Introduction

Early Cretaceous mesofossil floras from eastern North America and Portugal have yielded an extraordinary diversity of small angiosperm fruits and seeds in fossil assemblages that also include angiosperm flowers and other plant fragments (e.g. Friis et al. 2011). Most of these seeds have an exotestal seed coat in which the mechanical protective layer is in the outer layer of the outer integument. The features of these seeds indicate a relationship to extant Austrobaileyales and Nymphaeales, although in most cases the fossils cannot be placed in any extant family or order (Friis et al. 1999, 2011, 2018a; see also Friis et al. 2018b this issue). A smaller proportion of the Early Cretaceous seeds are endotestal, in which the mechanical protective layer is in the inner part of the outer integument and among these are taxa related to Magnoliales (Friis, Crane and Pedersen, work in progress) and especially extant Chloranthaceae (Friis and Pedersen 2011, Friis et al. 2015). Extant Chloranthaceae are clearly relictual with only four surviving genera (Ascarina J.R.Förster et G.Förster, Chloranthus O.Swartz, Hedysorus O.Swartz, and Sarcandra Gardner), which show a scattered pantropical distribution that includes occurrences in Asia, the Pacific Islands and Central and South America (Todzia 1993).
Today the family comprises ca. 75 extant species, many of which are putatively of relatively recent origin (e.g. Zhang and Renner 2003), but the extensive Early Cretaceous record of unequivocal chloranthoid flowers, fruits, seeds, stamens and pollen documents that the group had attained considerable diversity much earlier and an almost global distribution by the Albain (Early Cretaceous). Especially significant is the wide distribution of the characteristic pollen of Asteropollis Hedlund et Norris (Hedlund and Norris 1968), which has a tectum and aperture configuration almost indistinguishable from pollen of extant Hedysosmum (Walker and Walker 1984). Early Cretaceous records of Asteropollis extend from Antarctica to Greenland and from America and Europe to eastern Asia (for literature see Martinez et al. 2013). Dispersed pollen of Clavatipollenites Couper is also important for interpreting the early evolutionary history of chloranthoids and includes species that are closely similar to pollen of extant Ascarina (Couper 1960, Walker and Walker 1984, Archangelsky and Taylor 1993). However, since there is a considerable diversity among dispersed pollen grains assigned to Clavatipollenites they may not all be related to Chloranthaceae. More detailed analysis using scanning electron microscopy is needed if Clavatipollenites is to be used to indicate the past distribution of chloranthoids (Hughes 1994, Friis et al. 2011).

Interpreting the early fossil history of chloranthoids has been greatly facilitated by the discovery of a variety of chloranthoid mesofossils, including floral structures, fruits, seeds and stamens (Crane et al. 1989, Herendeen et al. 1993, Crane et al. 1994, Eklund et al. 1997, Friis et al. 2011, Hartkopf-Fröder et al. 2011). While much less abundant than dispersed pollen grains, such mesofossils are common in Early Cretaceous sediments from Portugal, and because they are relatively rich in systematically informative characters, they are especially valuable for understanding the early phases of chloranthoid evolution. Among these early chloranthoids are Hedysosmum-like flowers, fruits and staminate structures and several undescribed taxa, as well as floral structures, fruits, seeds and stamens assigned to species of the extinct genera Canrightia E.M.Friis et K.R.Pedersen and Canrightiopsis E.M.Friis, G.W.Grimm, M.M.Mendes et K.R.Pedersen (Friis et al. 1997, 2011, Friis and Pedersen 2011, Friis et al. 2015). Canrightia and Canrightiopsis are closely similar to extant Chloranthus, Sarcandra and Ascarina in having pendent, orthotropous, bitegmic and endostele ovules/seeds, in which the outer integument (testa) and the inner integument ( tegmen) are distinct. The mechanical layer is in the inner part of testa (endotesta) and consists of one layer of cubic to palisade-shaped crystal cells with endoreticulate fibrous infillings. Canrightia and Canrightiopsis differ from the extant genera of Chloranthaceae in several features and their discovery has been particularly important for unravelling the evolution of the unique dorsally displaced androecium of extant Sarcandra and Chloranthus (Friis et al. 2015).

Here we describe two new extinct chloranthoids, Rightcania kvacekii gen. et sp. nov. from the Puddledock flora of Virginia, USA, and Kvačekispernum rugosum gen. et sp. nov. from the Vale de Água locality, Portugal. Both genera have features of ovule organization and seed coat comparable to Canrightia, Canrightiopsis and related extant Chloranthaceae. Rightcania kvacekii is particularly similar to Canrightia in having more than one ovule/seed in the fruit, while Kvačekispernum is closely similar to seeds of Canrightiopsis. Rightcania kvacekii from the Puddledock flora is the first record of a member of the Canrightia-Canrightiopsis complex from North America, and together the two new genera provide further evidence of the extensive extinct diversity among early chloranthoid angiosperms that were widespread during the Early Cretaceous at a very early stage of angiosperm evolution.

Material and methods

The fossil specimens were recovered from Early Cretaceous sediments from the Puddledock and Vale de Água localities. Sediments at the Puddledock locality are of early to middle Albian age. They outcrop in a large clay pit, the former Tarmac Lone Star Industries (now Vulcan Materials Co.) sand and gravel pit, located south of Richmond and east of the Appomattox River in Prince George County, Virginia, USA (37° 15’ 52” N, 77° 22’ 10” W). Sediments at the Vale de Água locality are of late Aptian to early Albian age. They outcrop in a huge clay pit complex near the small villages of Vale de Água and Juncal, southwest of Batalha in the Lusitanian Basin (39° 37’ 15” N, 08° 51’ 30” W), western Portugal. Further information on the geological context and age of the plant fossils from the two localities is given in Friis et al. (2011). For comparison with the new material described here we also illustrate seeds of Canrightia (Friis and Pedersen 2011) and Canrightiopsis from the Early Cretaceous of Portugal (Friis et al. 2015).

The fossils were extracted from the sediments and cleaned for further analysis following standard procedures (e.g. Friis et al. 2009, 2018b this issue). They were studied using attenuation-based synchrotron radiation X-ray tomographic microscopy (SRXTM) at the TOMCAT beamline of the Swiss Light Source of the Paul Scherrer Institute, Villigen, Switzerland (Stampanoni et al. 2006, Friis et al. 2014). For SRXTM analyses specimens were mounted on brass stubs using nail polish and analyses were carried out at 10 keV with a sCMOS detector and a 20 μm thick LAG:Ce scintillator screen using a 10× objective (PP56562, PP56593, PP56599, S171512, S174004, S174039, S174159, S174951, S174952; isotopic pixel size 0.65 μm) or 20× objective (S174100, S174004; isotopic pixel size 0.325 μm) over 180°. Examination of specimen PP56562 used at 10 keV with a sCMOS detector and a 20 μm thick LAG:Ce scintillator screen using a 10× objective (PP56562, PP56593, PP56599, S171512, S174004, S174039, S174159, S174951, S174952; isotopic pixel size 0.65 μm) or 20× objective (S174100, S174004; isotopic pixel size 0.325 μm) over 180°. Examination of specimen PP56562 used horizontal two-fold expansion with projections over 360° (for details see Friis et al. 2014).

The fossil seeds are housed in the palaeobotanical collections of the Field Museum, Chicago (PP numbers) and in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm (S numbers), where also raw data are stored.

New names of fossil plants are being registered in the Plant Fossil Names Registry, which is hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany (IOP), each with a unique registry number.
Text-fig. 1. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images of *Rightcania kvacekii* gen. et sp. nov. from the Early Cretaceous Puddledock locality, Virginia, USA (Holotype, PP56562, Puddledock sample 185). a, b) Volume renderings showing surface of abraded fruit with four ovules/seeds in apical (a) and lateral (b) view; note irregularly arranged exotesta cells that give rise to a faintly undulate surface pattern. c, d) Transverse orthoslices through fruit and seeds from close to the base (c; orthoslice xy0852) and from the middle of the fruit (d; orthoslice xy0615) showing four ovules/seeds of which two are fully developed (1, 2) and two are aborted or underdeveloped (3, 4); outer integument composed of an outer layer of non-lignified cells (exotesta, oi-ex) and an inner layer (endotesta, oi-en) of crystal cells with endoreticulate infillings; inner integument composed of an outer layer (exotegmen, ii-ex) of smaller cells and inner layer of larger cells (meso- and endotegmen, ii-en); note that the meso- and endotegmen is well-preserved in the underdeveloped seeds, but crushed in the fully developed seeds. e) Transverse orthoslice (xy0997) through the basal part of a seed showing cells of exotesta (oi-ex), endotesta (oi-en), exotegmen (ii-ex) and partly preserved embryo (arrow). Scale bars = 500 µm (a–d); 250 µm (e).
Systematic palaeobotany

Subdivisio Angiospermae Lindley, 1830
Family Chloranthaceae R.Br. ex Sims, 1821
Genus Rightcania E.M.Friis, P.R.Crane et K.R.Peder sen gen. nov.

Type. Designated here, Rightcania kvacekii E.M.Friis, P.R.Crane et K.R.Peder sen gen. et sp. nov.

Plant Fossil Names Registry Number. PFN000104 (for new genus).

Etymology. Rightcania is an anagram of Canrightia to indicate similarity to this fossil genus.

Diagnosis. Fruit a berry with three to five ovules/seeds and a fruit wall of thin-walled parenchyma cells. Stigmatic area sessile, indistinct. Hypanthium fused to lower part of ovary wall. Ovules pendent, orthotropous
to semi-orthotropous, bitgmic, endotesta with a testa of multiple cell layers. Exotesta of several layers of slightly elongate, irregular wavy cells; endotesta a single layer of cubic to palisade-shaped cells containing densely spaced crystals and fibrous infillings. Outer surface of endotesta smooth. Tegmen several cell layers thick; exotegmen of elongated fibrous cells, mesotegmen and endotegmen with large, slightly elongate and thin-walled cells; inner layers of tegmen crushed in mature seeds. Embryo tiny; nutritive tissue of isodiametric thin-walled cells.

Comments on the genus. The fruit wall of Rightcania is abraded, but remains of the hypanthium are preserved in one specimen indicating that the floral organization was semi-inferior as in the extinct cloranthoid genus Canrightia (Friis and Pedersen 2011). Other floral features are unknown, but Rightcania is also similar to Canrightia in having several orthotropous ovules/seeds enclosed in a thin-walled, probably fleshy fruit, and in having seeds with a seed coat structure closely similar to that of extant and fossil Chloranthaceae. Rightcania is very rare in the Puddledock mesofossil assemblages and include three-, four- and five-seeded fruits, whereas in the more abundant Canrightia material from Portugal the number of seeds varies between two and five (Friis and Pedersen 2011).

Prominent resin bodies in the fruit wall are characteristic for Canrightia, but have not been observed in Rightcania. Whether this reflects poor preservation of the fruit wall or original absence is unknown. Rightcania also differs from Canrightia in its thicker outer testa composed of several layers of irregular sclerenchyma cells, as well as its thicker endotesta. In both genera the inner integument (tegmen) is several cells thick with the exotegmen consisting of thick-walled cells, and the meso- and endotegmen composed of larger and thin-walled cells. The cells of the tegmen are well preserved in ovules that are not mature, but they are collapsed or consumed in mature seeds. In Canrightia the endotegmen is developed as a distinctive endothelium of radially elongated cells, while in Rightcania the endotegmen is less distinct and less clearly differentiated from mesotegmen, as is also the case in Canrightiopsis. Canrightiopsis is distinguished from Rightcania by its one-seeded fruits and thicker cell walls of the meso- and endotegmen (Friis et al. 2015).

**Rightcania kvacekii** E.M. Friis, P.R. Crane et K.R. Pedersen sp. nov.

Text-figs 1–2

**Holotype.** Designated here, PP56562 (Puddledock sample 185; illustrated here on Text-figs 1a–e, 2a–d).

**Plant Fossil Names Registry Number.** PFN000105 (for new species).

**Paratypes designated here.** PP56566 – PP56568 (Puddledock sample 183); PP56564, PP56565 (Puddledock sample 185); PP56593, PP56599 (Puddledock sample 189).

**Repository.** Palaeobotanical Collections, Department of Geology, The Field Museum, Chicago, Illinois, USA (PP).

**Etymology.** The name kvacekii is in honor of Zlatko Kvaček for his contribution to palaeobotany.

**Type locality.** Puddledock locality, former Tarmac Lone Star Industries (Vulcan Materials Co.) sand and gravel pit, located south of Richmond and east of the Appomattox River in Prince George County, Virginia, USA (37° 15′ 52″ N, 77° 22′ 10″ W).

**Type stratum and age.** Basal part of Subzone IIB, Potomac Group; Early Cretaceous (early to middle Albian).

**Diagnosis.** As for the genus.

**Distinguishing features for Rightcania kvacekii.** As for the genus.

**Dimensions.** Length of fruit: 1.6‒2.9 mm; width of fruit: 1.1‒2.18 mm.

**Description and remarks.** Rightcania is based on about 40 dispersed fruits and seed fragments, all preserved as lignite. The fruits are mostly three- or four-seeded, rarely five-seeded. The fruits are abraded, and one four-seeded fruit has remains of a hypanthium fused to the fruit wall. There is no other information on the attachment or organization of the flower.

The fruits are obovate in lateral view, almost circular in transverse section (Text-fig. 1a–d), about 1.6‒2.9 mm long and 1.1‒2.18 mm in diameter, with three to five ovules/ovules/seed(s) enclosed in a thin-walled, probably fleshy fruit, and in having seeds with a seed coat structure closely similar to that of extant and fossil Chloranthaceae. Rightcania is very rare in the Puddledock mesofossil assemblages and include three-, four- and five-seeded fruits, whereas in the more abundant Canrightia material from Portugal the number of seeds varies between two and five (Friis and Pedersen 2011).
seeds. The fruit wall is preserved near the fruit apex and also in small, scattered regions over the seed surface, but it is generally abraded (Text-fig. 2a, c–e). It is composed of thin-walled, more or less isodiametric, parenchyma cells. Cavities that may indicate the former presence of ethereal oil cells are occasionally present in the ground tissue of the fruit wall, but unequivocal resin bodies that would provide more definitive evidence have not been observed.

Well-preserved internal details revealed by synchrotron radiation X-ray microtomographic microscopy (SRXMT) of a larger, four-seeded specimen (Holotype, PP 56562), show that this fruit was mature or close to maturity with two fully developed seeds and two underdeveloped or aborted ovules/seeds (Text-figs 1c–e, 2a). The fruit is unilocular and the seeds are radially arranged, perhaps indicating that the gynoecium is syncarpous and evolved from three to five carpels each with a single seed.

The ovules/seeds are attached apically (Text-fig. 2f) and are slightly shorter than the fruit. The ovules/seeds are elliptical to obconical in lateral view; rounded at the chalazal end (apical) and slightly pointed at the micropylar end (basal). The seeds are triangular to almost circular in transverse section with flattened or concave contact faces (Text-fig. 1a, c, d). The stigma is poorly preserved, but was apparently sessile.

The ovules/seeds are orthotropous to hemi-orthotropous, bitegmic and endotestal. The outer integument is composed of an exotesta and endotesta. The exotesta is composed of elongated sclerenchyma cells, several cell layers deep arranged longitudinally in an irregularly wavy pattern (Text-figs 1b, 2b). The separation between the exotesta of adjacent seeds is often not distinct, which can give the fruit the appearance of being septate. However, the separation is clear close to the fruit wall (Text-fig. 2e). The exotesta is up to 120 µm thick adjacent to the carpel wall and 70 µm thick between the seeds.

The endotesta has a smooth outer surface and is composed of cubic to palisade-shaped crystal cells, one cell layer deep. The cells have densely packed crystals internally that are seen as cubic imprints in the cell lumen, which is otherwise filled by an endoreticulate infilling of fibres (Text-figs 1c–e, 2a, c). The endotesta is about 60 µm thick adjacent
to the carpel wall and about 30 µm thick along the contact faces between the seeds.

In the holotype analysed using SRXTM the cells of the tegmen are mostly crushed in the fully developed seeds (Text-figs 1c–e, 2a), whereas in the two ovules/seeds that are thought to be underdeveloped or aborted (Text-figs 1c, d, 2a), the tegmen is better preserved. In the fully developed, and also in the underdeveloped or aborted ovules/seeds the exotegmen consists of narrow, thick-walled cells. Meso- and endotegmen are only well preserved in the aborted or undeveloped ovules/seeds, where they consist of several layers of larger, thin-walled cells. The tegmen probably served as a nutritive tissue for the developing embryo and was consumed in the two fully mature seeds.

A tiny embryo is partly preserved in one of the fully developed seeds (Text-figs 1c, e, 2a). It is positioned close to the micropyle and is formed of minute, almost isodiametric cells. The embryo is surrounded by larger, thin-walled cells that comprise the remains of the nutritive tissue and are interpreted as cells of the endosperm (Text-fig. 2a).

**Kvacekispermum E.M.Fris, P.R.Crane et K.R.Pedersen gen. nov.**

**Type.** Designated here, *Kvacekispermum rugosum* E.M.Fris, P.R.Crane et K.R. Pedersen gen. et sp. nov.

**Plant Fossil Names Registry Number.** PFN000106 (for new genus).

**Etymology.** The name *Kvacekispermum* is in honor of Zlatko Kvaček for his numerous contributions to palaeobotany.

**Diagnosis.** Seeds broadly obovate in lateral view and almost circular in transverse section with coarsely rugulate to reticulate surface formed from the uneven outer surface of endotesta in which the depressions are arranged in poorly defined grooves. Stigmatic area sessile on the fruit apex, slightly raised, hemispherical. Ovule pendent, orthotropous, bightemig, endotestal. Endotesta comprised of a single layer of palisade-shaped cells with densely spaced crystals and fibrous infillings. Tegmen crushed in mature seeds. Embryo tiny; nutritive tissue of isodiametric thin-walled cells.

**Comments on the genus.** The fruit wall of *Kvacekispermum* is abraded except in the region of the stigma. There is no indication of floral organization or pollen, and detailed comparison with the floral organization in *Canrightia* and *Canrightiopsis* is not possible. However, *Kvacekispermum* is similar to *Canrightiopsis* in having a pendent, orthotropous and bightemig ovule/seed with a thick endotestal seed coat. The shape of the seed, together
with the central position of the stigma, also indicate that *Kvacekispermum* had single-seeded fruits similar to *Canrightiopsis*. Both also have a tiny embryo surrounded by a nutritive tissue of small, equiaxial cells with thin cell walls. *Kvacekispermum* is distinguished from seeds of *Canrightiopsis* by the coarsely rugulate surface of the endotesta, which contrasts with the foveolate endotesta surface characteristic of all species of *Canrightiopsis*.

The fossil fruits and seeds of *Kvacekispermum* and *Canrightiopsis* share many features with fruits and seeds of extant *Ascarina*, *Sarcandra* and *Chloranthus*, but *Canrightiopsis* is distinguished from the extant taxa by features of its androecium. Floral organisation is not known for *Kvacekispermum*, but the seed is distinguished from seeds of extant taxa by its thicker seed coat and the coarsely rugulate surface of the endotesta.

*Kvacekispermum rugosum* E.M.Friis, P.R.Crane et K.R.Pedersen sp. nov.

*Text-figs* 3, 4

*Holotype*: Designated here, S174951 (Vale de Água 141; illustrated here on *Text-figs* 3a–f, 4a–f).
Plant Fossil Names Registry Number. PFN000107 (for new species).

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History (S).

Etymology. The specific epithet is from Latin rugosus: wrinkled.

Type locality. Vale de Água locality, Portugal (39° 37′ 15″ N, 08° 51′ 30″ W).

Type horizon and age. Early Cretaceous (late Aptian – early Albian; basal part of the Figueira da Foz Formation).

Diagnosis. As for the genus.

Distinguishing features for *Kvacekispermum rugosum*. As for the genus.

Dimensions. Length of seed: 1.14 mm; width of seed: 1.04 mm.

Description and remarks. *Kvacekispermum rugosum* is known from a single well-preserved seed. The seed is abraded, and the fruit wall is missing except near the apex where stigma is preserved. There is no information on organization of the flower, but synchrotron radiation X-ray microtomographic microscopy (SRXMT) of the seed (Holotype, S174951) has revealed fine details of the endotesta and nutritive tissue.

The seed is broadly obovate in lateral view, almost circular in transverse section, about 1.14 mm long and 1.04 mm in diameter, with rounded (apical) chalazal region and slightly pointed (basal) micropylar region (Text-figs 3a–f, 4a–e). The stigmas, at the seed apex is sessile, slightly raised and hemispherical (Text-fig. 3a–d). The position of the stigma and the shape of the seed, as well as comparison to fruits and seeds of *Canrightiopsis*, suggest that the fruits of *Kvacekispermum* were one-seeded.

The seed is orthotropous and pendent, bitegmic and endotestal. The seed surface is coarsely rugulate to reticulate due to differences in the size of the cells comprising the endotesta with the resulting depressions arranged in poorly defined grooves. The endotesta is 60–125 µm thick consisting of a single layer of palisade-shaped crystal cells with endoreticulate infillings of fibres and imprints of small cubic crystals (Text-figs 3c–e, 4a, c). The crystals appear to be more densely packed close to the outer surface of the irregular grooves in the coarsely rugulate to reticulate surface (Text-fig. 4c, d). The exotesta consists of small, thin-walled cells that are preserved only in small patches in the grooves of the endotesta. The tegmen is collapsed in the mature seed, but the narrow, longitudinally arranged cells of the exotegmen are well preserved (Text-fig. 4a–d, f).

The embryo is not preserved, but there is a very small well-defined embryo cavity (Text-figs 3c, f, 4a, e) indicating that the embryo was tiny. The surrounding nutritive tissue consists of thin-walled cells that do not show signs of shrinkage (Text-fig. 4a, b, d, e). Based on comparison with extant angiosperms the nutritive tissue is interpreted as endosperm.

Discussion

Comparison of *Rightcania kvacekii* and *Kvacekispermum rugosum* with other fossils

*Rightcania kvacekii* and *Kvacekispermum rugosum* are characterized by their pendent, orthotropous, bitegmic and endotestal ovules/ seeds, in which the endotesta is composed of one layer of crystalliferous cells infilled with fibrous endoreliculum. Among extant angiosperms this combination of features is known only in the ovules/ seeds of *Ascarina, Chloranthus* and *Sarcandra* (Chloranthaceae). Similar seeds are also characteristic of the extinct chloranthoid taxa *Canrightia* and *Canrightiopsis* from the Early Cretaceous of Portugal (Friis and Pedersen 2011, Friis et al. 2015), for fossil seeds associated with *Chloranthistemon* P.R. CRANE, E.M.FRIIS et K.R.PEDERSEN from the Late Cretaceous mesofossil floras of Åsen, Sweden, and for undescribed fossil seeds from Martha’s Vineyard, Massachusetts, USA (Friis, Crane and Pedersen, work in progress). *Zlatkokocarpus* J.KVAČEK et E.M.FRIIS from the early Cenomanian of the Czech Republic, is a further potentially related chloranthoid taxon with one-seeded fruits, but unfortunately details of the seed coat are unknown (Kvaček and Friis 2010).

The extinct genus *Rightcania* is especially similar to the extinct genus *Canrightia*. Both have fruits with a thin, probably fleshy, fruit wall and three to five (*Rightcania*) or two to five (*Canrightia*) seeds. It is also interesting that the...
fruits of *Canrightia* commonly include underdeveloped or aborted ovules/seeds together with fully developed seeds (Text-fig. 5f–h), as is also seen in *Rightcania*. In some cases all the seeds appear undeveloped or aborted (Text-fig. 5c, e).

Fruits and seeds of *Canrightia* are extremely common in Early Cretaceous mesofossil floras from Portugal. The number of seeds per fruit varies from two in almost all specimens from the Famalicão mesofossil flora (Text-fig. 5b, c, e, f), to three to five in specimens from the mesofossil floras of Arazede, Buarcos, Catefica, Vale de Agua and Vila Verde 2. All specimens from these localities are encompassed in a single species, *Canrightia resinifera* E.M.FRiis et K.R.pedeRsen (Friis and Pedersen 2011), although further refinement of species limits may be possible as additional specimens are discovered. A further species of *Canrightia* with three ovules/seeds (Text-fig. 5g, h) has recently been discovered from the Torres Vedras mesofossil assemblage (Friis, Crane and Pedersen, work in progress).

Most specimens of *Canrightia resinifera* have densely spaced resin bodies in the fruit wall that are thought to represent fossilized ethereal oil cells (Text-fig. 5a–f), but the occurrence of resin bodies is most pronounced in charcoalfied specimens from the Famalicão locality. Resin bodies are not as obvious in lignified specimens, for example from the type locality at Catefica. In specimens of *Rightcania* the fruit wall is generally abraded and there are no traces of resin bodies. It is uncertain whether this is because of abrasion or because they were not present in the original fruit wall.

*Rightcania* is known from about 40 specimens in the Puddledock flora, mostly with three and four seeds, rarely with five seeds. The number of seeds falls within the range of *Canrightia* although a larger sample may have documented a greater range. The main differences between the two genera are the much thicker seed coat in *Rightcania*, and nature of exotesta and tegmen (compare Text-figs 1–2 with Text-fig. 5). In *Rightcania* the endotesta is 30–60 µm thick while in *Canrightia* the thickness is 20 µm. In *Rightcania* the endotesta is also much thicker and very pronounced between the seeds, whereas in *Canrightia* it is thin and only seen as a very thin zone between the seeds (Text-fig. 5e, f). The most marked difference between the two genera is the nature of the tegmen. In underdeveloped or aborted ovules/seeds of *Canrightia* there is a distinct and evenly developed endothelium of radially elongate cells internal to the smaller cells of exo- and mesotegmen (Text-figs 5c, e, f), whereas in *Rightcania* the tegmen is less evenly developed and the cells of the meso- and endotegmen are of more or less similar size (Text-figs 1c, d, 2a). *Rightcania* is more like *Canrightiopsis* than *Canrightia* in features of the tegmen. In *Canrightiopsis* underdeveloped or aborted ovules/seeds the meso- and endotestal cells are of more or less equal size (Text-fig. 6e–g) and the tegmen is often fragmented.
perhaps partly reflecting consumption of the tegmen cells by the developing embryo.

Flowers of Canrightia were bisexual and perigynous, characterized by a short hypanthium fused to the ovary wall. The floral organization is not always clear, but there are specimens that clearly show the tips of tiny tepals on the rim of the hypanthium in a radially symmetrical arrangement. Each tepal has a stamen (stamen scar) that is opposite the tepal, not alternating as in the floral diagram of Doyle and Endress (2014). The fruit wall that encloses all the seeds (Text-figs. 5g, h) shows that the gynoecium of Canrightia develops into a single fruit and was not apocarpous as indicated by Doyle and Endress (2014). The fruit wall is abraded in Rightcania, but remains of the hypanthium are preserved in one specimen: this indicates a floral organization similar to that of Canrightia with semi-inferior ovary and hypanthium fused to the ovary wall. Also the apical and radial arrangement of ovules/seeds indicates that the gynoecium of Rightcania was syncarpous formed from three to five carpels. Although a possible scar is present at the top of the hypanthium it is not clear whether the flowers of Rightcania were bisexual. This, together with the differences in details of the seed coat, warrant the establishment of a new genus.

The seed of Kvacekispermum rugosum is closely similar to seeds of the extinct genus Canrightiopsis. In addition to similarities in seed coat and ovule/seed organization the two taxa are also very similar in the size of the embryo and cellular details of the endosperm (compare Text-figs 3, 4 with Text-fig. 6). Kvacekispermum differs, however, in the coarsely rugulate surface of the endotesta.

Canrightiopsis occurs abundantly among Early Cretaceous mesofossils from Portugal and includes three species, C. intermedia E.M.Friis, G.W.Grimm, M.M.Mendes et K.R. Pedersen, C. crassitesta E.M.Friis, G.W.Grimm, M.M.Mendes et K.R.Pedersen and C. dinisi E.M.Friis, G.W.Grimm, M.M.Mendes et K.R.Pedersen, as well as several taxa referred to as Canrightiopsis sp. (Friis et al. 2015). All seeds of Canrightiopsis have distinctly foveolate surface to the endotesta with small cavities in longitudinal furrows, which contrasts with the coarsely rugulate to reticulate surface of Kvacekispermum. Canrightiopsis also includes several well-preserved specimens in which the fruit wall is preserved and shows the scars of the stamens, conclusively demonstrating that the fruit was unilocular, one-seeded and with a dorsally displaced androecium of three separate stamens. In the single seed of Kvacekispermum only small patches of the tissues outside the endotesta (exotesta and fruit wall) are present and the poor preservation does not allow inferences about the androecium and hypanthium. The position of the stigma on top of the seed, together with the rounded transverse section of the seed, indicate that as in Canrightiopsis the seed was produced in a unilocular and one-seeded fruit.

Conclusion

The orthotropous organization of Rightcania and Kvacekispermum seeds, coupled with the characteristic structure of the endotesta, which is composed of a single layer of crystalliferous cells with endoreticulate infillings, place the fossils among chloranthaceous angiosperms. These two new genera therefore further expand the extinct diversity of chloranthoid angiosperms known before the end of the Early Cretaceous. Rightcania also provides the first evidence of the Canrightiopsis-Canrightiopsis complex outside of the Portuguese mesofossil floras, indicating that this group of extinct genera, which are closely related to Ascarina, Chloranthus and Sarcandra, were also widespread in parallel to the broad distribution of early Hedyosum-like forms.

Rightcania is also significant in demonstrating that extinct early chloranthoids with more than one seed were common among Early Cretaceous members of the group. This feature is not seen among the four extant genera of Chloranthaceae, which highlights the limitations of inferring detailed patterns of character evolution based on data from extant taxa alone. Together with abundant evidence of many other extinct taxa at this level of angiosperm evolution (Friis et al. 2018a, b) the potential impacts of extinct chloranthoid diversity on phylogenetic relationships at the base of the angiosperm tree could also be profound.

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