Friis EM, Crane PR, Pedersen KR, Stampanoni M, Marone F. 2015. Exceptional preservation of tiny embryos documents seed dormancy in early angiosperms. Nature 528: 551-554. doi:10.1038/nature16441

Published 2015-12-24:
http://www.nature.com/nature/journal/v528/n7583/full/nature16441.html

**Exceptional preservation of tiny embryos documents seed dormancy in early angiosperms**

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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 palaeontogical 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 SRXTM[19] 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 ago[3] (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 dimension[20]), 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 lineages[22-26]. 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 eumagnoliids[18]. 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 Nymphaeaceae[26].

*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 fruits[3] 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 Piperales[28]. 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 plants[30]. 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 0.16[17]) 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.

**Received** ; **accepted** .


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

**Acknowledgements** We thank Anna Lindström for assistance with the SRXTM analyses. Research reported here was supported by the Swedish Natural Science Research Foundation, **t**he Edward P. Bass Distinguished Visiting Fellowship and by the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement n. 312284 (for CALIPSO) for the SRXTM analyses at the SLS.

**Author Contributions** E.M.F., K.R.P. and P.R.C. collected and prepared the fossil material for analyses. The measurements and reconstructions were performed by E.M.F. F.M and M.S. developed the algorithms for the analyses and enhanced the measurements. The paper was prepared by the authors jointly.

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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 beamline[32] 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 regridding[33]. 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 Fiji[35] resulting in an embryo to seed ratio (E:S) comparable to that published by others[17].

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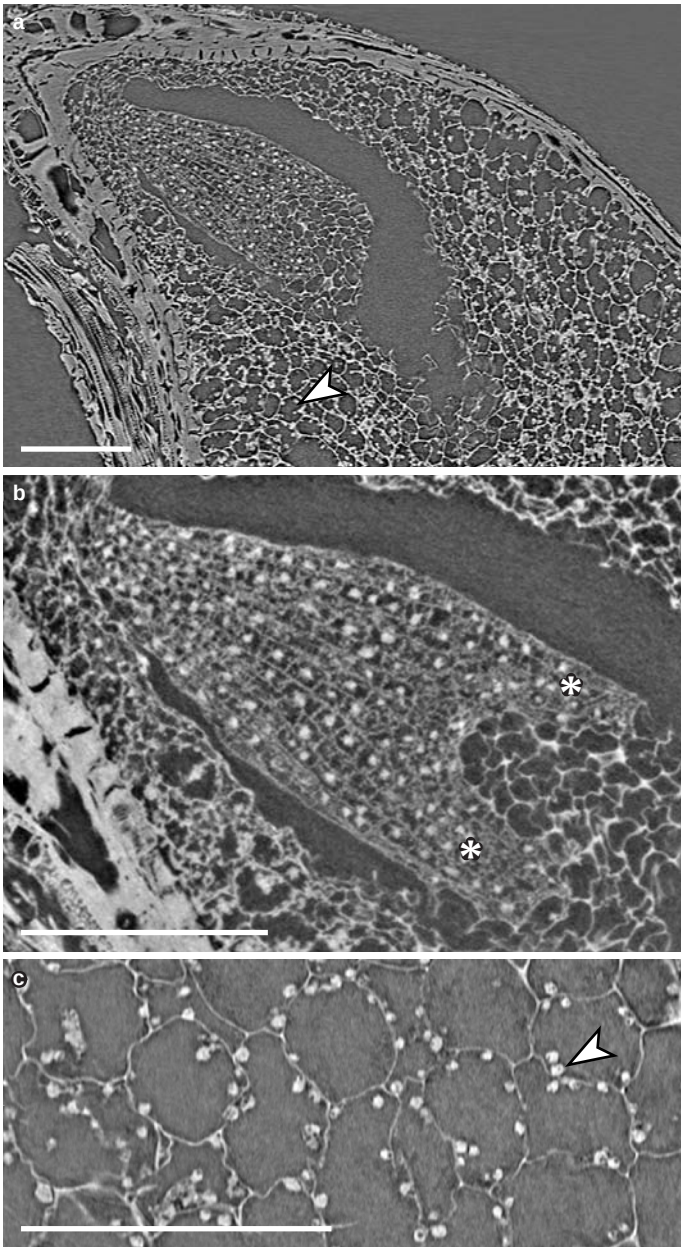
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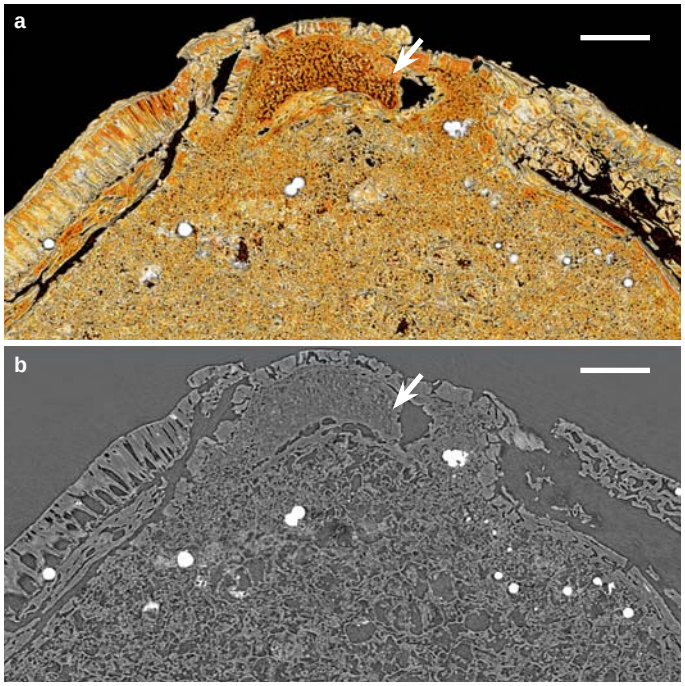
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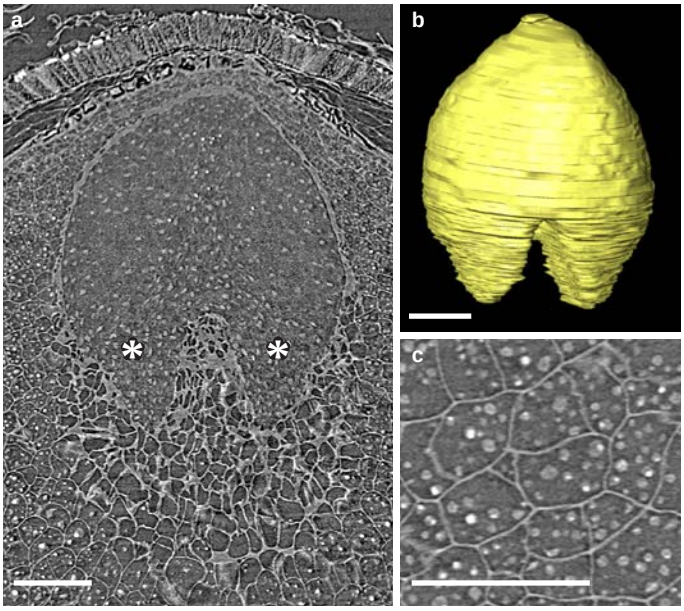
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Supplementary Table 1 | List of Early Cretaceous fruits with mature seeds and isolated, mature seeds studied using SRXTM. Currently undescribed seeds are here grouped into informal taxa numbered Taxon 1, Taxon 2 etc.

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 | *Anacostia marylandensis* | one-seeded fruit | exotestal | embryo preserved | nutritive tissue preserved, partly |
| PP54076 | Kenilworth 061 | *Anacostia marylandensis* | one-seeded fruit | exotestal | | seed empty |
| PP54084 | Kenilworth 175 | *Anacostia marylandensis* | one-seeded fruit | exotestal | | seed empty |
| PP54091 | Kenilworth 174 | *Anacostia marylandensis* | seed | exotestal | | seed empty |
| PP54092 | Kenilworth 174 | *Anacostia marylandensis* | one-seeded fruit | exotestal | | seed empty |
| PP54093 | Kenilworth 174 | *Anacostia marylandensis* | one-seeded fruit | exotestal | | nutritive tissue preserved, partly |
| PP54094 | Kenilworth 174 | *Anacostia marylandensis* | one-seeded fruit | exotestal | | nutritive tissue preserved, partly |
| PP54095 | Kenilworth 174 | *Anacostia marylandensis* | one-seeded fruit | exotestal | | nutritive tissue preserved, partly |
| PP54096 | Kenilworth 174 | *Anacostia marylandensis* | seed | exotestal | | seed empty |
| S172400 | Famalicão 25 | *Anacostia* sp. | seed | exotestal | | seed empty |
| S172401 | Famalicão 25 | *Anacostia* sp. | seed | exotestal | | nutritive tissue poorly preserved |
| S174031 | Famalicão 25 | *Anacostia* sp. | seed | exotestal | | seed empty |
| S174032 | Famalicão 25 | *Anacostia* sp. | seed | exotestal | embryo preserved, partly | nutritive tissue preserved |
| S174168 | Vale de Agua 408 | *Anacostia* sp. | seed | exotestal | | seed empty |
| PP54042 | Puddledock 082 | *Anacostia virginiensis* | one-seeded fruit | exotestal | embryo preserved, partly | nutritive tissue preserved, partly |
| PP54046 | Puddledock 082 | *Anacostia virginiensis* | one-seeded fruit | exotestal | | nutritive tissue preserved, partly |
| PP54034 | Puddledock 156 | *Appomattoxia ancistrophora* | one-seeded fruit | seed coat thin | empty space from embryo | nutritive tissue preserved, partly |
| PP54065 | Puddledock 156 | *Appomattoxia ancistrophora* | one-seeded fruit | seed coat thin | embryo preserved | |
| PP54067 | Puddledock 156 | *Appomattoxia ancistrophora* | one-seeded fruit | endotestal | | nutritive tissue preserved, partly |
| S153507 | Famalicão 25 | *Canrightia resinifera* | two-seeded fruit | endotestal | | nutritive tissue preserved, partly |
| S153508 | Famalicão 25 | *Canrightia resinifera* | two-seeded fruit | endotestal | | nutritive tissue preserved, partly |
| S170111 | Famalicão 25 | *Canrightia resinifera* | two-seeded fruit | endotestal | | nutritive tissue preserved, partly |
| S170112 | Famalicão 25 | *Canrightia resinifera* | two-seeded fruit | endotestal | | seed empty |
| S171506 | Catefica 50 | *Canrightia resinifera* | seed | endotestal | | seed empty |
| S171507 | Catefica 50 | *Canrightia resinifera* | seed | endotestal | | seed empty |
| S171508 | Catefica 50 | *Canrightia resinifera* | two-seeded fruit | endotestal | | seed empty |

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

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| S174151 | Famalicão 25 | *Canrightiopsis intermedia* | one-seeded fruit | endotestal | embryo preserved, poorly | nutritive tissue preserved, partly |
| S174152 | Famalicão 25 | *Canrightiopsis intermedia* | one-seeded fruit | endotestal | embryo preserved | nutritive tissue preserved, partly |
| S174153 | Famalicão 25 | *Canrightiopsis intermedia* | one-seeded fruit | endotestal | embryo preserved | nutritive tissue preserved, partly |
| S174155 | Famalicão 25 | *Canrightiopsis intermedia* | one-seeded fruit | endotestal | embryo preserved | nutritive tissue preserved, partly |
| S174156 | Famalicão 25 | *Canrightiopsis intermedia* | one-seeded fruit | endotestal | | seed empty |
| S174157 | Famalicão 25 | *Canrightiopsis intermedia* | one-seeded fruit | endotestal | empty space from embryo | nutritive tissue preserved, partly |
| S174174 | Vale de Agua 331 | *Canrightiopsis intermedia* | one-seeded fruit | endotestal | empty space from embryo | nutritive tissue preserved, partly |
| S172333 | Catefica 153 | *Canrightiopsis* sp. | seed | endotestal | | nutritive tissue preserved, partly |
| S174040 | Catefica 49 | *Canrightiopsis* sp. | one-seeded fruit | endotestal | | seed empty |
| S174149 | Famalicão 25 | *Canrightiopsis* sp. | one-seeded fruit | endotestal | | seed empty |
| S174309 | Catefica 154 | *Canrightiopsis* sp. | one-seeded fruit | endotestal | | seed empty |
| PP53966 | Puddledock 156 | *Couperites* sp. | one-seeded fruit | exotestal | | seed empty |
| PP53967 | Puddledock 156 | *Couperites* sp. | one-seeded fruit | exotestal | | seed empty |
| PP53967 | Puddledock 156 | *Couperites* sp. | one-seeded fruit | exotestal | | strongly compressed |
| PP54031 | Puddledock 156 | *Couperites* sp. | seed | exotestal | | seed empty |
| PP54032 | Puddledock 156 | *Couperites* sp. | seed | exotestal | | seed empty |
| PP54071 | Puddledock 156 | *Couperites* sp. | one-seeded fruit | exotestal | | seed empty |
| PP54072 | Puddledock 156 | *Couperites* 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 |

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| 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 Agua 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 |

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| 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 |

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| 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 |

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| 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 |

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| 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 |

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| 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 |