Welwitschioid diversity in the Early Cretaceous: evidence from fossil seeds with pollen from Portugal and eastern North America

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Abstract

Bicatia gen. et sp. nov. from the Early Cretaceous of the Northern Hemisphere is described based on three species of dispersed seeds: Bicatia costata from the Juncal and Famalicão localities (western Portugal) and the Kenilworth locality (eastern North America), B. juncalensis from the Juncal locality, and B. rugosa from the Puddledock locality (eastern North America). Seeds of B. costata and B. rugosa are known from both lignitised (Juncal, Kenilworth, Puddledock) and charcoalified specimens (Famalicão, Puddledock), whereas seeds of B. juncalensis are known only from lignitised material (Juncal). All three species have the same characteristic chlamydospermous organisation seen in the wide range of other Early Cretaceous seeds that have been assigned to the Bennettitales-Erdtmanithecales-Gnetales (BEG) group. However, the species of Bicatia differ from all previously described BEG seeds in having a disymmetrical and flattened seed envelope with more or less distinct lateral wings. All three species are also closely associated with polyplicate pollen grains that have a prominent distal colpus. Pollen grains of this kind are very similar to those of extant Welwitschia. The combination of seed and pollen features seen in Bicatia provides the strongest documentation so far of Welwitschia-like plants in the Northern Hemisphere during the Early Cretaceous.

Keywords: charcoal, chlamydospermous seeds, fossil seeds, Gnetales, mesofossils, polyplicate pollen, Portugal, Potomac Group, Welwitschia

Over the past 30 years, an unanticipated benefit of increased palaeobotanical exploration for Early Cretaceous angiosperms has been a dramatic expansion of the fossil record of Gnetales (Friis et al. 2011). Beginning with the recognition of Eoanthera zherikhini Krassilov from the Early Cretaceous of Siberia (Krassilov 1986) and Drewria potomacensis Crane & Upchurch in the Drewry’s Bluff leaf bed in the Potomac Group of eastern North America (Crane & Upchurch 1987), the early fossil record of Gnetales is now extensive. Probable Gnetales have been described co-occurring with early angiosperms in Early Cretaceous fossil floras from Brazil (Rydin et al. 2003; Dilcher et al. 2005; Kunzmann et al. 2009, 2011; Löwe et al. 2013; Ricardi-Branco et al. 2013), China (Rydin et al. 2006b; Yang 2010), Mongolia (Krassilov 1982), eastern North America (Crane & Upchurch 1987; Rydin et al. 2006a), Portugal (Rydin et al. 2004, 2006a) and Russia (Krassilov 1986). In particular, critical examination of mesofossil floras from eastern North America and Portugal has recovered a diverse complex of small seeds characterised by a distinctive chlamydospermous organisation in which a thickened seed envelope surrounds a thin integument that has a long micropylar tube (Friis et al. 2007, 2009, 2013). Some of these seeds are clearly of gnetalean affinity.

The pollen corresponding to most of the seeds of the Bennettitales-Erdtmanithecales-Gnetales (BEG)
group is unknown. However, some seeds (Erdtmanispermum Pedersen, Crane et Friis) contain pollen of Eucommidites Erdtman (Pedersen et al. 1989), while others (Raunsgaardispernum Mendes, Pais et Friis) contain smooth-walled monocolpate pollen grains (Mendes et al. 2008a). Several of the fossil seeds (assigned to Ephedrispermum Rydin, Pedersen, Crane et Friis and extant Ephedra L.) are very similar to the seeds of extant Ephedra and have ephedroid pollen in the micropyle (Rydin et al. 2004, 2006a).

In this paper, we add to the fossil record of BEG seeds through the description of a new genus based on mesofossils from the Juncal and Famalicão localities in the Lusitanian Basin of Portugal, and from the Kenilworth and Puddledock localities in the Potomac Group of Maryland and Virginia, eastern North America. A new genus with three species is described, and in all species, the closely associated polyplicate pollen is similar to that of extant Welwitschia Hook. f. in having a distinct distal colpus. Recognition of these seeds provides new information on the diversity of the BEG group and adds to the evidence that plants similar to extant Welwitschia were present in Early Cretaceous vegetation of the Northern Hemisphere.

Material and methods

The Early Cretaceous seeds described here are from the Juncal and Famalicão mesofossil floras collected in the Lusitanian Basin of Portugal, and from the Kenilworth and Puddledock localities in the Potomac Group of Maryland and Virginia, eastern North America. The age of these mesofossil floras ranges from Aptian-early Albian (Juncal and Famalicão) to early-middle Albian (Kenilworth, Puddledock). The geological context of the localities is described in more detail in Friis et al. (2011).

Extraction and initial preparation of the fossil seeds followed standard procedures (e.g. Friis et al. 2009). Isolated seeds were studied at high resolution using a Hitachi S-4300 Field Emission Scanning Electron Microscope at 2 kV at the Swedish Museum of Natural History, Stockholm, and 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). Specimens were mounted on aluminium stubs for scanning electron microscopy (SEM) and brass stubs for SRXTM using nail polish. Specimens mounted for SEM were coated with gold for about 60 seconds. All specimens analysed using SRXTM were also studied using SEM, either before or after the SRXTM analyses.

SRXTM imagining was carried out at 10 keV using a scCMOS detector and a 20 µm thick LAG:Ce scintillator screen. Specimens S172653, S174007 were analysed using a 10× objective (isotropic pixel size 0.65 µm), specimens S172654 and PP53915 were analysed using a 20× objective (isotropic pixel size 0.325 µm), while specimens PP53937–PP53941 were analysed using a 20× objective (isotropic pixel size 0.37 µm). For more information on the methods and their application to similar material, see Friis et al. (2014).

Seeds of extant Welwitschia for comparative studies were provided by Ernst van Jaarsveld, Kirstenbosch National Botanical Garden, South Africa.

The fossil seeds are housed in the palaeobotanical collections of the Swedish Museum of Natural History (S numbers) and in the Field Museum, Chicago (PP numbers). Specimens mounted for SEM and SXRTM have separate numbers. For each species, several unmounted specimens are also stored in box-slides under a single number.

Results

Description of the fossils

We use the term chlamydosperms for seeds with an organisation similar to that of seeds of extant
Gnetales, a group that in the older literature are often referred to as Chlamydospermae (see also Friis et al. 2013). The term is derived from Greek for cloak and seed. Chlamydospermous seeds have the nucellus surrounded by a thin, membranous integument and both the nucellus and integument enclosed by an outer, thicker layer, the seed envelope. The integument is extended apically into a long micropylar tube. The seed envelope is probably bract-derived.

Bennettitales-Erdtmanitcales-Gnetales (BEG)

Genus **Bicatia** gen. nov.

**Derivation of generic name.** – From the two-sided seed envelope (in Latin combinations: bi- for two-) and -catia’ indicating a broad similarity to other chlamydospermous seeds with a rugulate surface such as *Tomcatia*, *Cattomia* and *Acanthocatia*.

**Type species.** – *Bicatia costata* Friis, Pedersen et Crane sp. nov., designated here.

**Additional species.** – *Bicatia juncalensis* Friis, Pedersen et Crane sp. nov; *Bicatia rugosa* Friis, Pedersen et Crane sp. nov.

**Generic diagnosis.** – Seeds small, orthotropous. Integument free from seed envelope for its full length except at the base where the integument is broadly attached to the seed envelope. Integument apically extended into a long micropylar tube. Micropylar tube comprising an inner and outer epidermis. Inner epidermis lining the micropylar tube heavily cutinised. Micropylar canal open both apically and

Figure 2. SEM images showing cellular details of *Bicatia costata* sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. **A.** Outer surface of strongly compressed specimen showing epidermis of seed envelope with files of elongated cells. Note that many cells show distinctive circular thickenings (S174275). **B.** Detail of specimen shown in Figure 1D showing epidermis of seed envelope in the region of the midrib with narrow elongated cells over the midrib and wider cells laterally. Note closely spaced circular thickenings. **C.** Detail of seed in Figure 1B showing well-preserved epidermis of seed envelope with narrow elongated cells aligned in transverse rows that roughly span the space between two adjacent transverse ridges. **D.** Detail of sclerenchyma over seed body showing transversely elongated cells with thick walls and distinct fine pitting (S174280). Scale bars – 200 µm (A), 50 µm (B, D), 100 µm (C).
also farther down; without cellular closure. Seed envelope disymetric, two-winged and flattened, elliptical to obtriangular in dorsi-ventral view, narrowly elliptical in transverse section. One face typically convex, the other convex, flat or concave. A longitudinal midrib may or may not be present on one or both faces. Surface of seed envelope almost smooth, rugulose or rugose with transversely aligned ridges that may branch and anastomose. Seed envelope extended in the micropylar region into a short apical projection that supports the micropylar tube. Papillae absent in the micropylar region. Inner epidermis of seed envelope composed of relatively large, longitudinally elongated polygonal cells with thin cell walls. Outer epidermis of seed envelope composed of longitudinally elongated cells with a thick cuticle and sometimes with prominent circular thickenings. Sclerenchyma zone of seed envelope with several layers of narrow, elongated cells, that are aligned transversely over the main seed body, but aligned longitudinally laterally near the wings and towards the inside of the seed. Parenchyma zone of small equi-axial cells, especially well-developed laterally where this zone between the sclerenchyma and outer epidermis contributes to the formation of the wings. Pollen polyplicate, monocolpate.

**Distinguishing features of the genus.** – *Bicatia* is distinguished from all other currently known chlamydo- spermous fossil seeds by the flattened, disymetrical seed-envelope that is weakly or distinctly winged. Flattened of the seed envelope is probably dorsi-ventral. Sometimes both faces are convex. In other cases, one face is convex and the other face is flat or slightly concave. However, all seeds are found dispersed and there is no information how they were attached to the reproductive axes.

Seeds of *Acanthocatia* Friis, Pedersen et Crane, *Cattomia* Friis, Pedersen et Crane, *Quadrispernum* Friis, Pedersen et Crane, *Rugonella* Friis, Pedersen et Crane and *Tomcatia* Friis, Pedersen et Crane (Friis et al. 2009, 2013) are similar to seeds of *Bicatia* in their rugose surface, which results from the uneven distribution of sclerenchyma in the seed envelope. These previously described seeds are distinguished from seeds of *Bicatia* in having micropyle closure by the radial extension of the inner epidermal cells of the integument. Cellular closure of the micropyle tube has not been observed in any specimens of *Bicatia*. A similar open micropyle tube occurs in seeds of extant and fossil *Ephedra*, and apparently also in extant *Welwitschia* (see Discussion section). Seeds of extant *Welwitschia* are also similar to those of *Bicatia* in being chlamydospermous with lateral wings. However, in *Welwitschia* the wings and seed envelope are papery and are characterised by long fibres arranged in a chevron-like pattern: a feature not seen in *Bicatia*. A similar chevron-like pattern does occur, however, in the seed envelope of *Buarcospermum* Friis, Pedersen et Crane, another BEG seed described from the Early Cretaceous of Portugal and North America (Friis et al. 2009). Pollen associated with *Bicatia* is polyplicate, as in extant *Ephedra* and *Welwitschia*. However, while the pollen of *Ephedra* is acolpate, the pollen of both *Bicatia* and *Welwitschia* has a single, elongate colpus.

**Comments on the genus.** – Three species are currently included in the genus *Bicatia*, but the nature of their preservation varies and the generic diagnosis is based on information from both charcoa- lised and lignitised specimens. Charcoalified specimens typically have good cellular preservation (*B. costata* from the Famalíçao locality and *B. rugosa* from the Puddledock locality) and detailed information on the integument and other internal structures, such as lack of papillae in the micropylar region, has only been obtained from this material. Lignitised specimens (*B. juncalensis* and *B. costata* from the Juncal and Kenilworth localities and a single specimen of *B. rugosa* from the Puddledock locality) rarely have internal anatomical details preserved, but generally have good preservation of epidermal features and associated pollen.

SRXTM analysis of charcoalified specimens of *Bicatia costata* from Famalíçao and of *B. rugosa* from the Puddledock locality documents very similar organisation and structure of the seed envelope, which unites two different species of the genus from the two regions. Both species also have distinctive circular thickenings in the epidermis cells that are sometimes arranged in prominent rows. The association of all three species with the same kind of polyplicate and monocolpate welwitschioid pollen further corroborates their close relationship and justifies their inclusion in the same genus.

Wings are well-preserved in both of the species known from Portugal (*Bicatia juncalensis* and *B. costata*), which comprises mainly lignitised material, but they are only poorly developed in the North America species (*B. rugosa*), which comprises mainly charcoalified and abraded specimens. Whether wings were originally present in *B. rugosa* and were later abraded, or whether they were only poorly developed
is not possible to establish based on the material currently available.

*Bicatia costata* sp. nov.

Figures 1–4.

**Derivation of specific epithet.** – From the ribbed surface of the seed envelope.

**Specific diagnosis.** – As for the genus with the following additions: Seed envelope elliptical to ovate in outline with a pointed apical protrusion and a slightly concave base. Lateral wings narrow, of almost the same width from base to apex. Surface of seed envelope rugose with irregular transversely oriented ridges. Cells of outer epidermis of the seed envelope longitudinally aligned; narrowly elongate over the midrib, shorter laterally with small circular thickenings along the cell walls.

**Distinguishing features of the species.** – Seeds of *Bicatia costata* are similar to those of *B. juncalensis* in size, in having distinct wings, and in the general organisation of sclerenchyma cells of the seed envelope. They differ, however, in the pronounced rugose surface of the seed envelope, which is smooth to rugulose in *B. juncalensis*, and in the epidermal cells of the seed envelope, which are generally larger than in *B. juncalensis* and have distinct circular thickenings. Seeds of *B. costata* are also distinctive in their elliptical outline, which contrasts with the obtriangular outline of *B. juncalensis*. Seeds of *B. costata* are similar to those of *B. rugosa* in general organisation, but are distinguished by their smaller size and the presence of two distinct wings. In addition, in *B. rugosa* both faces of the seed envelope are typically convex, the transverse ridges are more pronounced and the surface pattern they form is more irregular. Pollen associated with *B. costata* is very similar to that of *B. juncalensis* in size and shape, but is considerably smaller than that of *B. rugosa*.

**Dimensions.** – Length of seeds: 0.65–0.85 mm; width of seeds: 0.5–0.75 mm (specimens from Juncal); length of seed: 1 mm; width of seed: 0.9 mm (specimens from Famalicão). Pollen grains: 15–18 µm long (specimens from Juncal).

**Holotype.** – S174086 (sample Juncal 70), designated here; illustrated in Figures 1A, H, 4B, D.

**Paratypes.** – S172654, S174087–S174091, S174260–S174283, S174293 (sample Juncal 70; in total 276 specimens); S174259, S174298 (sample Juncal 71; in total three specimens); S174306 (sample Juncal 64; one specimen).

**Other material.** – PP54027 (sample Kenilworth 061, in total two specimens).

**Other specimens examined.** – S174007, S174307 (sample Famalicão 25, in total two specimens).

**Type locality.** – Clay pit close to the village of Juncal, Portugal (39° 35′ 42″ N; 08° 54′ 00″ W).

**Type stratum.** – Famalicão Member, Figueira da Foz Formation (late Aptian–early Albian).

**Description and comments on the species.** – The material includes about 280 seeds from the Juncal locality and two seeds from the Famalicão locality. Two specimens have also been recovered from the Kenilworth locality in Maryland, USA. Specimens from Juncal and Kenilworth are lignitised and strongly compressed: Internal cellular structures are either not preserved, or are only poorly preserved. However, the specimen from Famalicão is charcoalfied and the cellular details of the seed envelope are well-preserved. Tissues internal to the seed envelope are homogenised and lack cellular details. There is a slight size difference between the specimens from the two localities, with the Famalicão seeds slightly larger (1 mm long and 0.9 mm wide) than the Juncal...
specimens (0.65–0.85 mm long and 0.5–0.75 mm wide). However, the specimens from both localities are sufficiently similar in morphology and in their epidermal features that we include them here in the same species. SRXTM analyses of the Famalicão specimen (S174007) provided information on cellular details. SRXTM of one specimen from the Juncal locality (S172654) provided only a rough overview of the distribution of sclerenchyma and softer tissue.

All seeds are found isolated and there is no information on their attachment to the reproductive axis. The seed envelope surrounding the seed proper is disymmetrical, flattened (Figures 1H, 3G) and elliptical to ovate in outline. The two lateral wings are of almost the same width from base to apex, and are typically about 0.15 mm wide. At the apex, the seed envelope is extended into a narrow projection around the micropyle, and at the base a distinct concave area marks the probable point of seed attachment (Figures 1A–E, 3A–C). The nucellus and integument are poorly preserved.

One face of the seed-envelope is typically convex with a raised longitudinal rib down the midline (Figures 1A, D, E, 3A). The other face is usually flat or concave and lacks the midrib (Figure 1C) although a midrib is occasionally present when the face is concave (Figure 1B). On both faces, the seed envelope has 7–11 irregular transversely oriented ridges. On the convex face, these transverse ridges typically extend from the inner borders of the wings to the longitudinal rib (Figures 1A, D, E, 3A), but they may also extend over it. On the flat or concave face, the transverse ridges often extend over the middle of the seed envelope (Figure 1C). In other cases, the ridges branch near the middle (Figure 1B).

The seed envelope is 50 µm thick over the main body of the seed. The outer epidermis is usually well-preserved and consists of longitudinally aligned,
Figure 5. SEM images (A–D) and SRXTM reconstructions (E, F) of lignitised specimens of Bicatia juncalenensis sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. A. Seed showing concave face of seed envelope, distinct apical elongation of the seed envelope around the micropylar tube, and lateral wings that broaden towards the apex giving the seed envelope an obtriangular outline (holotype; S172590). B. Seed showing concave face of seed envelope and well-developed lateral wings (S172591). C. Seed showing concave face of seed envelope. Note outlines of narrow elongated epidermis cells and the outline of transversely elongated sclerenchyma cells below the epidermis over the middle of the seed, as well as equiaxial cells of the wing (S174284). D. Detail of holotype showing the apical elongation of the seed envelope around the micropylar tube. Note pollen grain protruding from micropylar tube (see detail in Figure 7A). E. Voltex reconstruction of seed in oblique apical view showing convex face, indistinct transverse ridges, distinct midrib and thin lateral wings with equiaxial cells (arrow). F. Voltex reconstruction of the seed in Figure 5E showing the apical elongation of the seed envelope, the lateral wings composed of equiaxial cells (arrow) and the thickening of the sclerenchyma over the midrib and along the inner borders of the lateral wings (S172653). Scale bars – 500 µm (A–C, E, F), 100 µm (D).
narrow, elongated cells. Cells over the midrib are
narrower than those laterally (Figures 1G, 2A–C).
The cells form transverse rows that roughly span the
space between two adjacent transverse ridges
(Figure 2C). Small ring-shaped structures some-
times appear close to the anticlinal cell walls
(Figure 2A, B) and in the very narrow epidermal
cells over the midrib, they occur in a row
(Figure 2B). The details of these ring-shaped struc-
tures are unknown, but they may represent pores
with prominently thickened borders in the inner
anticlinal walls of the epidermal cells.

The seed envelope consists mainly of scleren-
chyma cells except for the wings, which are com-
posed of an epidermis that encloses parenchyma or
collenchyma cells. The sclerenchyma cells that
comprise most of the seed body are long and nar-
row, with thick, strongly pitted cell walls
(Figure 2D). Towards the inside, the sclerenchyma cells
are longitudinally elongated and are especially
well-developed close to the wings, whereas towards
the outside, the sclerenchyma cells are mainly trans-
versely elongated (Figures 2D, 3C, F, G). The
parenchyma or collenchyma cells comprising the
wings are almost isodiametric with relatively thin
and pitted cell walls (Figures 1F, 3B, C, E–G).
Cells close to the inner border of the wing are
larger, while those of the outer part of the wing are
smaller (Figure 3C, F, G).

Pollen grains were observed on two of the ligni-
tised specimens from Juncal (Figures 1A, H, 4A–D),
but not on the single charcoalified seed from
Famalicão. The grains are polyplicate, monocolepate
and broadly elliptical with rounded to slightly
pointed ends. They are 15–18 µm long and about
12 µm wide (Figure 4A–D). A single colpus extends
for almost the full length of the grain (Figure 4A–D).
It is broad with a granular to verrucate colpus mem-
brane (Figure 4A, C). The tectum is irregular, and
sometimes slightly sinuous along the margin of the
colpus (Figure 4A). About 20 ridges (plicae) sepa-
rated by narrow furrows (striae) extend parallel to
the long axis of the grain and are of various lengths.
The longest plicae and striae reach almost to the
ends of the grain. The tectum is psilate.

*Bicatia juncalensis* sp. nov.

Figures 5–7.

Derivation of specific epithet. – From the Juncal locality, where the fossils were collected.

Specific diagnosis. – As for the genus with the follow-
ing additions: Seed envelope obtriangular in outline with a pointed base. Lateral wings broader near apex of seed. Surface of seed envelope smooth, or with indistinct, transversely aligned ridges. Cells of outer epidermis of seed envelope narrowly elongated and longitudinally aligned.
Distinguishing features of the species. – See distinguishing features for Bicatia costata.

Dimensions. – Length of seeds: 0.8 mm; width of seeds: 0.9 mm. Pollen grains: about 17 µm long.

Holotype. – S172590 (sample Juncal 70), designated here; illustrated in Figures 5A, D, 7A.

Paratypes. – S172588, S172589, S172591, S172653, S174092, S174284—S174288 (sample Juncal 70; in total 16 specimens), S174258 (sample Juncal 71; one specimen); S174304, S174305 (sample Juncal 64; in total two specimens).

Type locality. – Clay pit close to the village of Juncal, Portugal (39° 35′ 42″ N; 08° 54′ 00″ W).

Type stratum. – Famalicão Member, Figueira da Foz Formation (late Aptian–early Albian).

Description and comments on the species. – Specimens assigned to this species have only been recovered from the Juncal locality. The material includes 20 specimens, all found isolated. All are lignitised and strongly compressed. There is no information on how they were attached to the reproductive axis.

The seed envelope is obtriangular in outline and flattened, with lateral wings that are broader near the apex and narrow towards the base (Figure 5A–C, E, F). One face is typically slightly concave with a more or less distinct longitudinal rib down the middle of the seed (Figures 5F, 6C). The other face is usually flat or slightly concave with or without midrib. Apically, the seed envelope tapers into a long projection around the micropyle (Figure 5A–F). The attachment area at the base of the seed envelope is slightly pointed or truncate. The outer epidermis of the seed envelope is well-preserved and composed of longitudinally elongated cells. The cells over the midrib are narrower than those in more lateral positions (Figure 6A). The surface of the seed envelope appears smooth, but SXRTM reveals faint transverse ridges that extend from the inner borders of the wings to the midrib (Figure 5E).

Internal cellular details are not well-preserved, but SXRTM analyses show the same general organisation of the seed envelope as in Bicatia costata. The main body of the seed envelope is thick, and probably composed of sclerenchyma cells. These
sclerenchyma cells are narrow and longitudinally elongated in the lateral parts of the seed envelope (Figure 6B). Over the middle of the seed envelope the sclerenchyma cells are transversely elongated (Figure 5C). The cells of the wing are equiaxial, thin-walled and strongly compressed (Figure 6C).

Polyplicate pollen grains have been found inside the micropylar tube of the holotype (Figure 7A) and similar grains occur attached to the surface of the seed envelope of another specimen (S172589; Figure 7B–D). The grains are elliptical to almost spherical in polar view, about 17 µm long and about 10–17 µm wide. The single colpus extends for almost the full length of the grains, but grains with the distal face exposed are not well-preserved (Figure 7B). The tectum is psilate. The number of plicae is estimated to about 20. They are of various lengths with some reaching almost to the ends of the grains (Figure 7A, C, D).

*Bicatia rugosa* sp. nov.

Figuers 8–10.

*Derivation of specific epithet.* – From the irregular transverse ribs that give the surface of the seed envelope a distinctly rugose appearance (Lat. *rugosus* for ‘wrinkled/rugose’).

*Specific diagnosis.* – As for the genus with the following additions: Seed narrow to broadly elliptical in outline with pointed apex and rounded to pointed base. Lateral wings not well-developed (or not well-preserved). Surface of seed envelope rugose with irregular, transversely oriented, sometimes anastomosing, ridges. Median part of both faces raised, but lacking distinct midrib. Transverse ridges usually divide over the median ridge. Outer cells of the epidermis longitudinally aligned.

*Distinguishing features of the species.* – Seeds of *Bicatia rugosa* are similar to those of *B. costata* and *B. junca-lensis* in the general organisation of the seed envelope, sclerenchyma cells and the presence of transverse ridges. However, *B. rugosa* differs from both in the more irregular arrangement of the transverse ridges, which often branch and anastomose. In *B. rugosa*, the lateral wings also appear poorly developed compared to those of *B. costata* and *B. junca-lensis*. However, most specimens of *B. rugosa* are abraded with only the sclerenchyma tissue preserved. It is therefore possible that wings were present, but abraded prior to preservation. Pollen grains associated with *B. rugosa* are considerably larger (24–30 µm) than those of *B. junca-lensis* and *B. costata* (17.5 µm and 15–17.5 µm respectively).

*Dimensions.* – Length of seeds: 0.8–1.3 mm; width of seeds: 0.8–1.0 mm. Pollen grains: 24–30 µm long.

*Holotype.* – PP53939 (sample Puddledock 082), designated here; illustrated in Figures 8A–C, 9A–D, F, G, I.

*Paratypes.* – PP53915–PP53922, PP53937, PP5338, PP53940, PP53941, PP54000–PP54006 (sample Puddledock 082; in total about 135 specimens); PP53897, PP54007 (sample Puddledock 083; in total four specimens).

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

*Type stratum.* – Basal part of Subzone IIIb, Potomac Group; Early Cretaceous (early–middle Albian).

*Description and comments on the species.* – The material includes 140 specimens from the Puddledock locality, most of which are charcoaled. However, there are also a few lignitised specimens. Six specimens were studied using SXRTM (PP53915, PP53937–PP53941).

None of the seeds are found attached to the reproductive axis and how they were borne is...
unknown. The seeds are chlamydospermous with the integument almost completely enclosed in the seed envelope. The seed envelope is elliptical and flattened with a short apical projection around the micropyle and slightly pointed or rounded base (Figure 8A, C, E). In transverse sections, the seed envelope is disymmetrical and flattened (Figure 9B–E), except in the micropylar region where it is rounded (Figures 8B, D, 9A). Both faces of the seed-envelope are usually convex (Figure 9D, E), but one face may be only slightly convex or flat. There is usually a broad, indistinct midrib or raised area on both seed surfaces. Both surfaces also have irregular transversely aligned ridges, which usually divide and anastomose over the raised area/midrib to form a coarse irregular reticulate pattern (Figures 8A, C, E, 10A).

The integument is membranous and typically is not well-preserved, except apically where it forms a distinct micropylar tube that is circular in transverse section and contains the micropylar canal (Figures 8B, D, F, 9A–C, G). The integument is free from the seed envelope (Figures 8D, 9E) except at the base where it is broadly attached. The micropylar tube (Figures 8B, D, 9A–C) consists of only two cell layers, the outer and the inner epidermis. Both layers are well-preserved in several of the specimens studied by SXRTM. The inner epidermis is distinctive in being heavily cutinised and is the only cell layer present near the extreme apex of the micropylar tube (Figures 8F, 9A, B, G). The outer epidermis is more delicate and is present only farther down the tube (Figure 9C). In transverse section, the micropylar tube is seen as a ring around the micropylar canal and is open for its full length, down as far as the top of the nucellus (Figure 9A–C, G).

The seed envelope is thick and consists mainly of sclerenchyma cells. Most specimens are abraded and the outer epidermis of the seed envelope is either not preserved or is poorly preserved. In a few cases, the remains of narrow, elongated and longitudinally aligned cells are preserved. Circular thickenings are observed in the epidermal cells, very similar to those of Bicatia costata. The inner epidermis of the seed envelope consists of narrow, thin-walled cells that are longitudinally aligned (Figure 8F). The inner part of the seed wall lining the micropylar tube is smooth without papillae (Figures 8D, F, 9A, B, G, H).

In most specimens, the seed envelope is represented only by a thick layer of sclerenchyma cells. These cells vary considerably in shape and size as well as in their orientation (Figure 9D, E, H, I). Typically, however, they are long and narrow with thick, strongly pitted cell walls. The sclerenchyma layer has a thin inner zone of longitudinally elongated cells. These longitudinally aligned cells are most conspicuous along the lateral margins of the seed, bordering the narrow wings (Figure 9D, E, H), but also occur over the main body of the seed (Figure 9D, E). In the middle part of the sclerenchyma layer, there is a distinct zone of narrow cells that are transversely elongated (Figure 9D, E, H) and towards the outside, there is another layer of larger, more irregular cells. These larger, outer sclerenchyma cells have characteristic wall thickenings composed of variously oriented narrow ridges (Figures 8B, 9D, E, I). Cells forming the wings are small and equiaxial (Figure 9D, E), perhaps parenchymatic or bulliform.

Numerous pollen grains were observed on the surface of a single lignitised specimen (PP53915, Figure 10A, B). The grains are polypricate, 24–30 μm long and 10–12 μm wide. The single colpus is distinct and extends for almost the full length of the grains (Figure 10B, E, F). Plicae are of various lengths with approximately every second plica longer.
and the intermediate plicae shorter (Figure 10D–G). The long plicae extend almost the full length of the pollen grains leaving only a very small smooth region without plicae at both ends of the grains. Plicae are dense on the proximal face (Figure 10D, G), but more sparse on the distal face where there is usually a broad laevigate zone bordering the colpus (Figure 10 E, F). A granular infratectal layer is seen in a few damaged pollen grains (Figure 10C).

**Discussion**

Occurrence of Bicatia in Early Cretaceous mesofossil floras. – Except for two specimens of Bicatia costata from the Famalicão locality, Bicatia is in Portugal restricted to the Juncal mesofossil assemblage, in which it is particularly conspicuous. In North America, Bicatia is known currently only from the Kenilworth and Puddledock localities. At all
localities, *Bicatia* occurs in a diverse assemblage of angiosperms, other seed plants and remains of ferns and lycopsids. However, the abundance of *Bicatia* in these mesofossil floras varies considerably. At the Juncal locality, a light-coloured bed with a diverse macrofossil flora, consisting mainly of angiosperm leaf impressions occurred between darker layers of soft clays and silt with mesofossils. These Juncal mesofossil assemblages are relatively poor both in the number of species and in the number of specimens, but some samples are dominated by seeds of *Bicatia*. From Juncal sample 70, about 400 seeds and other mesofossil were picked, of which almost 300 are seeds of *Bicatia* (277 specimens of *B. costata* and 17 specimens of *B. juncalensis*). A single seed of *Quadrispernum parvum* Friis, Pedersen et Crane is the only other representative of the BEG group in this sample. There are only few angiosperm species in the Juncal mesofossil flora, and the individual species are typically represented by a single or few specimens only. In the associated macrofossil flora, there are no remains that can be ascribed confidently to *Bicatia*. Instead, the macrofossil flora is dominated by diverse angiosperm remains (Friis et al. 1994b).

The two seeds of *Bicatia costata* in the Famalicão mesofossil flora contrast strongly with its abundance at Juncal. The two mesofossil floras are strikingly different. While Juncal is depauperate both in species and number of specimens, Famalicão is rich both numerically and in species diversity. The Famalicão mesofossil flora includes thousands of specimens, most of them angiosperms. A preliminary survey identified more than 100 different species of angiosperms (Eriksson et al. 2000) of which *Camriottia resinifera* Friis et Pedersen is particularly abundant (Friis & Pedersen 2011). There are also a variety of other seeds related to the BEG group in the Famalicão flora including species assigned to *Ephedrispernum, Lobospermum* Friis, Pedersen et Crane, *Quadrispernum* Friis, Pedersen et Crane and *Tomicatia* (Friis et al. 2009, 2013).

The Puddledock mesofossil flora is more like that from Famalicão than that from Juncal. It is also diverse and includes thousands of specimens. As in the Famalicão flora, angiosperms predominate (Crane et al. 1994) and several species have been named (Friis et al. 1994a, 1997; von Balthazar et al. 2007, 2011). The BEG group is also well-represented in the Puddledock flora. In addition to the *Bicatia* fossils described here, there are also seeds assigned to *Acanthocatia, Cattonia, Buarcospermum, Lignerispernum* Friis, Pedersen et Crane, *Lobospermum, Quadrispernum, Rugonella* and *Tomicatia* as well as several taxa that remain to be described.

The Kenilworth mesofossil flora has been less intensively studied than the three other mesofossil floras mentioned here although it is rich both in specimens and in species. The plant assemblage is dominated by fruits and seeds of angiosperms, of which only *Anacostia* Friis, Crane et Pedersen has been investigated in detail (Friis et al. 1997). *Anacostia* is also abundant in the Famalicão flora. In addition to angiosperm fossils, the Kenilworth mesofossil flora also comprises diverse seeds assignable to the BEG group including *Lignerispernum* and several undescribed forms.

**Comparison to extant plants**

While seeds with a chlamydospermy organisation comparable to that seen in *Bicatia* were diverse during the Early Cretaceous, among extant plants, they are known only in the three genera of Gnetales: *Ephedra, Gnetum* L. and *Welwitschia*. In both seed and pollen characters, *Bicatia* is most comparable to *Welwitschia*. Like *Bicatia*, *Welwitschia* has bilateral symmetrical and winged seeds. In *Welwitschia*, the seed envelope and wings are formed from a pair of bracts, which may also have been the case in *Bicatia*, to judge from the midrib on both surfaces of the seed envelope in some *Bicatia* seeds. *Bicatia* and *Welwitschia* are also similar in having polylicate and monocolpate pollen with a long, broad colpus and psilate colpus margin. However, while the pollen associated with *Bicatia* is similar to that of extant *Welwitschia* in shape, morphology, aperture configuration, and presence of granular infratectal layer, it is considerably smaller than the relatively large pollen grains of the extant genus.

Seeds of *Ephedra* and *Gnetum* differ from those of *Bicatia* and *Welwitschia* in having a seed envelope that lacks wings and that may be four-, three- or sometimes two-parted. In some species of *Ephedra*, such as *Ephedra alata* Decne., a wing may be present, but is then formed from other bracts associated with the seeds, not from the seed envelope (Rydin et al. 2010). The rugulate arrangement of transverse ridges seen in the seed envelope of a few extant species of *Ephedra*, such as *Ephedra rhytidosperma* Pachomova, is also different from those of *Bicatia*. In *Ephedra*, the ridges are formed by thickening of the cuticle (Ickert-Bond & Rydin 2011), while in *Bicatia*, the ridges are formed from sclerenchyma cells. Pollen of *Ephedra* also differs from that of *Bicatia*. *Ephedra* pollen is polylicate, but there is no distinct colpus. Pollen of *Gnetum* is non-plicate and also lacks a distinct colpus.

The details of the micropyle in *Welwitschia* and *Bicatia* are also similar. In *Welwitschia*, the integument around the micropyle is extended into a long
tube and the inner epidermis is strongly cutinised. It forms a straight hollow tube around the micropylar canal (Pearson 1909; Sykes 1911; Martens 1971; Carafa et al. 1992). Both *Bicatia* and *Welwitschia* also lack the cellular closing mechanism of the micropylar canal that is characteristic of extant *Gnetum* (Berridge 1911) as well as many fossil chlamydospermous seeds (Friis et al. 2006, 2009, 2013). An open micropylar tube and canal, as seen in *Welwitschia* and *Bicatia*, is also seen in *Ephedra*. However, in *Ephedra* the seed envelope has a papillate lining around the micropyle (Thoday & Berridge 1912; Martens 1971; Rydin et al. 2010). This has not been observed in *Bicatia* and *Welwitschia*.

Notwithstanding the strong similarities between the seeds of *Bicatia* and *Welwitschia* several distinguishing features preclude placing the fossils in the living genus. Most notably, seeds of *Welwitschia* have large papery wings and the sclerenchyma cells of the seed envelope form a distinct chevron pattern. Pollen of *Welwitschia* is also much larger, than that associated with *Bicatia*, around 60 µm long (see illustrations in Rydin & Friis 2005) in contrast to around 15–18 µm in *B. costata* and *B. juncaensis*, and around 24–30 µm in *B. rugosa*.

**Comparison to other fossil chlamydospermous seeds**

Fossil seeds with a chlamydospermous organisation are common and diverse in the Early Cretaceous mesofossil floras of Portugal and North America. Currently, about 30 species have been identified. Of these, 17 species have been formally named and assigned to eleven extinct genera (*Acanthocatia*, *Buarcospermum*, *Cattomia*, *Ephedrispermum*, *Erdmanispernum*, *Lignierspermum*, *Lobospermum*, *Quadrispermum*, *Raunsgaardispernum*, *Rugonella*, *Tomcatia*) or to the extant genus *Ephedra* (Pedersen et al. 1989; Rydin et al. 2006a; Mendes et al. 2008a, 2008b; Friis et al. 2009, 2013). Several of these seeds have a rugulate surface formed by the uneven distribution of sclerenchyma cells in the seed envelope as occurs in *Bicatia*, but none of them have the combination of features seen in the three new *Bicatia* species and none have so far been associated with *Welwitschia* type pollen.

The fossil chlamydospermous seeds assigned to *Acanthocatia*, *Buarcospermum*, *Cattomia*, *Ephedra*, *Ephedrispermum*, *Lignierspermum*, *Lobospermum*, *Quadrispermum*, and *Tomcatia* all have a four-parted seed envelope, while the seed envelope of *Rugonella* and *Erdmanispernum* is three-parted. Among previously described BEG seeds only those of *Raunsgaardispernum* are disymmetric like those of *Bicatia*, but in this case there are other important differences. Most notably, the seed envelope of *Raunsgaardispernum* has a smooth outer surface, there are no lateral wings, and there are papillae on the inner surface of the envelope that surrounds the micropyle. Pollen of *Raunsgaardispernum* is also non-plicate. Polyplicate grains similar to those of *Bicatia* have been observed in the micropyle of *Ephedra portugallicia* Rydin, Pedersen, Crane et Friis (Rydin et al. 2006a) and in a new species of *Ephedrispermum* (E. M. Friis, pers. observation, 2013). However, these grains lack a colpus. They are more like pollen of extant *Ephedra* than the colpate welwitschioid pollen associated with *Bicatia*.

**Comparison to dispersed polyplicate-monocolpate pollen from Early Cretaceous strata**

The fossil pollen grains associated with *Bicatia* are closely similar to several kinds of dispersed polyplicate and monocolpate grains described from Early Cretaceous palynofloras, but there is particularly similarity to the dispersed pollen grains associated with the fossil plant *Drewria potomacensis* described from the Drewry’s Bluff locality of the Potomac Group (Crane & Upchurch 1987). These pollen grains range in size from about 18 to 32 µm, which is broadly comparable to the size of pollen associated with *B. rugosa* (24–30 µm), which is also from the Potomac Group. The pollen grains associated with *D. potomacensis* are ellipsoid with a broad colpus that extends for almost the full length of the grains, as in *Bicatia*. These grains also have plicate that are similar in distribution and length to those seen in pollen grains associated with *B. rugosa*. Crane and Upchurch (1987) compared the pollen associated with *Drewria* to that of extant *Welwitschia*. They also noted several similarities to extant *Welwitschia* in the vegetative and reproductive structures of *D. potomacensis* (see later).

Dispersed polyplicate and monocolpate pollen grains assigned to extant *Welwitschia* as well as to the fossil genera *Fjugella* N. Mchedlishvili et Shakhmoundes, *Chomsipites* Smirnova and some species of *Ephedripites* Bolkhovitina ex Potonié are similar to those of *Bicatia*. Pollen grains assigned to *Welwitschia* from the Late Cretaceous (Campanian) of Spain are of comparable size (about 27–34 µm) to pollen of *B. rugosa*, but have a much greater density of more narrow ribs (Médu 1987). Even more similar are the grains assigned to the paleotaxon Barremian-monomosixeen from Barremian strata of the Warlingham Borehole, southern England. These grains closely resemble the grains associated with *Bicatia* in morphology and aperture configuration and are also comparable in size (c. 27–35 µm: Hughes 1994). Pollen grains of *Ephedripites* sp. 1 from the Early Cretaceous of Tuscany, Italy
(Trevisan 1980), are larger (33–53 µm) than those of Bictia, but otherwise similar in shape, aperture configuration as well as distribution and length of the plicae.

Chumisipites was described based on pollen grains from the Albain–Cenomanian of central Lebanon. In addition to the type species C. libanicus Smirnova, two other species from the Albain–Cenomanian of the Caspian region (C. pyriformis Smirnova and C. dzubae Smirnova) have been included in the genus. Smirnova (2010) also transferred Ephedripites zaklinskaiae Azema et Boltenhagen from the Albain–Turonian of Gabon to the genus and suggested relationship to Welwitschia for all species of the genus.

Dispersed pollen of Jugella was interpreted initially as pollen of early Araceae (Mtchedlishvili & Shakhmoundes 1973). However, comparable polyplicate pollen grains in Araceae are acolpate and Friis et al. (2004) suggested that Jugella pollen was probably more similar to that of extant Welwitschia. Pollen of the type species j. sibrica N. Mtchedlishvili et Shakhmoundes from the Barremian of Siberia is larger (45.3–47.9 µm long) than grains of the three Bictia species, but otherwise, the shape of the grains, the form of the colpus, and the spacing and distribution of plicae, is closely comparable to that associated with Bictia. Jugella claribaculata N. Mtchedlishvili et Shakhmoundes reported from the Late Hauterivian–Barremian of the Pricaspian Depression (also reported from the Barremian–Aptian Yixian Formation of north-eastern China; Li 2003) and J. gracilis N. Mtchedlishvili et Shakhmoundes from the Valanginian of the Pricaspian Depression, as well as the Berriasian of northern Ustyrt, also have pollen that is larger (around 58 µm and 50 µm respectively) than that observed for Bictia. Pollen of J. caspica N. Mtchedlishvili et Shakhmoundes from the late Barremian of the Pricaspian Depression is only slightly larger (30.1–43.3 µm) than pollen of B. rugosa, but considerably larger than that associated with the two Portuguese species of Bictia.

Dispersed pollen grains assigned to different species of Jugella have also been reported from the latest Jurassic of Argentina and Tanzania (see references in Schrank 2010). These grains are comparable in general morphology to those found in association with Bictia, but all are larger (38–52 µm). Grains of J. semistrigata Schrank also have a much broader non-plicate zone bordering the aperture (Schrank 2010). Other records of polyplicate pollen from the Early Cretaceous of Gondwana, most notably from the Crato Formation (Osborn et al. 1993), are generally of the ephedroid type that lack a colpus. Welwitschioid pollen grains have not yet been associated with any of the several macrofossils from the Crato Formation that have been linked to Welwitschia (see later).

The fossil record of Welwitschia-like plants

While the Mesozoic fossil record of polyplicate pollen is extensive, such grains are especially widespread and abundant during the Cretaceous. Most lack a distal colpus and broadly resemble pollen of extant Ephedra. However, polyplicate welwitschioid pollen grains, which are characterised by their single broad colpus, have also been described, mainly from Early Cretaceous sediments (see earlier). These records support the idea that welwitschioid plants may have been widely distributed in the Early Cretaceous and that the restricted and ecologically constrained distribution of extant Welwitschia is relictual. The discovery of bilaterally symmetrical, winged chlamydspermous seeds with associated welwitschioid pollen from the Northern Hemisphere is consistent with this conclusion.

While the extinct plants that produced fossil welwitschioid pollen and Bictia seeds are not known, the compression/impression fossils of Drevoria potomacensis (Crane & Upchurch 1987) may provide an insight into what the plants that produced Bictia seeds were like. Drevoria potomacensis was a tiny plant with stems 1–3 mm in diameter, and simple oblong leaves that were borne in an opposite and decussate arrangement. The leaves also had an unusual chevron-shaped venation resembling that of the seedling leaves of Welwitschia. Seeds of Drevoria also resemble those of Bictia in being flat, sometimes with a midrib on both faces, and in having a long micropylar tube extending beyond the seed body. However, it is not clear whether the seeds were winged as in Bictia and Welwitschia and unfortunately the preservation of Drevoria does not allow more detailed examination.

Cratonia coyledon Rydin, Mohr et Friis, a well-preserved seedling from the Early Cretaceous Crato Formation, is another macrofossil with chevron-shaped leaf venation, as well as other features that indicate a relationship with Welwitschia (Rydin et al. 2003). Other plant macrofossils from the Crato Formation that have been suggested as probably related to welwitschioid plants include the young stem Welwitschiella austroamericana Dilcher, Bernardes-de-Oliveira, Pons et Lott, isolated leaves of Welwitschiophyllum brasiliense Dilcher, Bernardes-de-Oliveira, Pons et Lott, and reproductive axes of Welwitschiostrobus murilli Dilcher, Bernardes-de-Oliveira, Pons et Lott (Dilcher et al. 2005). Friedselloella gracilifolia Löwe, Mohr, Coiffard et Bernardes-de-Oliveira, also from the Crato Formation, is a ‘whole plant’ with Ephedra-like
vegetative parts that have opposite and decussate phyllotaxis (Löwe et al. 2013). Pollen grains from male cones were described as polylicate and inaperturate, but details are lacking. Unfortunately details of the seed envelope of F. gracilifolia are also unclear, which precludes further comparison with the seeds of Bicatia.

Gurvanella dictyoptera Krassilov first described from localities in Mongolia (Krassilov 1982) and later from several localities in the Yixian Formation of north-eastern China (Duan 1998; Sun et al. 2001) is a further macrofossil of possible welwitschioid affinity from the Early Cretaceous. The genus is known mainly as compressions/impressions of isolated winged seeds, but seeds have also been found attached to axes with opposite and decussate phyllotaxis that are broadly Ephedra-like in their appearance (Duan 1998). Seeds of G. dictyoptera are much larger than those of Bicatia with large, apparently papery wings. These seeds are superficially similar to the winged seeds of Welwitschia, but their preservation as impression or thin compressions precludes more detailed anatomical comparison and confirmation of their chlamydosperous organisation.

Conclusion

The combination of seed and pollen features seen in the three Bicatia species described here provides the strongest documentation so far of Welwitschia-like plants during the Early Cretaceous. In all three species, the seeds have the same characteristic chlamydosperous organisation as in extant Gnetales, which is also seen in a wide range of other Early Cretaceous seeds that have been assigned to the BEG group. However, the seeds of Bicatia are distinctive in their disymmetrical and flattened seed envelope that has more or less distinct lateral wings, and in these respects they are similar to seeds of extant Welwitschia. Pollen grains associated with the Bicatia seeds differ from those of other species of the BEG group in being polylicate and monocolpate, again similar to pollen of extant Welwitschia. Seeds of Bicatia and Welwitschia share the heavily cutinised inner epidermis of the integument, which forms a straight tube around the micropylar canal. A significant difference between the two genera is that both the seeds and pollen in Bicatia are much smaller than extant Welwitschia, perhaps suggesting that the Bicatia plant was very different in habit from its closest living relative. Very likely it was much smaller, perhaps resembling Drewria. Many aspects of the biology and ecology of Early Cretaceous welwitschioid plants and extant Welwitschia were most likely different; however, it is interesting to note that Drewria was interpreted as a coloniser of open habits (Crane & Upchurch 1987), as is also characteristic of extant Ephedra and Welwitschia.

The link between welwitschioid seeds and welwitschioid pollen provided here by the Bicatia fossils corroborates earlier ideas that many Early Cretaceous polylicate and monocolpate pollen represent extinct Welwitschia relatives, which in turn suggests that extant Welwitschia is a relic of a once more widespread and more diverse lineage. During the Early Cretaceous, welwitschioid plants were present not only in Gondwanan regions of Africa and South America in the Southern Hemisphere, but also in north-eastern China, Central Asia, and Europe to eastern North America in the Northern Hemisphere. The long history of the welwitschioid clade established by fossils such as Bicatia, combined with greater diversity in the past and the relictual status of the extant genus, may account in part for its long branch length in phylogenetic analyses based on molecular data (McCoy et al. 2008), which in turn undoubtedly contributes to the difficulty of establishing the relationships of Welwitschia, Ephedra and Gnetum to other groups of extant plants based on molecular data. During the Early Cretaceous, the evidence from Bicatia, Ephedrispermum and other fossils of the BEG group indicates substantial extinct diversity. Ephedra, Welwitschia, and perhaps also Gnetum, are the only living survivors and descendants.

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