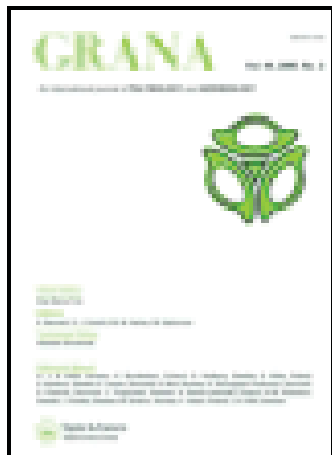


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Else Marie Friis^a, Kaj Raunsgaard Pedersen^b & Peter R. Crane^c

^a Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden

^b Department of Earth Sciences, University of Aarhus, Aarhus, Denmark

^c School of Forestry & Environmental Studies, Yale University, New Haven, USA

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

ELSE MARIE FRIIS¹, KAJ RAUNSGAARD PEDERSEN² & PETER R. CRANE³

¹Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden, ²Department of Earth Sciences, University of Aarhus, Aarhus, Denmark, ³School of Forestry & Environmental Studies, Yale University, New Haven, USA

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 charcoalfied 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 *Eoantha zherikhinii* Krassilov from the Early Cretaceous of Siberia (Krassilov 1986) and *Drewria potomacensis* Crane et 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.

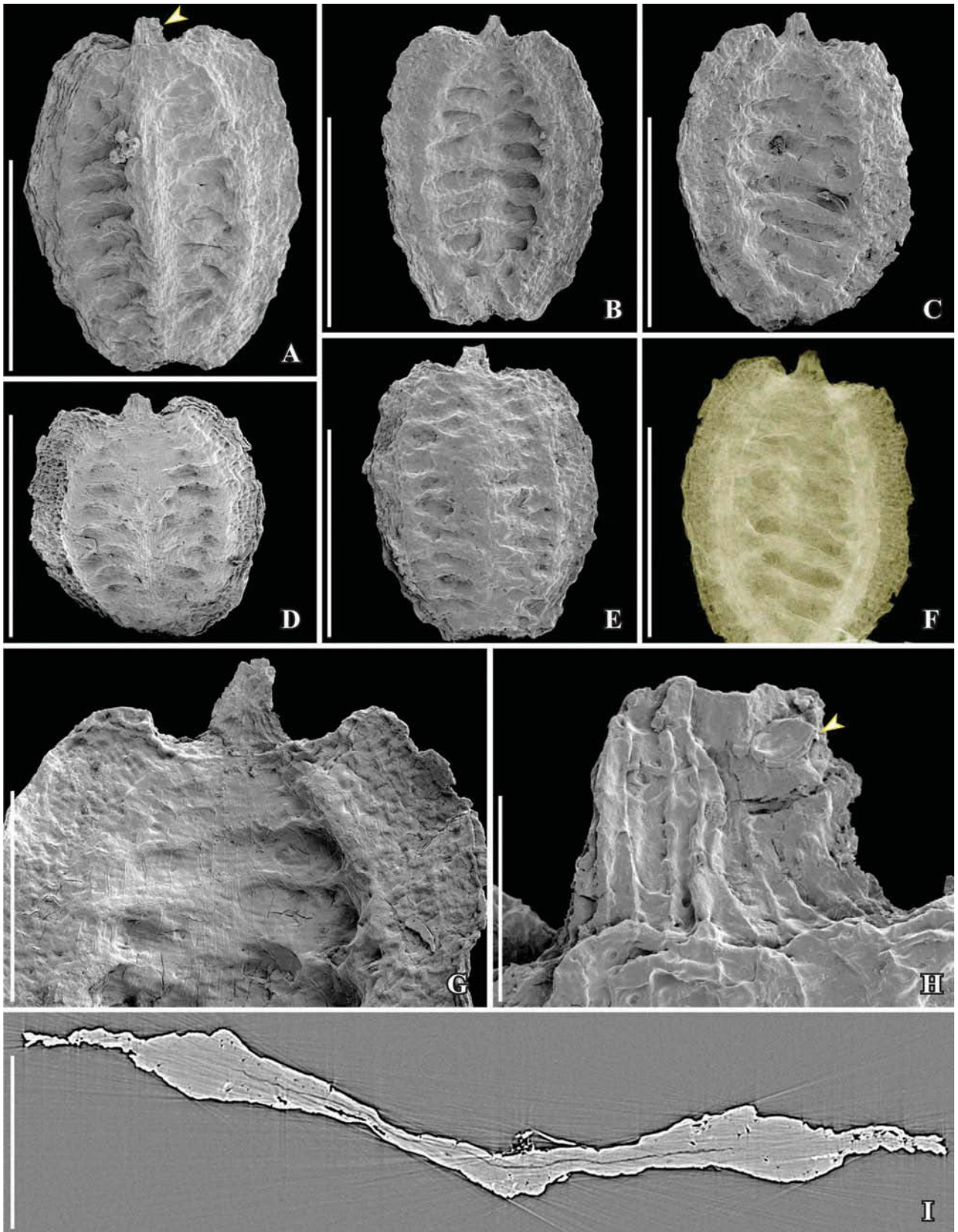
The pollen corresponding to most of the seeds of the Bennettitales-Erdtmanithecales-Gnetales (BEG)

Correspondence: Else Marie Friis, Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.
E-mail: else.marie.friis@nrm.se

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group is unknown. However, some seeds (*Erdtmanispermum* Pedersen, Crane et Friis) contain pollen of *Eucommidites* Erdtman (Pedersen et al. 1989), while others (*Raumsgaardispermum* 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, Portugal, and from the Kenilworth and Puddledock mesofossil floras collected in sediments of the Potomac Group, in 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 imaging was carried out at 10 keV using a sCMOS 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 SRXTM 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 chlamydospermous for seeds with an organisation similar to that of seeds of extant

←
Figure 1. SEM images and SRXTM reconstructions of lignitised specimens of *Bicatia costata* sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. **A.** SEM of convex face of seed showing seed envelope with narrow lateral wings, a median, longitudinal rib and two lateral ribs bordering the wings. Note the well-developed transverse ridges and the apical protrusion of the seed envelope with an adhering pollen grain (*arrowhead*) (holotype; S174086). **B, C.** SEM of concave face of seed showing seed envelope with lateral wings. Note that the midrib is poorly or only weakly developed on this face and that the transverse ridges sometimes continue over the middle of the seed or divide (**B:** S174089; **C:** S172654). **D, E.** SEM of convex face of seed showing the midrib and transverse ridges. Note the equiaxial cells of the lateral wings (**D:** S172654; **E:** S174088). **F.** SRXTM voltex reconstruction of the specimen in Figure 1C. Note the distinct equiaxial cells of the lateral wings. **G.** SEM of the apical part of seed showing the well-preserved outer epidermis of seed envelope and outlines of the equiaxial cells of the lateral wings. Note the projection of the seed envelope around the micropyle (S174270). **H.** SEM of apex of specimen in Figure 1A showing pollen grain (*arrow*) adhering to the micropylar region. **I.** SRXTM reconstruction (orthoslice) of transverse section of specimen in Figure 1C and 1F, showing the thicker sclerenchyma of the seed envelope over the seed proper and the thin lateral wings. Note that the sclerenchyma is especially well-developed along the inner borders of the wings in the position of the lateral ribs and also over the mid-rib. Scale bars – 500 µm (A–F), 200 µm (G), 50 µm (H), 100 µm (I).

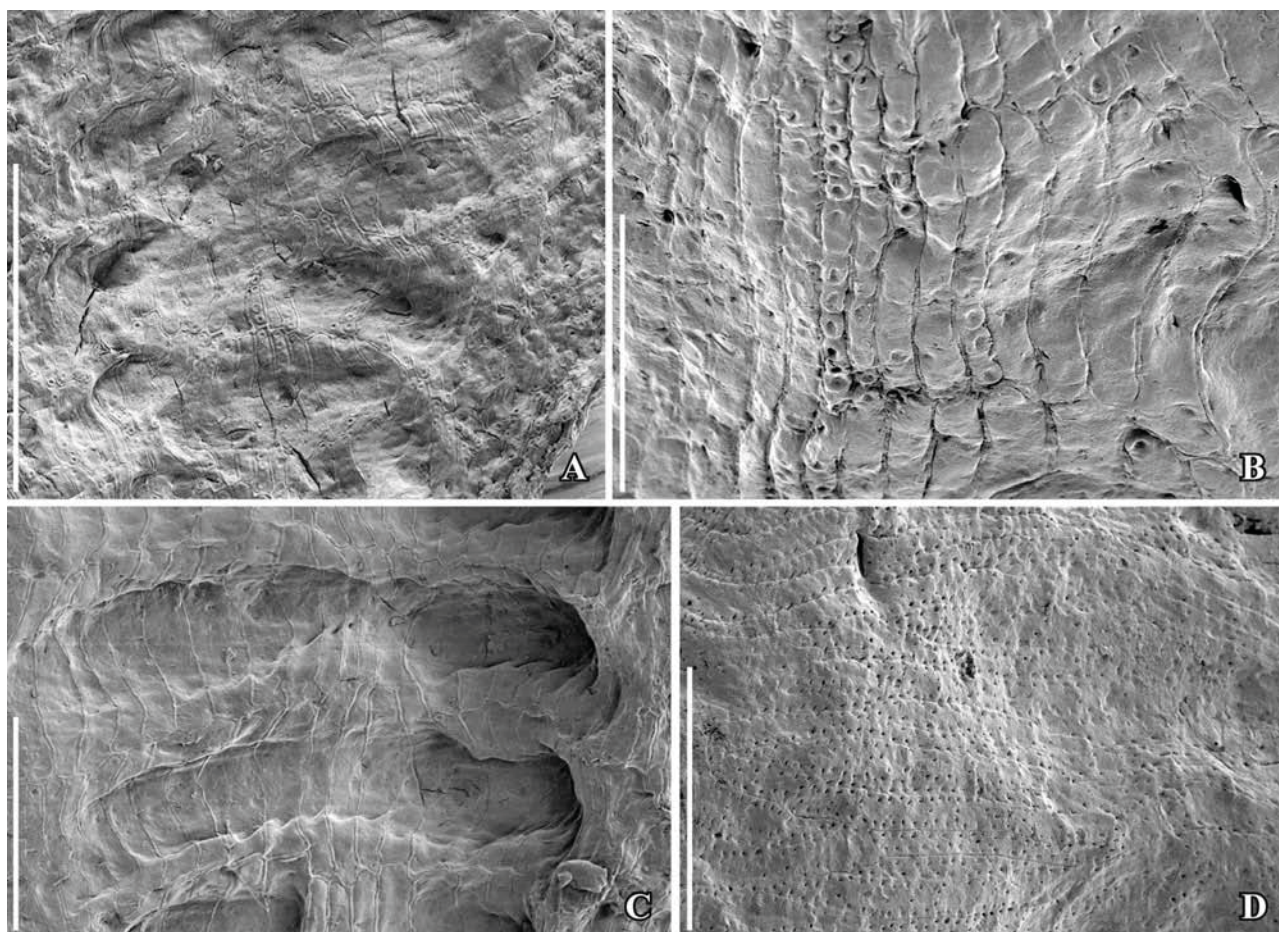


Figure 2. SEM images showing cellular details of *Bicatia costata* sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. **A.** Outer surface of strongly compressed specimen showing epidermis of seed envelope with files of elongated cells. Note that many cells show distinctive 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).

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–Erdtmanithecales–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

also farther down; without cellular closure. Seed envelope disymmetric, 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 equiaxial 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 chlamydospermous fossil seeds by the flattened, disymmetrical seed-envelope that is weakly or distinctly winged. Flattening 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.

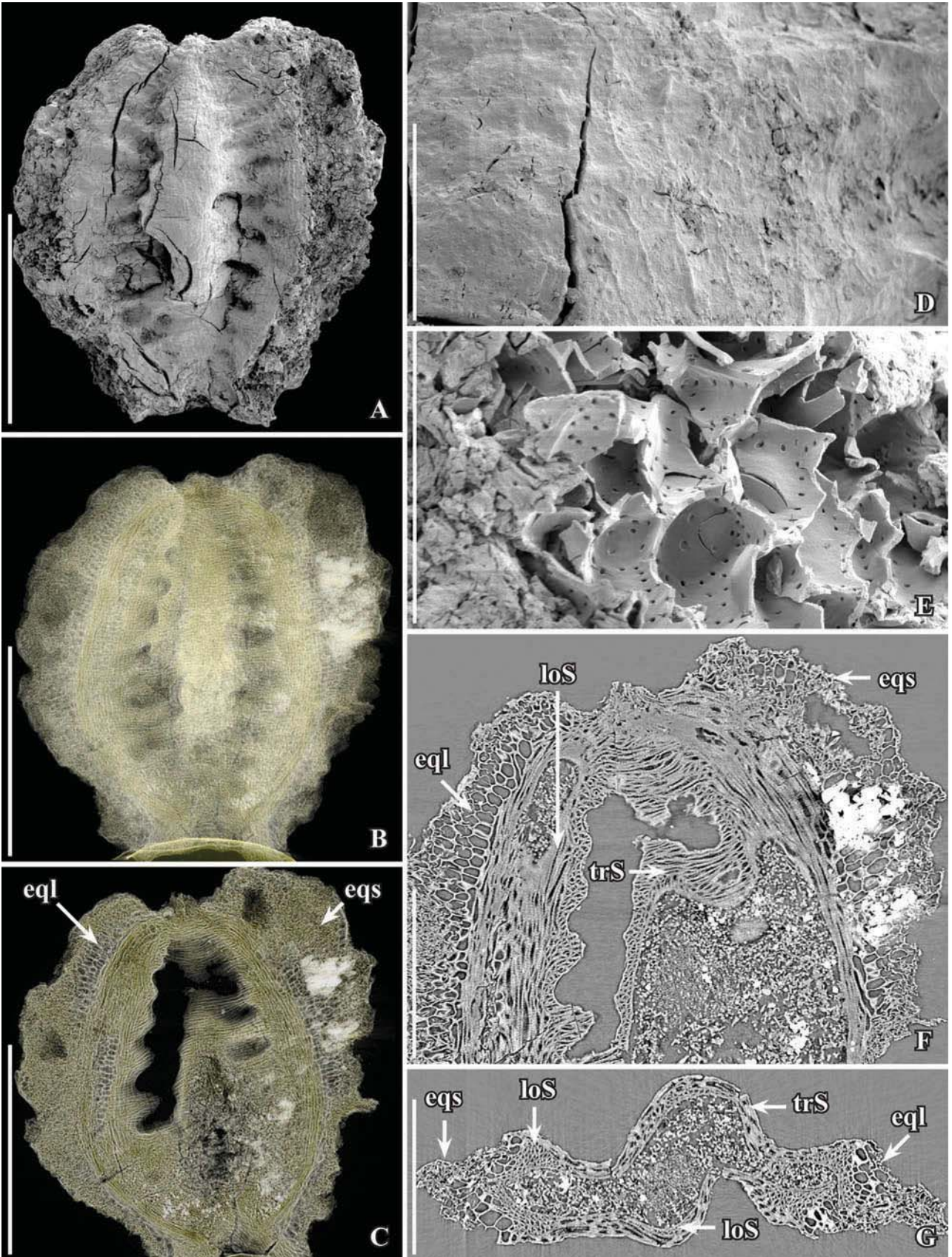
Seeds of *Acanthocatia* Friis, Pedersen et Crane, *Cattomia* Friis, Pedersen et Crane, *Quadrispermum* Friis, Pedersen et Crane, *Rugonella* Friis, Pedersen et Crane and *Tomcatia* Friis, Pedersen et Crane (Friis et al. 2009, 2013) are similar to seeds of *Bicatia* in their rugose surface, which results from the uneven distribution of sclerenchyma in the seed envelope. These previously described seeds are distinguished from seeds of *Bicatia* in having micropylar closure by the radial extension of the inner epidermal cells of the integument. Cellular closure of the micropylar tube has not been observed in any specimens of *Bicatia*. A similar open micropylar 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 charcoalified and lignitised specimens. Charcoalified specimens typically have good cellular preservation (*B. costata* from the Famalicão 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. juncaensis* 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 Famalicão 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 juncaensis* 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 (specimen 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 charcoallified 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

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Figure 3. SEM images (A, D, E) and SRXTM reconstructions (B, C, F, G) of a charcoallified specimen of *Bicatia costata* sp. nov. (S174007) from the Early Cretaceous Famalicão locality (sample Famalicão 25), Portugal. **A.** Convex face of seed envelope showing distinct midrib, narrow lateral wings and transverse ridges. **B.** Voltex reconstruction of seed showing equiaxial cells of lateral wings and narrow elongated sclerenchyma cells bordering the wings. **C.** Longitudinal section (SRXTM reconstruction, cut voltex between orthoslices 140 and 200) showing size differences among the equiaxial cells of the lateral wings, with the smaller cells (*eqs*) towards the outside and the larger cells (*eql*) towards the inside. Note the distinct, narrow, longitudinally elongated sclerenchyma cells bordering the wings and transversely aligned sclerenchyma cells over the middle of the seed. **D.** Detail of seed envelope showing outer epidermis with circular thickenings close to the anticlinal cell walls. **E.** Detail through broken part of wing showing equiaxial cells with distinctive pitting. **F.** Orthoslice reconstruction in longitudinal section showing larger (*eql*) and smaller (*eqs*) equiaxial cells of the lateral wings and narrow, elongate, transversely aligned sclerenchyma cells (*trS*) over the middle of the seed. Note longitudinally aligned sclerenchyma cells (*loS*) laterally. **G.** Orthoslice reconstruction of transverse section showing smaller (*eqs*) and larger (*eql*) equiaxial cells of the lateral wings. Note also the inner layer of sclerenchyma cells that are longitudinally elongated (*loS*) laterally and over the median part of the seed and the outer layer of sclerenchyma cells that are transversely elongated (*trS*) over most of the seed body. Scale bars – 500 µm (A–C), 50 µm (D, E), 250 µm (F, G).

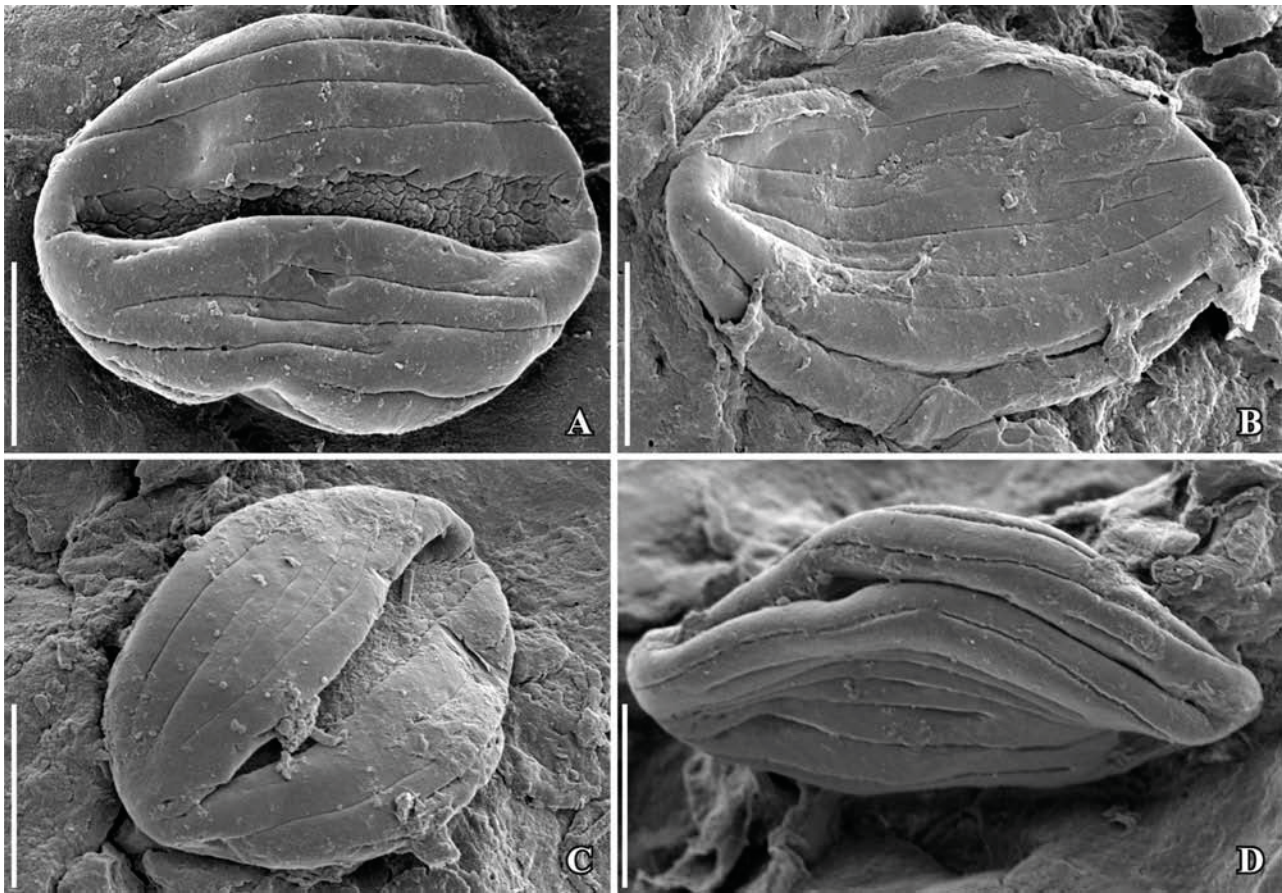


Figure 4. SEM images of pollen grains associated with lignitised specimens of *Bicatia costata* sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. **A.** Pollen grain adhering to surface of seed envelope of specimen in Figure 1E showing longitudinal ridges (plicae) and furrows (striae) as well as the long prominent colpus with a granular aperture membrane. **B.** Detail of pollen grain from holotype in Figure 1A and 1H in lateral (equatorial) view showing longitudinal ridges and furrows. Note collapse of the grain over the colpus. **C.** Pollen grain from specimen in Figure 1E showing longitudinal ridges and prominent colpus with a granular aperture membrane. **D.** Pollen grain from holotype in Figure 1A and 1H showing longitudinal ridges and furrows. Note grain folded concealing the colpus. Scale bars – 5 µm (A–D).

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 1I, 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,

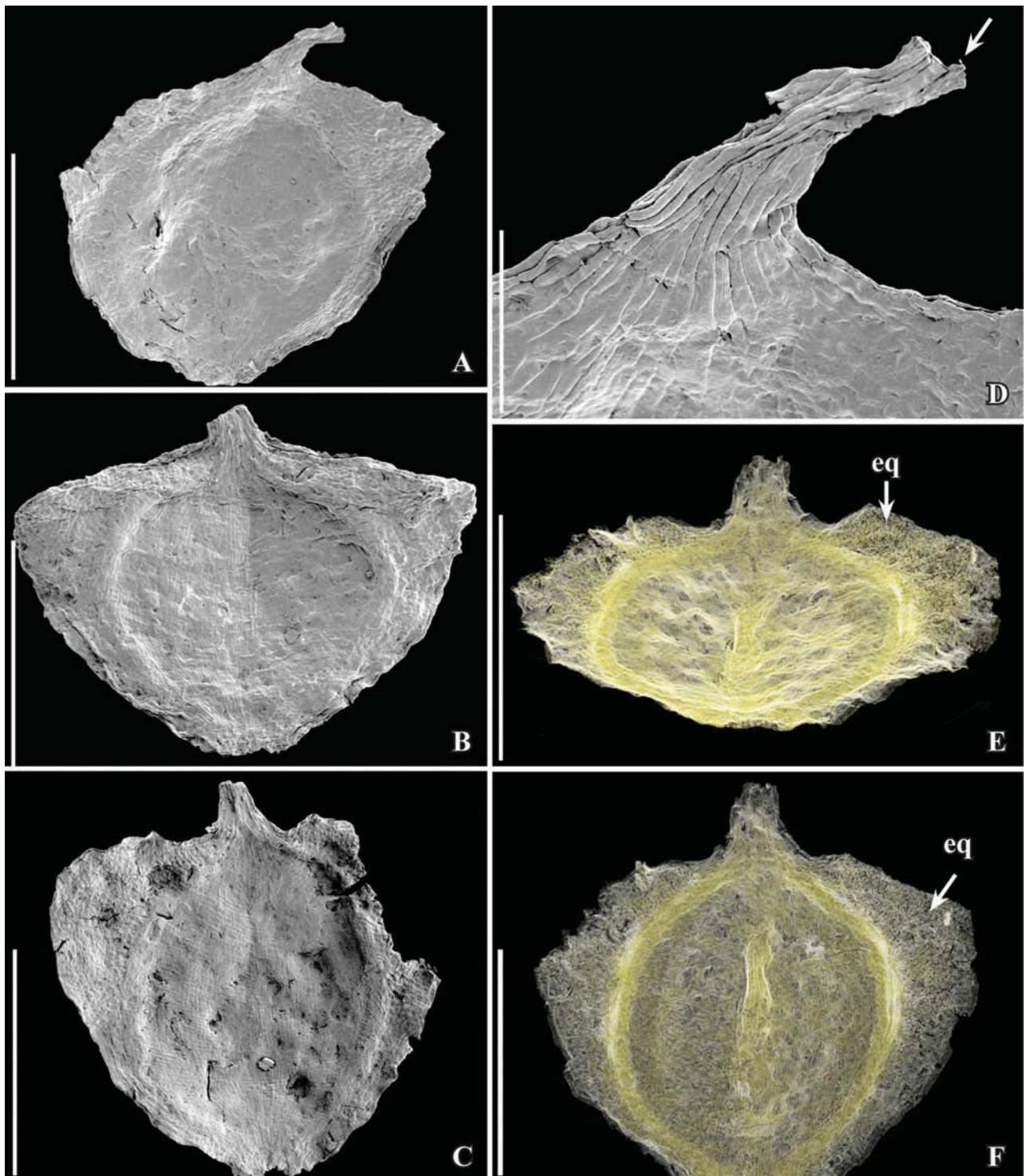


Figure 5. SEM images (A–D) and SRXTM reconstructions (E, F) of lignitised specimens of *Bicatia jumcalensis* sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. **A.** Seed showing concave face of seed envelope, distinct apical elongation of the seed envelope around the micropylar 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).

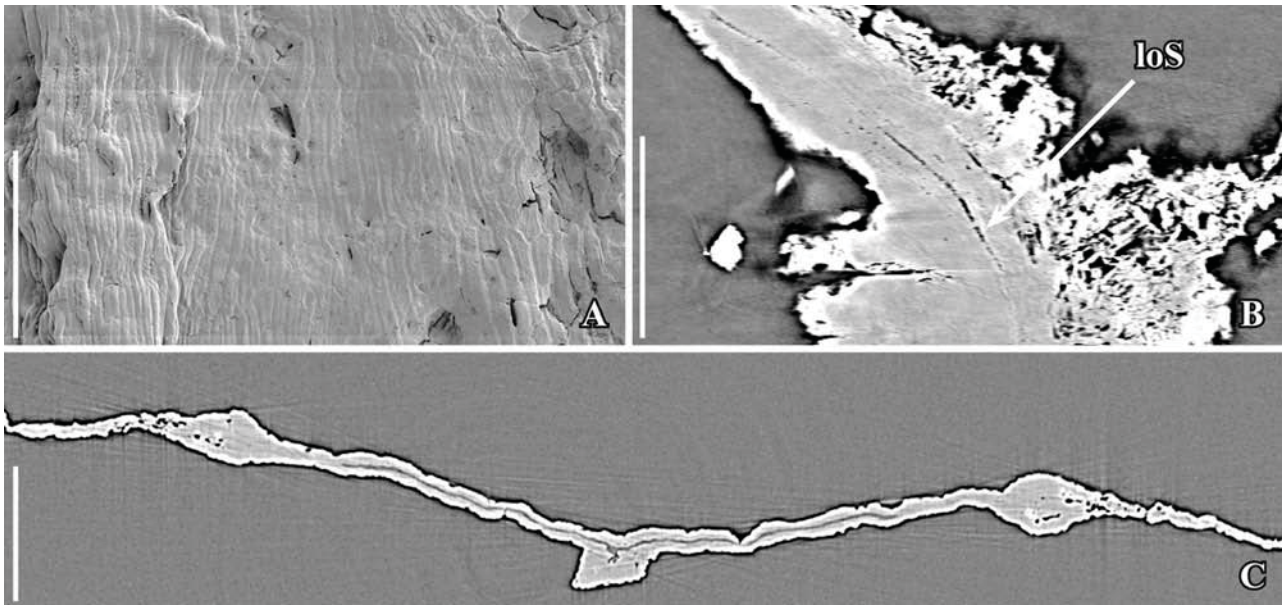


Figure 6. SEM image (A) and SRXTM reconstructions (B, C) of lignitised specimens of *Bicatia juncaensis* sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. A. Outer surface of seed showing epidermis of seed envelope with files of narrow elongated cells over the midrib and slightly wider cells closer to the margins (S172588). B. Orthoslice reconstruction of longitudinal section showing longitudinally aligned narrow sclerenchyma cells (*loS*) bordering the wing. C. SRXTM reconstruction (orthoslice) of transverse section of specimen in Figure 5E and 5F showing the thick sclerenchyma over the body of the seed and thin lateral wings. Note that sclerenchyma is particularly thick along the inner borders of the wings and over the midrib. Scale bars – 100 μm .

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 sometimes 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 structures 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 sclerenchyma cells except for the wings, which are composed of an epidermis that encloses parenchyma or collenchyma cells. The sclerenchyma cells that comprise most of the seed body are long and narrow, 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 transversely 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 lignitised specimens from Juncal (Figures 1A, H, 4A–D), but not on the single charcoaled seed from Famalicão. The grains are polyplicate, monocolpate 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 membrane (Figure 4A, C). The tectum is irregular, and sometimes slightly sinuous along the margin of the colpus (Figure 4A). About 20 ridges (plicae) separated 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 juncaensis 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 following 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.

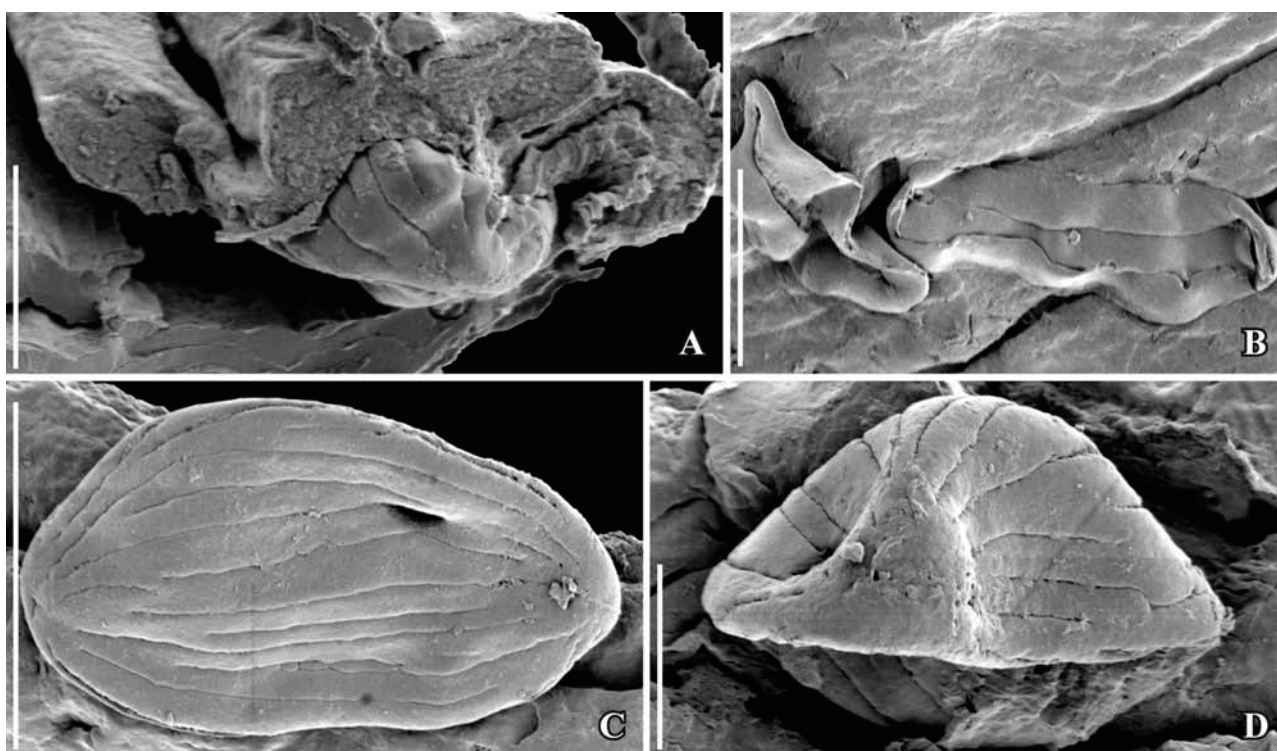


Figure 7. SEM images of pollen grains *in situ* and adhering to lignitised specimens of *Bicatia juncalensis* sp. nov. from the Early Cretaceous Juncal locality (sample Juncal 70), Portugal. **A.** Single pollen grain protruding from the micropylar tube of the holotype shown in Figure 5A and 5D. **B.** Distal view of two fragmentary pollen grains showing broad colpus (S172589). **C.** Proximal view of single pollen grain showing ridges (plicae) and furrows (striae) (S172589). **D.** Pollen grains seen from the end (equator) showing the almost smooth region and the ridges, which are flat in profile and separated by furrows of unequal length (S172589). Scale bars – 5 μ m (A), 10 μ m (B–D).

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 μ m 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).

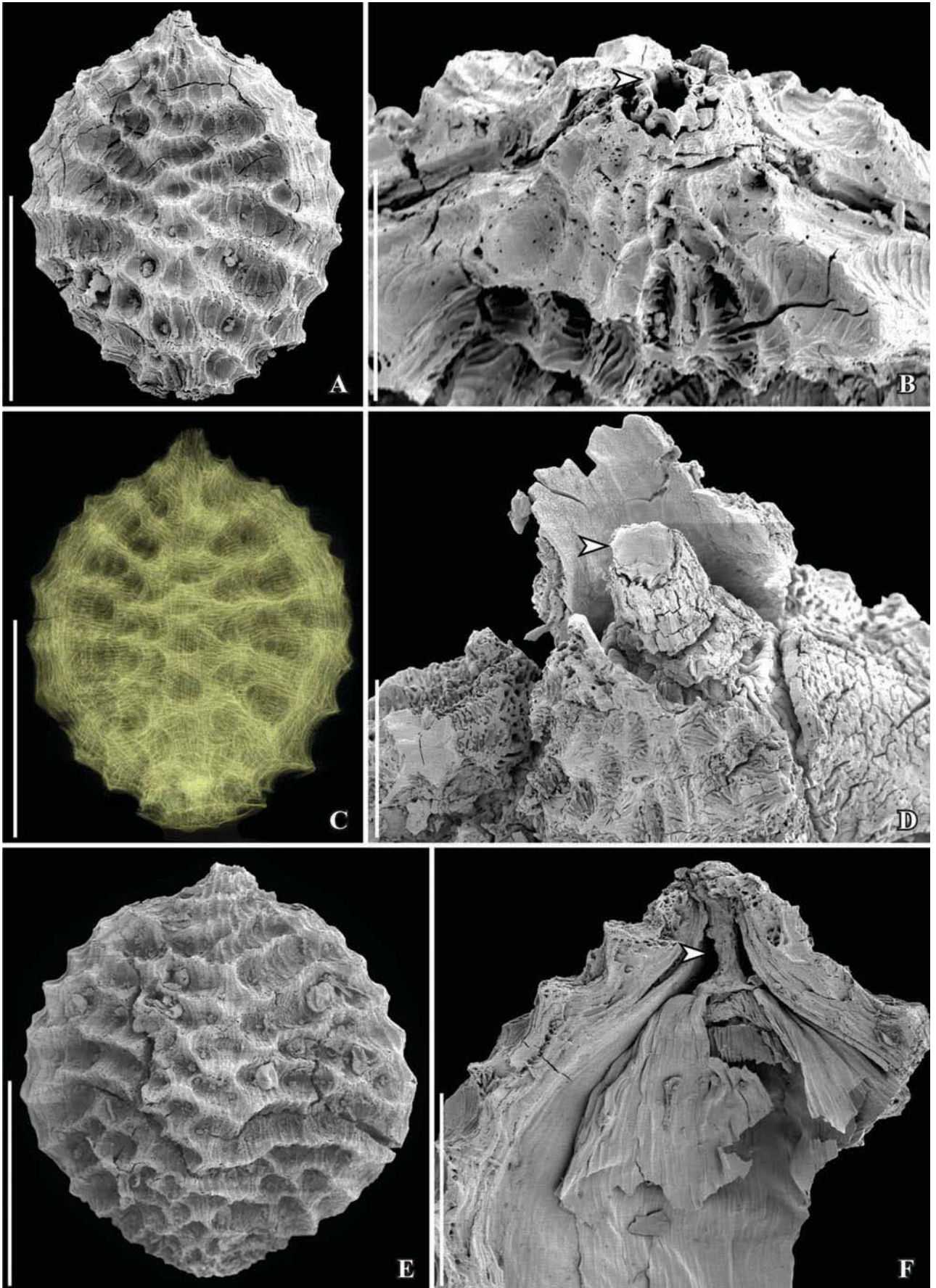
Type stratum. – Famalicão Member, Figueira da Foz Formation (late Aptian–early Albian).

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 (Figure 5E, F), 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.

Figures 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. juncaensis* and *B. costata* 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. juncaensis*. 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. juncaensis* 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 Appomattox River in Prince George County, Virginia, USA (37° 15' 52" N; 77° 22' 10" W).

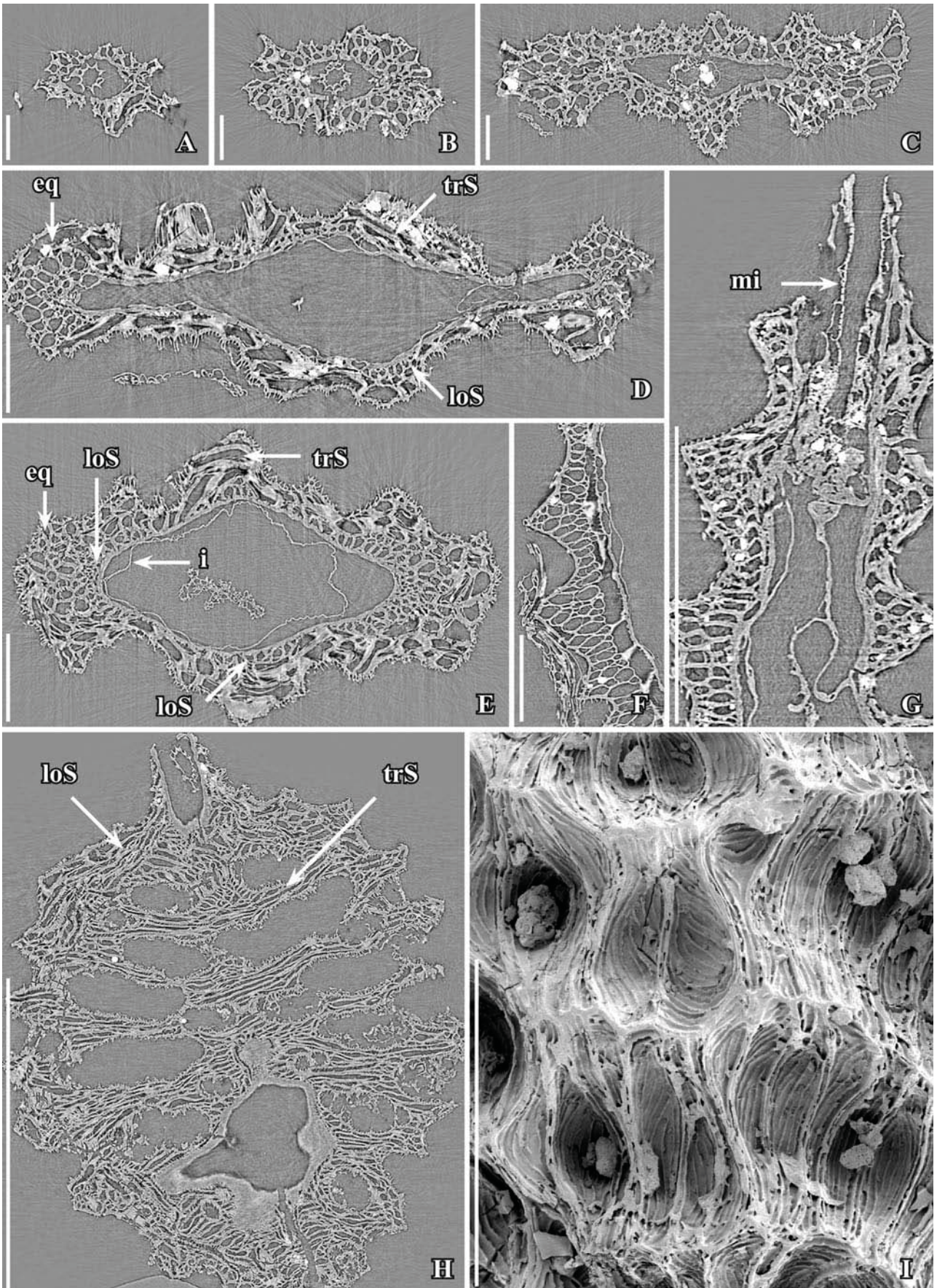
Type stratum. – Basal part of Subzone IIB, Potomac Group; Early Cretaceous (early–middle Albian).

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

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Figure 8. SEM images (A, B, D–F) and SXRTM reconstruction (C) of charcoaled seeds of *Bicatia rugosa* sp. nov. from the Early Cretaceous Puddledock locality, Virginia, eastern North America. **A.** Seed showing rounded base, slightly pointed apex and rugulate surface of seed envelope (holotype; PP53939; sample Puddledock 082). **B.** Detail of holotype showing slightly protruding micropylar tube with heavily cutinised cells of inner epidermis (*arrowhead*) surrounded by sclerenchyma cells of the seed envelope. **C.** Voltex reconstruction of holotype showing rugulate arrangement of sclerenchyma cells. Note narrow sclerenchyma cells that are transversely elongated over seed body, but longitudinally elongated in the median region and along the inner borders of the narrow wings. **D.** Oblique apical view of a broken seed showing the elongated micropylar tube and the surrounding envelope. Note that the micropylar tube is plugged by an apparent secretion (*arrowhead*) and that the inner lining of the seed envelope is smooth (PP53922; sample Puddledock 082). **E.** Broadly elliptical seed with slightly pointed base and apex, and coarsely rugulate surface of seed envelope (PP53897; sample Puddledock 083). **F.** Apical portion of a broken seed showing the thick sclerenchyma cells of the seed envelope and the thinner, partially shrivelled, integument with an elongated micropylar tube (*arrowhead*) (PP53920; sample Puddledock 082). Scale bars – 500 µm (A, C, E), 100 µm (B, D), 250 µm (F).



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 preserved 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 collenchymatic.

Numerous pollen grains were observed on the surface of a single lignitised specimen (PP53915, Figure 10A, B). The grains are polyplicate, 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

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Figure 9. SRXTM reconstructions (A–H) and SEM image (I) of charcoalfied seeds of *Bicatia rugosa* sp. nov. from the Early Cretaceous Puddledock locality (sample Puddledock 082), Virginia, eastern North America. A–C. Orthoslice reconstructions of transverse sections of holotype through the apical part of integument and surrounding seed envelope from apex (A) and downwards (B, C) in the micropylar region. Note the thick, cutinised wall of the inner epidermis of integument in (A) and (B). The first cells of outer epidermis of the integument are seen in (C). Note also that micropylar canal is open from top to much farther down. D. Orthoslice reconstruction of holotype in transverse section through the middle part of the seed showing poorly preserved remains of integument and distinct sclerenchyma cells of seed envelope. Note equiaxial cells (*eq*) of the narrow lateral wings, transversely elongated (*trS*) and longitudinal elongated (*loS*) cells of seed envelope. Outermost cells of sclerenchyma zone larger with narrow ridges. E. Orthoslice reconstruction of transverse section through middle part of seed showing integument (*i*), perhaps surrounding remains of nucellus, and the enclosing seed envelope composed of sclerenchyma. Equiaxial cells (*eq*) form the narrow lateral wings, and longitudinally (*loS*) and transversely elongated (*trS*) sclerenchyma cells form the main body of seed (PP53937). F. Orthoslice reconstruction in longitudinal section through the seed envelope of the holotype showing section through transversely elongated sclerenchyma cells and remains of epidermal cells towards the outside. G. Longitudinal section (orthoslice) of the holotype through the micropylar tube (*mi*) showing the open micropylar canal surrounded by heavily cutinised epidermis cells of integument and the seed envelope. H. Orthoslice reconstruction of longitudinal section through the rugulate surface of the seed envelope showing the characteristic transversely elongated cells (*trS*) over the middle of the seed and the longitudinally elongated cells (*loS*) along the inner borders of the narrow wings (PP53941). I. Detail of abraded surface of holotype showing outer sclerenchyma cells of seed envelope. Scale bars – 50 µm (A–C), 100 µm (D–F), 200 µm (G, I), 500 µm (H).

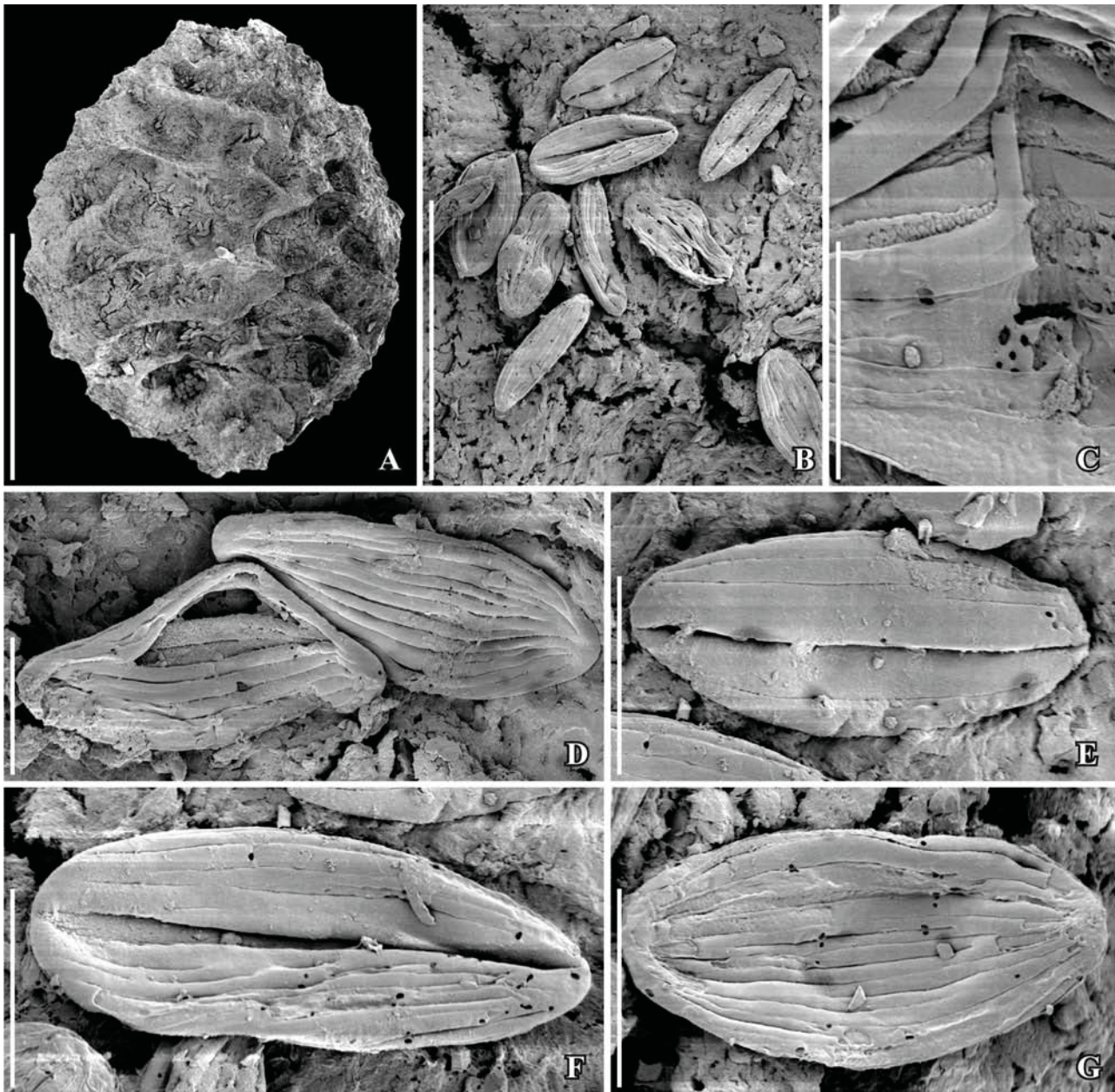


Figure 10. SEM images of pollen grains associated with a lignitised specimen of *Bicatia rugosa* sp. nov. from the Early Cretaceous Puddledock locality, Virginia, eastern North America (PP53915; sample Puddledock 082). **A.** Lateral view of seed showing rugulate surface of the seed envelope and numerous adhering pollen grains. **B.** Cluster of pollen grains on the surface of the seed envelope. **C.** Detail of pollen grain showing granular infratectum protruding from between the thickened ridges (plicae). **D.** Two pollen grains in proximal view. **E.** Distal view of a single pollen grain showing distinct distal colpus flanked by two broad ridges. **F.** Distal view of a single pollen grain showing distinct distal colpus. **G.** Proximal view of a polyplcate pollen grain showing narrow ridges. Scale bars – 500 μm (A), 50 μm (B), 5 μm (C), 10 μm (D–G).

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 lycopods. 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. jumcalensis*). A single seed of *Quadrispermum 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 *Canrightia 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 *Ephedrispermum*, *Lobospermum* Friis, Pedersen et Crane, *Quadrispermum* Friis, Pedersen et Crane and *Tomcatia* (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*, *Cattomia*, *Buarcospermum*, *Lignierispermum* Friis, Pedersen et Crane, *Lobospermum*, *Quadrispermum*, *Rugonella* and *Tomcatia* 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 *Lignierispermum* and several undescribed forms.

Comparison to extant plants

While seeds with a chlamydospermous 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 polyplcate 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 rhytidosperra* 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 polyplcate, 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*, *Erdtmanispermum*, *Lignierispermum*, *Lobospermum*, *Quadrispermum*, *Raunsgaardispermum*, *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*, *Lignierispermum*, *Lobospermum*, *Quadrispermum*, and *Tomcatia* all have a four-parted seed envelope, while the seed envelope of *Rugonella* and *Erdtmanispermum* is three-parted. Among previously described BEG seeds only those of *Raunsgaardispermum* are disymmetric like those of *Bicatia*, but in this case there are other important differences. Most notably, the seed envelope of

Raunsgaardispermum 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 *Raunsgaardispermum* is also non-plicate. Polyplicate grains similar to those of *Bicatia* have been observed in the micropyle of *Ephedra portugallica* 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 plicae 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 *Jugella* N. Mtchedlishvili et Shakhmoundes, *Chomsiipites* 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 (Médus 1987). Even more similar are the grains assigned to the paleotaxon Barremian-monosixteen 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 *Bicatia*, but otherwise similar in shape, aperture configuration as well as distribution and length of the plicae.

Chomsiipites was described based on pollen grains from the Albian–Cenomanian of central Lebanon. In addition to the type species *C. libanicus* Smirnova, two other species from the Albian–Cenomanian of the Caspian region (*C. pyriformis* Smirnova and *C. dzyubae* Smirnova) have been included in the genus. Smirnova (2010) also transferred *Ephedripites zaklinskaiae* Azéma et Boltenhagen from the Albian–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. sibirica* N. Mtchedlishvili et Shakhmoundes from the Barremian of Siberia is larger (45.3–47.9 μm long) than grains of the three *Bicatia* 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 *Bicatia*. *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 Ustyurt, also have pollen that is larger (around 58 μm and 50 μm respectively) than that observed for *Bicatia*. 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 *Bicatia*.

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 *Bicatia*, but all are larger (38–52 μm). Grains of *J. semistriata* 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 chlamydospermous seeds with associated welwitschioid pollen from the Northern Hemisphere is consistent with this conclusion.

While the extinct plants that produced fossil welwitschioid pollen and *Bicatia* seeds are not known, the compression/impression fossils of *Drewria potomacensis* (Crane & Upchurch 1987) may provide an insight into what the plants that produced *Bicatia* seeds were like. *Drewria 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 *Drewria* also resemble those of *Bicatia* 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 *Bicatia* and *Welwitschia* and unfortunately the preservation of *Drewria* does not allow more detailed examination.

Cratonia cotyledon 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 murili* Dilcher, Bernardes-de-Oliveira, Pons et Lott (Dilcher et al. 2005). *Friedsellowia 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 chlamydospermous 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 chlamydospermous 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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