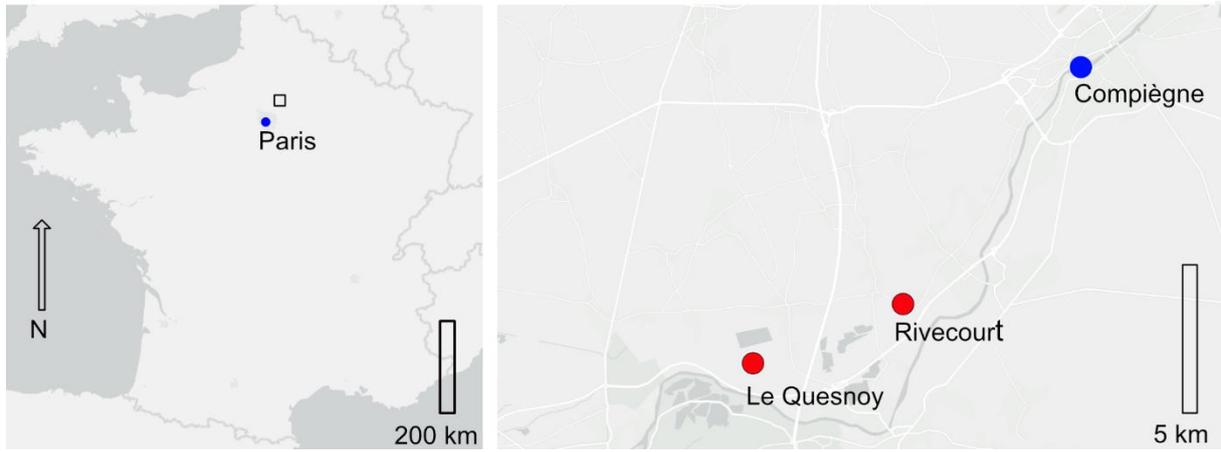


Figure 1 Map of the former outcrop area and location of the studied sites.

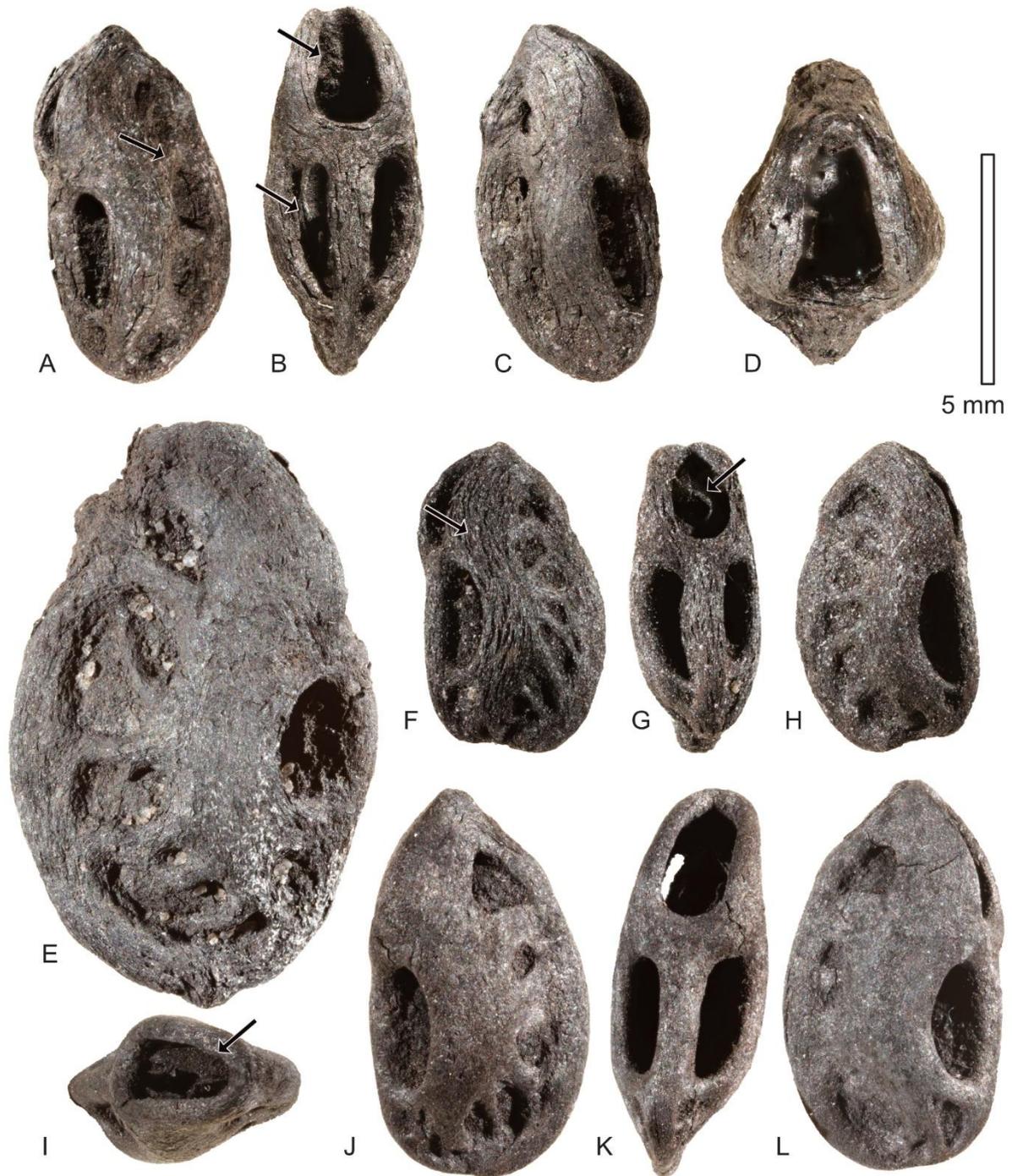


Figure 2 Endocarp of *Cyrtocarpa biapertura* C. Del Rio, E. Kara & D. De Franceschi *sp. nov.* from Rivecourt. A. Lateral view of Riv. PPB 17 (Holotype) arrow = lateral ribs forming a reticulation, B. Ventral view of A, upper arrow = curved germination pore, lower arrow = ventral apertures, C. Second lateral view, D. Apical view of the germination pore, E. Lateral view of Riv. PPB 198, F. Lateral view of Riv. PPB 201, arrow = fibrous surface, G. Ventral view of F, arrow = remnants of the locular envelope preserved inside the apical pore, H. second lateral view, I. Distal pore with likely recessed bilabiate germination, J. Lateral view of Riv. PPB 207, K. Ventral view of J, L. Second lateral view. Scale bar at top right applies to all images.

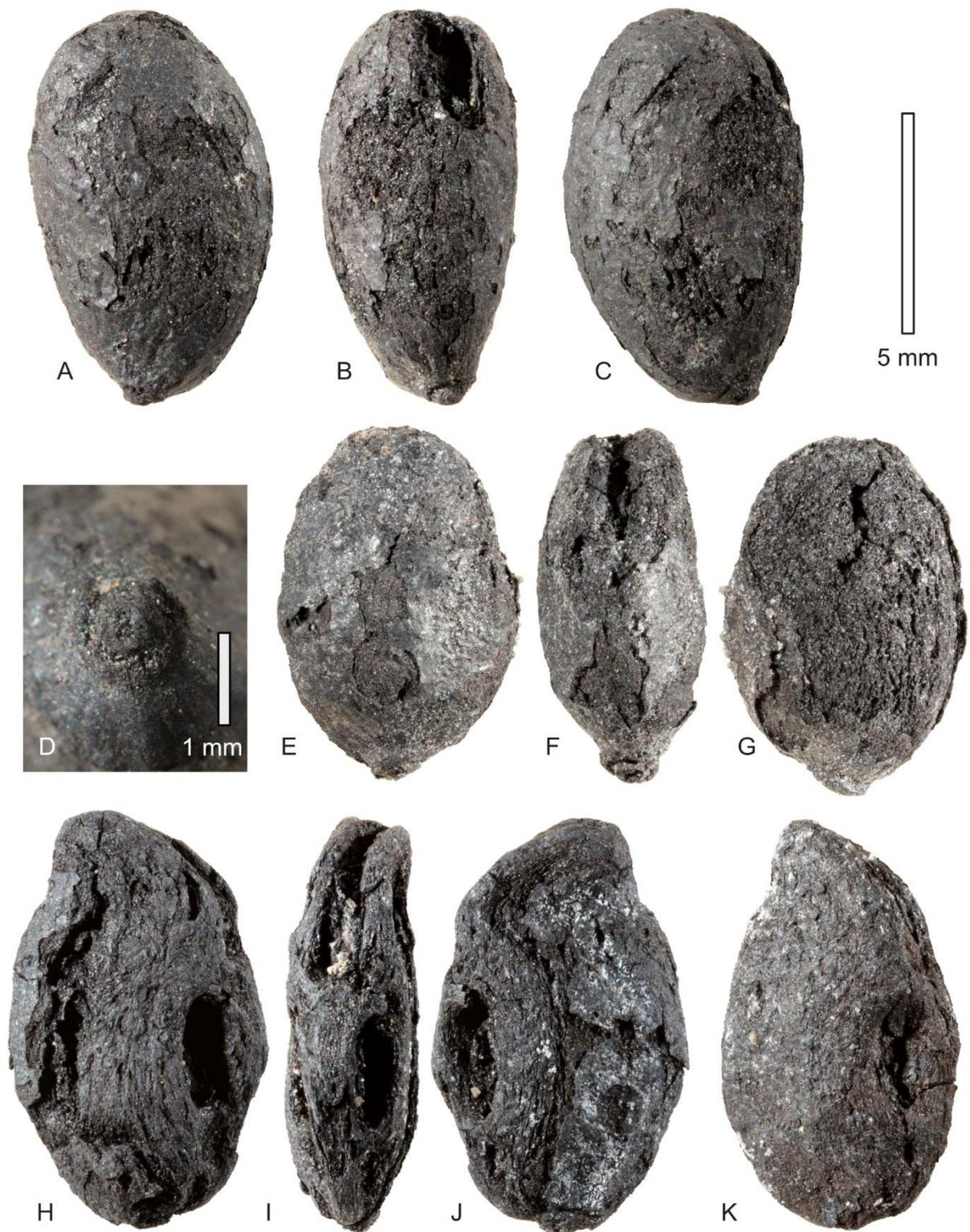


Figure 3 Fruits of *Cyrtocarpa biapertura* C. Del Rio, E. Kara & D. De Franceschi sp. nov. from Le Quesnoy. A-G. Specimens from QNY1. A. Lateral view of MNHN.F.50220., B. Ventral view of A, C. second lateral view, D. same specimen, circular basal attachment, E. Lateral view of MNHN.F.50221., F. Ventral view of E, G. Second lateral view. H-K. Specimens from QNY2. H. Lateral view of MNHN.F.50203., I. Ventral view of H, J. Second

lateral view, K. Lateral view of MNHN.F.50201. Scale bar at top right applies to all images except D.

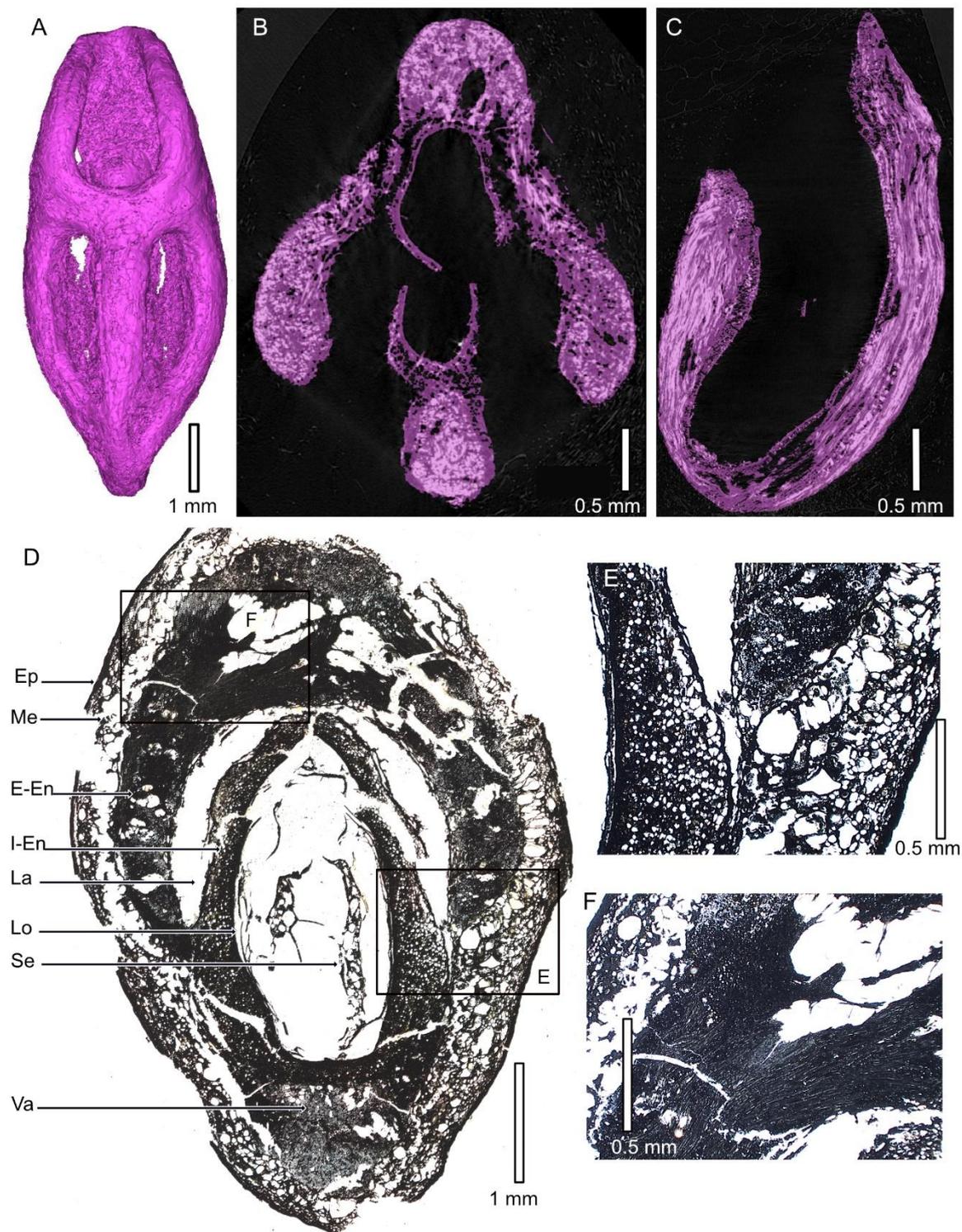


Figure 4 Internal information from *Cyrtocarpa biapertura* C. Del Rio, E. Kara & D. De Franceschi sp. nov. A. 3D reconstruction of the Holotype using CT scan (Riv. PPB17), B. Transverse section of A., C. Sagittal section of A., D. Transverse section of the fruit of MNHN.F.50217. Ep = Epicarp, Me = Mesocarp, E-En = External endocarp, I-En = Internal endocarp, La= Lacuna, Lo = Locule, Se = seed, Va= vascular trace, E., Enlargement of part of

of D showing the endocarp mesocarp and part of the lacuna, F. Enlargement of part of D showing the fibrous external endocarp and mesocarp.

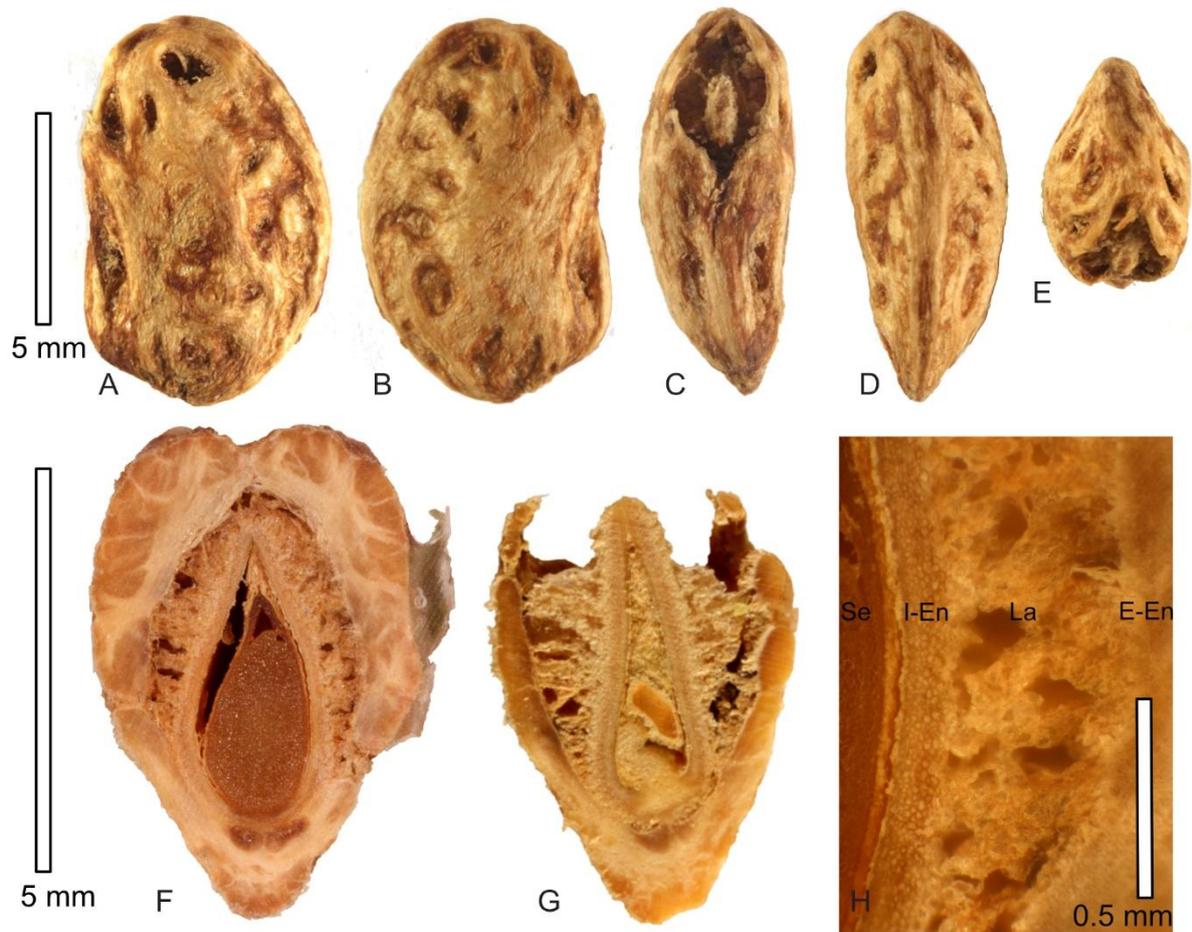


Figure 5 Modern specimen of endocarp of *Cyrtocarpa caatingae* J.D. Mitch. & Daly (voucher = A. Carvalho et al. 3762, NY herbarium). A-B. Lateral views showing the reticulated ribbed surface, C. Ventral view showing the ventral concavities and the germination pore, D. Dorsal view, E. Apical view, F. Fruit cut transversally showing central locule surrounded by two lacunae filled by parenchyma. G. Fruit cut transversally at the level of the ventral apertures. H. Anatomical details of F, Se = Seed, I-En = internal Endocarp, La = Lacuna, E-En = External endocarp. Upper left scale applies to A-E, lower left scale applies to F-G.

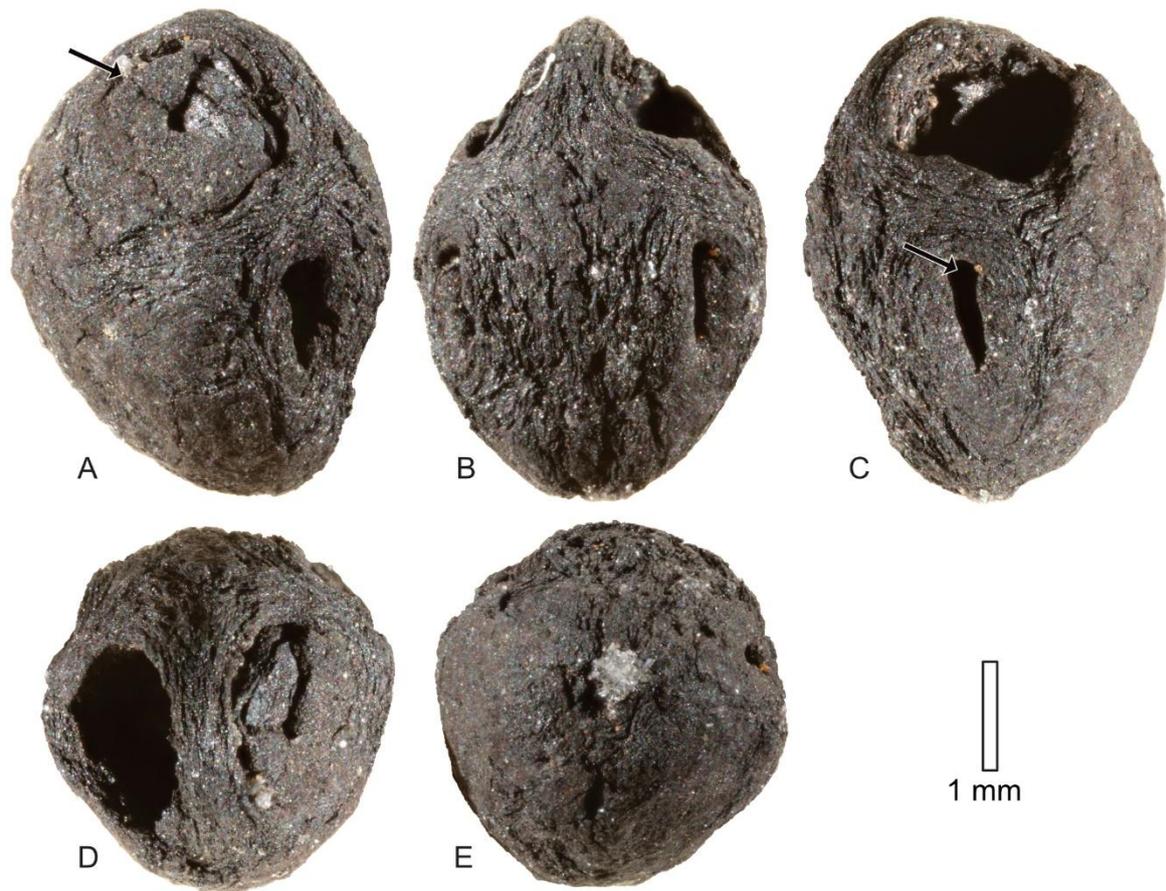


Figure 6 Endocarp of cf. *Lannea europaea* (Reid and Chandler) Chandler (MNHN.F. 50222), A. Lateral view, arrow = simple operculum, B. Ventral view, C. Second lateral view, arrow = elongate aperture, D. Apical view, E. Basal view. Scale bar applies to all images.