Exceptional preservation of tiny embryos documents seed dormancy in early angiosperms

ELSE MARIE FRIIS^{1,2}, PETER R. CRANE², KAJ RAUNSGAARD PEDERSEN^{2,3},
MARCO STAMPANONI^{4,5} & FEDERICA MARONE⁴

¹Department of Palaeobiology, Swedish Museum of Natural History, SE-104 05 Stockholm, Sweden. ²Yale School of Forestry and Environmental Studies 195 Prospect Street, New Haven, CT 06511, USA. ³Department of Earth Science, University of Aarhus, DK-8000 Aarhus, Denmark. ⁴Swiss Light Source, Paul Scherrer Institute, CH-5232 Villigen PSI, Switzerland. ⁵Institute for Biomedical Engineering, ETZ F 85, Swiss Federal Institute of Technology Zurich, Gloriastrasse 35, 8092 Zurich, Switzerland.

The rapid diversification of angiosperms through the Early Cretaceous, between about 130 and 100 million years ago initiated fundamental changes in the composition of terrestrial vegetation and is increasingly well-understood based on a wealth of palaeobotanical discoveries over the last four decades^{1–5}, and their integration with improved knowledge of living angiosperms^{3,6}. Prevailing hypotheses, based on evidence from both living and fossil plants, emphasize that the earliest angiosperms were plants of small stature^{7–12} with rapid life cycles^{7,8,12,13} that exploited disturbed habitats^{3,9,11,13,14} in open^{3,9,11,13,14}, or perhaps understory conditions^{15,16}. However, direct palaeontological data relevant to understanding the seed biology and germination ecology of Early Cretaceous angiosperms are sparse. Here we report the discovery of embryos and their associated nutrient storage tissues in exceptionally well-preserved angiosperm seeds from the Early Cretaceous. Synchrotron radiation X-ray tomographic microscopy (SRXTM) of the fossil embryos from many taxa reveals that all were tiny at the time of dispersal. These results support hypotheses based on extant plants that tiny embryos and seed dormancy are basic for angiosperms as a whole^{17,18}. The minute size of the fossil embryos, and the modest nutrient storage tissues dictated by the overall small seed size, is also consistent with the interpretation that many early angiosperms were opportunistic, early successional colonizers of disturbance-prone habitats^{2,15,16}.

As part of a broader survey of Early Cretaceous angiosperm reproductive structures using SRXTM¹⁹ we analysed the internal structure of mature seeds from about 75 different angiosperm taxa recovered from rich assemblages of angiosperm flowers, fruits and seeds in 11 mesofossil floras from eastern North America and Portugal that range in age from

Barremian-Aptian to early or middle Albian, ca. 125-110 million years ago³ (see Methods). SRXTM revealed exquisite preservation of three-dimensional cellular structure, often including traces of nuclei and subcellular nutritive bodies. In mature fossil fruits and seeds, the seed coat is generally well-developed and cellular preservation is usually excellent. Softer tissues such as embryo and nutrient storage tissues may be degraded or distorted, but of the roughly 250 Early Cretaceous mature seeds examined about half show cellular structure inside the seed coat (Supplementary Table 1). Often only the nutrient storage tissue is preserved, with an empty space at the micropylar end of the seed indicating the maximum size, and former position of the embryo and its immediately surrounding cells. In about 50 seeds complete or partially preserved embryos occur along with remains of the surrounding nutrient storage tissue. Minimal shrinkage of the seeds during preservation is indicated by the typically straight cell walls and the fact that the nutrient storage tissue often fills out the whole seed volume inside the seed coat.

All Early Cretaceous angiosperm seeds studied here are small (< 2.5 mm in maximum dimension²⁰), and in all the fossil seeds in which it can be observed the embryo is tiny. Some embryos have two small cotyledon primordia; in others the cotyledons are not clearly differentiated. None have fully developed cotyledons or a radicle. All were preserved during a dormant phase in their development. Further growth of the embryo inside the seed would be required prior to germination.

Here we illustrate six different fossils that are representative of the diversity of embryo structure seen among all the specimens studied (Figs 1-3). Three of these fossils can be assigned to extinct genera (*Anacostia*, *Appomattoxia*, *Canrightiopsis*) that have already been described and assessed systematically^{3,21}. The three other taxa (Taxon 1, 2 and 3) remain to be described and formally named. Taxon 1 and Taxon 3 are isolated exotestal seeds. Taxon 2 is a small, thin-walled seed enclosed in a one-seeded fruiting unit.

In all six kinds of seeds, the tiny embryo is surrounded by nutrient storage tissue that occupies the bulk of the space inside the seed coat (Figs 2a and 3), but the size and form of the embryo varies. The cotyledons are not clearly differentiated in Taxon 3, and in *Canrightiopsis* and Taxon 1 they are rudimentary. In the other three taxa cotyledon primordia are larger. *Canrightiopsis* has the smallest embryo (ca. 120 μm long) and *Appomattoxia* the largest (ca. 296 μm long). The embryos of *Anacostia*, Taxon 1, and Taxon 2 are intermediate in size (*Anacostia* ca. 240 μm long; Taxon 1 ca. 250 μm long; Taxon 2 ca. 240 μm long). The embryo in Taxon 3 is distinct in being wider than long (ca. 250 μm wide; 160 μm long). In all

seeds examined the embryo size relative to the seed size (E:S; 2D area, see Methods) is very small, ranging from 0.015 in Taxon 1 to 0.034 in *Anacostia*.

Cellular preservation of the embryos in all six taxa is excellent. Cells are small, rectangular, often elongated parallel to the longitudinal axis and vary in length from 10-20 μm . In each cell there is typically a central body about 4-6 μm in diameter (Fig. 2b) that is similar in size and position to the nuclei seen in the embryo cells of extant early diverging angiosperm lineages. The nutrient storage tissue consists of cells that range from about 40 to 70 μm in diameter and have thin, usually straight, walls. Cells in the nutritive storage tissue often contain small rounded structures (Figs 2a, c and 3) that are most likely remains of the protein and lipid bodies that occur in the equivalent seed tissues of many extant angiosperms.

The nutrient storage tissue immediately around the embryo is often partly or fully decomposed, but in seeds with particularly good preservation, these cells are usually distinguished by their smaller size, thinner walls and lack of nutritive bodies. Very similar cellular differentiation occurs in the endosperm of modern *Sarcandra* (Fig. 4a, c) and other extant early diverging angiosperm lineages²²⁻²⁶. As in extant taxa the contents of the cells immediately around the embryo were apparently consumed very early in the development of the young plant.

Taxon 1 (Fig. 1a, b), Taxon 3 (Fig. 3) and *Canrightiopsis* (Fig. 1c-e) all have rudimentary or poorly differentiated embryos, as occur in early diverging lineages of living angiosperms (Amborellaceae, Austrobaileyaceae, Schisandraceae, Nymphaeaceae and Chloranthaceae)²²⁻²⁶, as well as in some eumagnoliids¹⁸. The distinctive exotestal seeds of Taxon 1 and Taxon 3 are also indicative of a relationship to Schisandraceae or Nymphaeaceae, and the broad embryo of Taxon 3 is very similar to the embryos in seeds of extant Nymphaeaceae²⁶.

Canrightiopsis is phylogenetically close to the common ancestor of extant *Ascarina*, *Sarcandra* and *Chloranthus* (Chloranthaceae)²¹. Comparison of the almost spherical *Canrightiopsis* embryo with that of extant *Sarcandra* shows strong similarities and the same cellular features. However, the seeds and embryos of *Canrightiopsis* are much smaller. In *Canrightiopsis* the length of the embryo is ca. 120 μm (Fig. 1d, e) whereas in the specimen of extant *Sarcandra* illustrated here it is ca. 470 μm (Fig. 4b). Endosperm and perisperm may be difficult to distinguish in mature seeds, but in this case comparison with extant *Sarcandra* strongly suggests that the nutrient storage tissue preserved in *Canrightiopsis* is endosperm.

Anacostia (Fig. 1f, g) and *Appomattoxia* (Fig. 1h, i) are particularly similar in embryo shape and size. Along with Taxon 2 (Fig. 1j, k) they have minute embryos with more distinct

cotyledons (“underdeveloped linear”²⁷). Embryos of this kind are characteristic of certain lineages among Austrobaileyales^{23, 24}, eumagnoliids and early diverging eudicots (e.g., Ranunculales, Trochodendrales)¹⁸. *Anacostia* and *Appomattoxia* both have abundant monoaperturate pollen on the stigmatic surfaces of their fruits³ making a relationship to eudicots unlikely. Pollen grains of *Anacostia* suggest a relationship to monocots, while other features indicate a position close to Schisandraceae^{3,6}. *Appomattoxia* has features suggesting a relationship to extant Piperales²⁸. In both cases, the minute dicotyledonous embryos are unlike those of the proposed modern relatives, adding further uncertainty to understanding the relationships of these extinct taxa.

Information on the embryos and provisioning of angiosperm seeds from the Early Cretaceous provides new data for assessing their relationships, but also contributes significantly to knowledge of the biology and ecology of early angiosperms. Seed size, based on the new material examined here, and previous work, is invariably small^{20,29}, as expected from the small stature documented for some Early Cretaceous angiosperms^{5,9,12} and consistent with the strong relationship between small seed size and small stature seen among living plants³⁰. However, in addition, none of the Early Cretaceous seeds studied here have fully developed embryos at the time of dispersal. In all cases the embryos are minute and the embryo to seed ratio (E:S) is much smaller than occurs in most extant angiosperms. It is also smaller than the E:S ratio hypothesized for the ancestral angiosperm embryo (E:S of 0.16¹⁷) by an order of magnitude, emphasizing the additional diversity of extinct taxa close to the base of the angiosperm phylogenetic tree, and the limitations of inferring ancestral characteristics solely by extrapolation from the features of extant taxa.

Seed dormancy associated with the minute fossil embryos ensured that the seeds of early angiosperms could survive until conditions for germination and seedling establishment were favourable. However, the tiny embryo size and modest nutrient reserves were also an intrinsic developmental constraint on the rapidity with which early angiosperms could germinate in response to short-lived moisture availability. Early angiosperms would have been unable to match the very rapid germination of many angiosperms that evolved later and ultimately proved even more effective in exploiting ephemeral ecological opportunities.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Text to figures:

Figure 1 Minute embryos with two cotyledon primordia in Early Cretaceous angiosperms. SRXTM reconstructions of embryos embedded in seeds (**a, c, f, h, j**) and

isolated from seeds (**b, d, e, g, i, k**). **a, b**, Exotestal seed and embryo (Taxon 1; S170235, Famalicão). **c-e**, *Canrightiopsis* with seed and embryo (S174005, Famalicão). **f, g**, *Anacostia* fruit with seed and embryo (PP54021, Kenilworth). **h, i**, *Appomattoxia* with seed and embryo (PP54064, Puddledock). **j, k**, Fruit with seed and embryo (Taxon 2; PP53991, Kenilworth). Scale bars, 500 μm (**a, c, f, h, j**), 100 μm (**b, d, e, g, i, k**).

Figure 2 Cellular preservation of embryos and associated nutrient storage tissue in Early Cretaceous angiosperm seeds. Longitudinal orthoslices through SRXTM volumes. **a**, Apical part of fruit in figure 1j (Taxon 2) showing embryo and surrounding storage tissue with remains of nutritive bodies (arrow). **b**, Detail of embryo in 2a showing the cotyledon primordia (asterisks) and embryo cells with a central body that may represent remains of the nucleus; thin-walled storage tissue is preserved between the cotyledons. **c**, Details of nutrient storage tissue from an Early Cretaceous exotestal seed (PP53973, Puddledock) with remains of nutritive bodies (arrow). Scale bars, 100 μm .

Figure 3 Minute and broad embryo and associated nutrient storage tissue in an Early Cretaceous seed (Taxon 3). Longitudinal 2D SRXTM reconstructions of micropylar region of exotesal seed (S174472, Famalicão 25) showing the broad shape and poorly differentiated embryo (arrow). **a**, Cut volume rendering (between orthoslices 1380-1420) coloured to emphasize the shape and position of embryo. **b**, Single orthoslice (orthoslice 1420) in same position as in 3a. Scale bars, 100 μm .

Figure 4 Embryo and nutrient storage tissue of extant *Sarcandra* (Chloranthaceae). 2D (**a, c**) and 3D (**b**) SRXTM reconstructions. **a**, Longitudinal orthoslice through seed showing rudimentary embryo with two cotyledon primordia (asterisks) embedded in copious nutrient storage tissue (endosperm); cells in the vicinity of the embryo lack the nutritive bodies that are abundant in other endosperm cells. **b**, Surface rendering of embryo showing the two small cotyledon primordia. **c**, Detail of endosperm with nutritive bodies (protein and lipids). Scale bars, 100 μm .

Methods

The fossil seeds studied here were isolated from 11 mesofossil floras preserved in soft unconsolidated sediments from eastern North America (Kenilworth, Maryland; Dutch Gap and Puddledock, Virginia) and Portugal (Arazede, Buarcos, Catefica, Famalicão, Juncal-Chicalhão, Torres Vedras, Vale de Água, Vila Verde) that range from Barremian-Aptian to early or middle Albian in age^{3,21,28,31}. Mesofossils preserved in these floras are often exquisitely preserved in three dimensions as charcoalified or lignitic specimens and include complete and fragmentary flowers, as well as abundant fruits and seeds. Fossils were isolated from the sediments by sieving in water, remaining mineral matrix was removed using HF and HCl, and the fossils were then rinsed in water and air-dried. A large number of specimens of mature seeds, from the full range of taxa preserved, were analysed using synchrotron radiation X-ray tomographic microscopy (SRXTM). Six fossils representative of the material examined were selected to illustrate common features of embryos and nutritive storage tissues. Specimens examined with SRXTM were mounted on brass-stubs with nail polish and analysed at the TOMCAT beamline³² at the Swiss Light Source, Villigen, Switzerland. For optimized contrast, measurements were made at 10 keV. For each data set, 1501 projections equiangularly spaced over 180 degrees were acquired. The transmitted and refracted X-ray radiation was converted to visible light by a thin scintillating screen (20 µm thick LAG:Ce or 5.9 µm thick LSO:Tb depending on the spatial resolution required), magnified by ×10 and ×20 objective lenses for overviews, and ×40 objective lens for details, and digitized by a CCD (PCO.2000) or a sCMOS (PCO.edge) camera. The sample-detector distance was on the order of few mm. The raw projections were dark and flat-field corrected and subsequently reconstructed using an efficient algorithm based on the Fourier method with regridding³³. The resulting volumetric data have voxel sizes of 0.65-0.74, 0.325 and 0.1625 µm, for measurements done with the x10, x20 and x40 objectives respectively.

To boost contrast in the detailed scan of specimen PP53991 (Fig. 2b and 2c), prior to tomographic reconstruction, the corrected projections were phase retrieved according to the single distance algorithm by Paganin et al.³⁴.

Embryo tissue was identified in the reconstructed SRXTM orthoslices and Avizo software was used to manually label individual slices to generate the three-dimensional embryo shapes. To illustrate the relationship of seed and embryo volume, the embryo surface was coloured yellow and the three-dimensional shape of the seeds/fruits shown by transparent voltex rendering in green (Fig. 1). The 2D area of embryo and seed inside the integuments

was measured in pixels on longitudinal sections through the middle of the seeds and embryos using the free software Fiji³⁵ resulting in an embryo to seed ratio (E:S) comparable to that published by others¹⁷.

A list of the mature seeds analysed here is available in Supplementary Table 1. The fossil material is stored in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm (S) and the Field Museum, Chicago (PP). Raw data from the SRXTM are stored at the Swedish Museum of Natural History.

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Supplementary Table 1 | List of Early Cretaceous fruits with mature seeds and isolated, mature seeds studied using SRXTM. Currently undescribed seeds are here grouped into informal taxa numbered Taxon 1, Taxon 2 etc.

List of Early Cretaceous fruits with mature seeds and isolated, mature seeds studied using SRXTM. Currently undescribed seeds are here grouped into informal taxa numbered Taxon 1, Taxon 2 etc.

Specimen no	Sample no	Taxon	Unit studied	Seed coat	Embryo	Nutritive storage tissue
PP54021	Kenilworth 061	<i>Anacostia marylandensis</i>	one-seeded fruit	exotestal	embryo preserved	nutritive tissue preserved, partly
PP54076	Kenilworth 061	<i>Anacostia marylandensis</i>	one-seeded fruit	exotestal		seed empty
PP54084	Kenilworth 175	<i>Anacostia marylandensis</i>	one-seeded fruit	exotestal		seed empty
PP54091	Kenilworth 174	<i>Anacostia marylandensis</i>	seed	exotestal		seed empty
PP54092	Kenilworth 174	<i>Anacostia marylandensis</i>	one-seeded fruit	exotestal		seed empty
PP54093	Kenilworth 174	<i>Anacostia marylandensis</i>	one-seeded fruit	exotestal		nutritive tissue preserved, partly
PP54094	Kenilworth 174	<i>Anacostia marylandensis</i>	one-seeded fruit	exotestal		nutritive tissue preserved, partly
PP54095	Kenilworth 174	<i>Anacostia marylandensis</i>	one-seeded fruit	exotestal		nutritive tissue preserved, partly
PP54096	Kenilworth 174	<i>Anacostia marylandensis</i>	seed	exotestal		seed empty
S172400	Famalicão 25	<i>Anacostia</i> sp.	seed	exotestal		seed empty
S172401	Famalicão 25	<i>Anacostia</i> sp.	seed	exotestal		nutritive tissue poorly preserved
S174031	Famalicão 25	<i>Anacostia</i> sp.	seed	exotestal		seed empty
S174032	Famalicão 25	<i>Anacostia</i> sp.	seed	exotestal	embryo preserved, partly	nutritive tissue preserved
S174168	Vale de Agua 408	<i>Anacostia</i> sp.	seed	exotestal		seed empty
PP54042	Puddledock 082	<i>Anacostia virginensis</i>	one-seeded fruit	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
PP54046	Puddledock 082	<i>Anacostia virginensis</i>	one-seeded fruit	exotestal		nutritive tissue preserved, partly
PP54034	Puddledock 156	<i>Appomattoxia ancistrophora</i>	one-seeded fruit	seed coat thin	empty space from embryo	nutritive tissue preserved, partly
PP54065	Puddledock 156	<i>Appomattoxia ancistrophora</i>	one-seeded fruit	seed coat thin	embryo preserved	
PP54067	Puddledock 156	<i>Appomattoxia ancistrophora</i>	one-seeded fruit	endotestal		nutritive tissue preserved, partly
S153507	Famalicão 25	<i>Canrightia resinifera</i>	two-seeded fruit	endotestal		nutritive tissue preserved, partly
S153508	Famalicão 25	<i>Canrightia resinifera</i>	two-seeded fruit	endotestal		nutritive tissue preserved, partly
S170111	Famalicão 25	<i>Canrightia resinifera</i>	two-seeded fruit	endotestal		nutritive tissue preserved, partly
S170112	Famalicão 25	<i>Canrightia resinifera</i>	two-seeded fruit	endotestal		seed empty
S171506	Catefica 50	<i>Canrightia resinifera</i>	seed	endotestal		seed empty
S171507	Catefica 50	<i>Canrightia resinifera</i>	seed	endotestal		seed empty
S171508	Catefica 50	<i>Canrightia resinifera</i>	two-seeded fruit	endotestal		seed empty

S171509	Catefica 50	<i>Canrightia resinifera</i>	three-seeded fruit	endotestal		seed empty
S171510	Famalicão 25	<i>Canrightia resinifera</i>	seed	endotestal		nutritive tissue preserved, partly
S171511	Famalicão 25	<i>Canrightia resinifera</i>	seed	endotestal		nutritive tissue preserved, partly
S171512	Famalicão 25	<i>Canrightia resinifera</i>	seed	endotestal		nutritive tissue preserved, partly
S171513	Famalicão 25	<i>Canrightia resinifera</i>	seed	endotestal		nutritive tissue preserved, partly
S174008	Catefica 50	<i>Canrightia resinifera</i>	two-seeded fruit	endotestal		seed empty
S174312	Catefica 153	<i>Canrightia resinifera</i>	three-seeded fruit	endotestal		seed empty
S174100	Torres Vedras 38	<i>Canrightia</i> sp.	three-seeded fruit	endotestal		nutritive tissue preserved, partly
S174039	Catefica 49	<i>Canrightiopsis crassitesta</i>	one-seeded fruit	endotestal		seed empty
S174159	Catefica 49	<i>Canrightiopsis crassitesta</i>	one-seeded fruit	endotestal	empty space from embryo	nutritive tissue preserved, partly
S174248	Catefica 49	<i>Canrightiopsis crassitesta</i>	one-seeded fruit	endotestal		seed empty
S174310	Catefica 154	<i>Canrightiopsis crassitesta</i>	one-seeded fruit	endotestal		nutritive tissue preserved, partly
S174311	Catefica 343	<i>Canrightiopsis crassitesta</i>	one-seeded fruit	endotestal		seed empty
P0311	Juncal-Chicalhão	<i>Canrightiopsis dinisii</i>	one-seeded fruit	endotestal		seed empty
S174004	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal		seed empty
S174005	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	embryo preserved	nutritive tissue preserved, partly
S174006	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	empty space from embryo	nutritive tissue preserved, partly
S174023	Famalicão 25	<i>Canrightiopsis intermedia</i>	seed	endotestal		seed empty
S174024	Famalicão 25	<i>Canrightiopsis intermedia</i>	seed	endotestal	embryo preserved, poorly	nutritive tissue preserved, partly
S174025	Famalicão 25	<i>Canrightiopsis intermedia</i>	seed	endotestal		nutritive tissue preserved, partly
S174026	Famalicão 25	<i>Canrightiopsis intermedia</i>	seed	endotestal		seed empty
S174027	Famalicão 25	<i>Canrightiopsis intermedia</i>	seed	endotestal	empty space from embryo	nutritive tissue preserved, partly
S174028	Famalicão 25	<i>Canrightiopsis intermedia</i>	seed	endotestal		seed empty
S174033	Famalicão 25	<i>Canrightiopsis intermedia</i>	seed	endotestal		nutritive tissue preserved, partly
S174104	Buarcos 157	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal		nutritive tissue preserved, partly
S174105	Buarcos 157	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal		nutritive tissue preserved, partly
S174107	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	empty space from embryo	nutritive tissue preserved, partly
S174108	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal		nutritive tissue preserved, partly
S174148	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	embryo preserved, poorly	nutritive tissue preserved, partly
S174150	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal		nutritive tissue preserved, partly

S174151	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	embryo preserved, poorly	nutritive tissue preserved, partly
S174152	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	embryo preserved	nutritive tissue preserved, partly
S174153	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	embryo preserved	nutritive tissue preserved, partly
S174155	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	embryo preserved	nutritive tissue preserved, partly
S174156	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal		seed empty
S174157	Famalicão 25	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	empty space from embryo	nutritive tissue preserved, partly
S174174	Vale de Agua 331	<i>Canrightiopsis intermedia</i>	one-seeded fruit	endotestal	empty space from embryo	nutritive tissue preserved, partly
S172333	Catefica 153	<i>Canrightiopsis</i> sp.	seed	endotestal		nutritive tissue preserved, partly
S174040	Catefica 49	<i>Canrightiopsis</i> sp.	one-seeded fruit	endotestal		seed empty
S174149	Famalicão 25	<i>Canrightiopsis</i> sp.	one-seeded fruit	endotestal		seed empty
S174309	Catefica 154	<i>Canrightiopsis</i> sp.	one-seeded fruit	endotestal		seed empty
PP53966	Puddledock 156	<i>Couperites</i> sp.	one-seeded fruit	exotestal		seed empty
PP53967	Puddledock 156	<i>Couperites</i> sp.	one-seeded fruit	exotestal		seed empty
PP53967	Puddledock 156	<i>Couperites</i> sp.	one-seeded fruit	exotestal		strongly compressed
PP54031	Puddledock 156	<i>Couperites</i> sp.	seed	exotestal		seed empty
PP54032	Puddledock 156	<i>Couperites</i> sp.	seed	exotestal		seed empty
PP54071	Puddledock 156	<i>Couperites</i> sp.	one-seeded fruit	exotestal		seed empty
PP54072	Puddledock 156	<i>Couperites</i> sp.	one-seeded fruit	exotestal		seed empty
S170235	Famalicão 25	Taxon 01	seed	exotestal	embryo preserved	nutritive tissue preserved
S170236	Famalicão 25	Taxon 01	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174034	Famalicão 25	Taxon 01	seed	exotestal		nutritive tissue preserved, partly
S174346	Famalicão 25	Taxon 01	seed	exotestal		seed almost empty
S174348	Famalicão 25	Taxon 01	seed	exotestal		seed empty
S174349	Famalicão 25	Taxon 01	seed	exotestal		seed almost empty
S174350	Famalicão 25	Taxon 01	seed	exotestal		nutritive tissue preserved, partly
S174351	Famalicão 25	Taxon 01	seed	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
S174431	Famalicão 25	Taxon 01	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174432	Famalicão 25	Taxon 01	seed	exotestal		seed empty
S174433	Famalicão 25	Taxon 01	seed	exotestal		seed almost empty
S174471	Famalicão 25	Taxon 01	seed	exotestal		seed empty

S174473	Famalicão 25	Taxon 01	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
PP53991	Puddledock 156	Taxon 02	one-seeded fruit	seed coat thin	embryo preserved	nutritive tissue preserved
PP54069	Puddledock 156	Taxon 02	seed	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
S170238	Famalicão 25	Taxon 03	seed	exotestal		nutritive tissue preserved, partly
S170239	Famalicão 25	Taxon 03	seed	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
S174035	Famalicão 25	Taxon 03	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174343	Famalicão 25	Taxon 03	seed	exotestal		seed empty
S174345	Famalicão 25	Taxon 03	seed	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
S174352	Famalicão 25	Taxon 03	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174353	Famalicão 25	Taxon 03	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174467	Famalicão 25	Taxon 03	seed	exotestal	embryo preserved, partly	nutritive tissue preserved
S174469	Famalicão 25	Taxon 03	seed	exotestal	embryo preserved	nutritive tissue preserved
S174470	Famalicão 25	Taxon 03	seed	exotestal	embryo preserved, partly	nutritive tissue preserved
S174472	Famalicão 25	Taxon 03	seed	exotestal	embryo preserved	nutritive tissue preserved
S174474	Famalicão 25	Taxon 03	seed	exotestal	embryo preserved	nutritive tissue preserved
S105218	Famalicão 25	Taxon 04	seed	exotestal		seed almost empty
S170234	Famalicão 25	Taxon 04	seed	exotestal		seed empty
S174336	Famalicão 25	Taxon 04	seed	exotestal		nutritive tissue preserved, partly
S174354	Famalicão 25	Taxon 04	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174430	Famalicão 25	Taxon 04	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174435	Famalicão 25	Taxon 04	seed	exotestal		seed almost empty
S174468	Famalicão 25	Taxon 04	seed	exotestal	embryo preserved	nutritive tissue preserved
S174171	Vale de Água 408	Taxon 05	seed	exotestal		nutritive tissue preserved, partly
S154533	Famalicão 25	Taxon 06	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S172316	Catefica 49	Taxon 07	seed	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
S170237	Famalicão 25	Taxon 08	seed	exotestal		nutritive tissue preserved, partly
S174337	Famalicão 25	Taxon 08	seed	exotestal		seed empty
S174338	Famalicão 25	Taxon 08	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174339	Famalicão 25	Taxon 08	seed	exotestal		nutritive tissue preserved, partly
S174340	Famalicão 25	Taxon 08	seed	exotestal		seed empty

S174341	Famalicão 25	Taxon 08	seed	exotestal		nutritive tissue preserved, partly
S174347	Famalicão 25	Taxon 08	seed	exotestal		nutritive tissue preserved, partly
S174358	Arazede 374	Taxon 08	seed	exotestal		nutritive tissue preserved, partly
S174179	Vale de Agua 141	Taxon 09	seed	exotestal		seed empty
S174338	Famalicão 25	Taxon 09	seed	exotestal	empty space from embryo	nutritive tissue preserved
S174036	Vale de Agua 265	Taxon 10	seed	exotestal		seed empty
S174189	Vale de Agua 141	Taxon 10	seed	exotestal		seed empty
S174363	Arazede 374	Taxon 10	seed	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
S170110	Famalicão 25	Taxon 11	seed	exotestal		seed empty
S170232	Famalicão 25	Taxon 11	seed	exotestal		seed empty
S170233	Famalicão 25	Taxon 11	seed	exotestal		seed empty
S172332	Catefica 153	Taxon 11	seed	exotestal		seed empty
S174177	Vale de Agua 141	Taxon 11	seed	exotestal		seed empty
S174178	Vale de Agua 141	Taxon 11	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174344	Famalicão 25	Taxon 11	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174187	Vale de Agua 329	Taxon 12	one-seeded fruit	endotestal?	embryo preserved, partly	nutritive tissue preserved, partly
S170240	Famalicão 25	Taxon 13	seed	seed coat thin	embryo preserved	nutritive tissue preserved, partly
S174424	Famalicão 25	Taxon 13	seed	seed coat thin		nutritive tissue preserved, partly
S174425	Famalicão 25	Taxon 13	seed	seed coat thin	embryo preserved	nutritive tissue preserved, partly
S170241	Famalicão 25	Taxon 14	seed	endotestal		seed empty
S170242	Famalicão 25	Taxon 14	seed	endotestal	embryo preserved, partly	nutritive tissue preserved, partly
S174029	Famalicão 25	Taxon 14	seed	endotestal		seed empty
S174030	Famalicão 25	Taxon 14	seed	endotestal	embryo preserved, poorly	nutritive tissue preserved, partly
S174422	Famalicão 25	Taxon 14	seed	endotestal		seed empty
S170108/ S174095	Famalicão 25	Taxon 15	three-seeded fruit	endotestal		seed empty
S170109	Famalicão 25	Taxon 15	three-seeded fruit	endotestal		seed empty
S170229	Famalicão 25	Taxon 15	three-seeded fruit	endotestal	embryo preserved, partly	nutritive tissue preserved, partly
S170230	Famalicão 25	Taxon 15	four-seeded	endotestal	embryo preserved, partly	
S170231	Famalicão 25	Taxon 15	three-seeded fruit	endotestal		seed empty
S170227	Famalicão 25	Taxon 16	three-seeded fruit	endotestal		nutritive tissue preserved, partly

S170228	Famalicão 25	Taxon 16	three-seeded fruit	endotestal		seed empty
S171535	Torres Vedras 43	Taxon 16	four-seeded fruit	endotestal		nutritive tissue preserved, partly
S174158	Famalicão 25	Taxon 16	two-seeded fruit	endotestal		seed empty
S174169	Vale de Agua 408	Taxon 16	two-seeded fruit	endotestal		nutritive tissue preserved, partly
S174176	Vale de Agua 364	Taxon 16	two-seeded fruit	endotestal		seed empty
S174360	Arazede 374	Taxon 16	two-seeded fruit	endotestal		seeds empty
S174361	Arazede 374	Taxon 16	one-seeded fruit	endotestal		seeds empty
S174434	Famalicão 25	Taxon 16	three-seeded fruit	endotestal		seed empty
S174439	Famalicão 25	Taxon 16	three-seeded fruit	endotestal		seeds empty
S174098	Torres Vedras 38	Taxon 17	seed	?		too compressed
S172321	Catefica 49	Taxon 18	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S172323	Catefica 49	Taxon 18	one-seeded fruit	seed coat thin		seed empty
S174162	Catefica 342	Taxon 18	one-seeded fruit	seed coat thin		seed empty
S135459	Vale de Agua 383	Taxon 19	two-seeded fruit	seed coat thin		seeds empty
S174163	Vale de Agua 408	Taxon 19	two-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S174172	Vale de Agua 363	Taxon 19	two-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S174173	Vale de Agua 363	Taxon 19	three-seeded fruit	seed coat thin		seed empty
S174436	Vale de Agua 328	Taxon 19	two-seeded fruit	seed coat thin	embryo preserved	nutritive tissue preserved, partly
S174037	Vale de Agua 265	Taxon 20	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S174314	Catefica 153	Taxon 21	one-seeded fruit	seed coat thin	empty space from embryo	nutritive tissue preserved, partly
S174188	Vale de Agua 363	Taxon 22	one-seeded fruit	exotestal	empty space from embryo	nutritive tissue preserved, partly
S174362	Arazede 374	Taxon 22	one-seeded fruit	exotestal		nutritive tissue preserved, partly
S174420	Famalicão 25	Taxon 22	one-seeded fruit	exotestal		seed empty
S171515	Catefica 343	Taxon 23	several-seeded fruit	seed coat thin		seeds empty
S171524	Catefica 50	Taxon 23	several-seeded fruit	seed coat thin		seeds empty
S172313	Catefica 49	Taxon 24	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S172324	Catefica 49	Taxon 24	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S172325	Catefica 49	Taxon 24	one-seeded fruit	seed coat thin		strongly compressed

S172328	Buarcos 371	Taxon 24	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S174186	Vale de Agua 329	Taxon 24	one-seeded fruit	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
S174419	Famalicão 25	Taxon 25	seed	testal-tegmic?		seed empty
S174190	Vale de Agua 141	Taxon 26	seed	exotestal		nutritive tissue preserved, partly
S170243	Famalicão 25	Taxon 27	seed	exotestal		seed empty
S174426	Famalicão 25	Taxon 28	seed	exotestal		nutritive tissue preserved, partly
S174428	Famalicão 25	Taxon 28	seed	exotestal		nutritive tissue preserved, partly
S174429	Famalicão 25	Taxon 28	seed	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
S156205	Buarcos 157	Taxon 29	one-seeded fruit	seed coat thin		strongly compressed
S153503	Catefica 364	Taxon 30	one-seeded fruit	seed coat thin	embryo preserved	nutritive tissue preserved, partly
S154531	Arazede 372	Taxon 30	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
S174115	Vila Verde 2	Taxon 30	one-seeded fruit	seed coat thin		seed empty
S156372	Buarcos 157	Taxon 31	one-seeded fruit	seed coat thin		strongly compressed
S172317	Catefica 49	Taxon 32	seed	exotestal		seed empty
S172319	Catefica 49	Taxon 33	seed	exotestal		seed empty
S174417	Famalicão 25	Taxon 34	seed	exotestal		strongly compressed
S174342	Famalicão 25	Taxon 35	seed	exotestal		seed empty
S174427	Famalicão 25	Taxon 36	one-seeded fruit	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
S174175	Vale de Agua 141	Taxon 37	seed	seed coat thin	embryo preserved, partly	
PP53965	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		seed empty
PP53989	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		seed empty
PP53990	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP53992	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin	embryo preserved	
PP54037	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		seed empty
PP54068	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		seed empty
PP54101	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP54102	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
PP54103	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		seed empty
PP54104	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
PP54105	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		seed empty

PP54106	Puddledock 156	Taxon 38	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP53952	Puddledock 151	Taxon 39	one-seeded fruit	seed coat thin	embryo preserved	nutritive tissue preserved
PP53957	Puddledock 151	Taxon 39	one-seeded fruit	seed coat thin		seed empty
PP53958	Puddledock 156	Taxon 39	one-seeded fruit	seed coat thin		seed empty
PP53959	Puddledock 156	Taxon 39	one-seeded fruit	seed coat thin		seed empty
PP53995	Puddledock 073	Taxon 40	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP53978	Puddledock 083	Taxon 41	one-seeded fruit	seed coat thin		seed empty
PP53964	Puddledock 156	Taxon 42	one-seeded fruit	seed coat thin		seed empty
PP54107	Puddledock 156	Taxon 42	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP54112	Puddledock 156	Taxon 42	one-seeded fruit	seed coat thin		seed empty
PP54111	Puddledock 156	Taxon 43	one-seeded fruit	seed coat thin	empty space from embryo	nutritive tissue preserved, partly
PP54153	Puddledock 185	Taxon 44	one-seeded fruit	exotestal		seed almost empty
PP54088	Kenilworth 174	Taxon 45	one-seeded fruit	seed coat thin		strongly compressed
PP54089	Kenilworth 174	Taxon 45	one-seeded fruit	seed coat thin		strongly compressed
PP54090	Kenilworth 174	Taxon 45	one-seeded fruit	seed coat thin		strongly compressed
PP54100	Kenilworth 061	Taxon 45	one-seeded fruit	seed coat thin		strongly compressed
PP53968	Puddledock 082	Taxon 46	one-seeded fruit	seed coat thin		seed empty
PP53969	Puddledock 082	Taxon 46	one-seeded fruit	seed coat thin		seed empty
PP53970	Puddledock 082	Taxon 46	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP54086	Kenilworth 175	Taxon 47	one-seeded fruit	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
PP54056	Puddledock 143	Taxon 48	two-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP54048	Kenilworth 174	Taxon 49	one-seeded fruit	seed coat thin		nutritive tissue preserved
PP54022	Kenilworth 060	Taxon 50	one-seeded fruit	seed coat thin		nutritive tissue preserved, partly
PP54025	Dutch Gap 098	Taxon 51	seed	?		seed empty
PP53972	Puddledock 082	Taxon 52	seed	exotestal	embryo preserved, partly	nutritive tissue preserved, partly
PP53973	Puddledock 082	Taxon 52	seed	exotestal	embryo preserved	nutritive tissue preserved, partly
PP53993	Puddledock 156	Taxon 52	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
PP54039	Puddledock 156	Taxon 52	seed	exotestal	embryo preserved, partly	
PP54052	Kenilworth 174	Taxon 53	seed	exotestal	empty space from embryo	nutritive tissue preserved
PP54075	Kenilworth 061	Taxon 53	seed	exotestal		seed empty

PP54082	Kenilworth 175	Taxon 53	seed	exotestal	empty space from embryo	nutritive tissue preserved
PP53999	Puddledock 073	Taxon 54	one-seeded fruit	seed coat thin		seed empty
PP54041	Puddledock 082	Taxon 55	seed	exotestal	empty space from embryo	nutritive tissue preserved, partly
PP54035	Puddledock 156	Taxon 56	seed	exotestal		seed empty
PP53974	Puddledock 082	Taxon 57	one-seeded fruit	seed coat thin		seed empty
PP53975	Puddledock 082	Taxon 57	one-seeded fruit	seed coat thin		seed empty
PP53976	Puddledock 082	Taxon 57	one-seeded fruit	seed coat thin		seed empty
PP54110	Puddledock 156	Taxon 58	seed	exotestal		seed empty
PP54062	Puddledock 151	Taxon 59	seed	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
PP54108	Puddledock 156	Taxon 59	seed	seed coat thin	embryo preserved	nutritive tissue preserved, partly
PP54109	Puddledock 156	Taxon 59	seed	seed coat thin		nutritive tissue preserved, partly
PP54073	Puddledock 156	Taxon 60	seed	seed coat thin	embryo preserved, partly	nutritive tissue preserved, partly
PP54074	Puddledock 156	Taxon 61	seed	seed coat thin		nutritive tissue preserved, partly
PP54098	Kenilworth 174	Taxon 62	five-seeded fruit	endotestal?		seed empty
PP54038	Puddledock 156	Taxon 63	two-seeded fruit	endotestal?		seed empty
PP54083	Kenilworth 175	Taxon 64	seed	seed coat thin		seed empty
PP54043	Puddledock 082	Taxon 65	two-seeded fruit	exotestal		nutritive tissue preserved, partly
PP54049	Kenilworth 174	Taxon 66	two-seeded fruit	exotestal		seed empty
PP54014	Kenilworth 061	Taxon 67	seed	exotestal		seed empty