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## ***Paisia*, an Early Cretaceous eudicot angiosperm flower with pantoporate pollen from Portugal**

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### **Abstract**

A new fossil angiosperm, *Paisia pantoporata*, is described from the Early Cretaceous Catefica mesofossil flora, Portugal, based on coalified floral buds, flowers and isolated floral structures. The flowers are actinomorphic and structurally bisexual with a single whorl of five fleshy tepals, a single whorl of five stamens and a single whorl of five carpels. Tepals, stamens and carpels are opposite, arranged on the same radii and tepals are involute at the base clasping the stamens. Stamens have a massive filament that grades without a joint into the anther. The anthers are dithecate and tetrasporangiate with extensive connective tissue between the tiny pollen sacs. Pollen grains are pantoporate and spiny. The carpels are free, apparently plicate, with many ovules borne in two rows along the ventral margins. *Paisia pantoporata* is the oldest known flower with pantoporate pollen. Similar pantoporate pollen was also recognised in the associated dispersed palynoflora. *Paisia* is interpreted as a possibly insect pollinated, herbaceous plant with low pollen production and low dispersal potential of the pollen. The systematic position of *Paisia* is uncertain and *Paisia pantoporata* most likely belongs to an extinct lineage. Pantoporate pollen occurs scattered among all major groups of angiosperms and a close match to the fossils has not been identified. The pentamerous floral organisation together with structure of stamen, pollen and carpel suggests a phylogenetic position close to the early diverging eudicot lineages, probably in the Ranunculales.

**Keywords:** *Almargem Formation, apocarpous, basal eudicots, Ranunculales, SRXTM, synchrotron radiation x-ray microtomography*

Pantoaperturate (pantoporate and pantocolpate) pollen grains occur scattered among all major groups of angiosperms and are reported both among early diverging lineages and in more derived groups. Their occurrence in basal lineages is particularly interesting in the light of the diversity of this kind of pollen in the Early Cretaceous, but the importance of pantoaperturate pollen in early angiosperm evolution has not yet been explored. The dispersed pollen record documents pantoporate/polyporate pollen already in the Aptian and by the Albian this

pollen type is almost globally distributed and represented by a diversity of forms (Chlonova 1986; Ibrahim et al. 2017). Among early diverging angiosperms pantoporate pollen is reported for Trimeniaceae (Austrobaileyales) and Chloranthaceae (Sampson & Endress 1984; Endress 1986), and in early diverging monocots pantoporate pollen characterises all extant Alismataceae and Limnocharitaceae (Argue 1973, 1974, 1976; Chanda et al. 1988; Furness & Banks 2010). Pantocolpate and pantoporate pollen grains are also common in early diverging lineages of

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eudicots including the Ranunculales and Buxales. In the Ranunculales, pantoaperturate pollen is recorded for the Eupteleaceae, Papaveraceae (Fumarioideae and Papaveroideae), Berberidaceae and Ranunculaceae (e.g. Wodehouse 1936; Pragłowski 1974; Nowicke & Skvarla 1981, 1982; Blackmore et al. 1995; Emadzade et al. 2010). *Euptelea*, usually resolved as sister to all other members of the Ranunculales, has mainly apolar and pantocolpate or sometimes partly pantoporate pollen, while tricolpate pollen is rare (Pragłowski 1974). Nevertheless, Eupteleaceae and all other families of Ranunculales were scored as having tricolpate pollen in the phylogenetic discussion of pollen characters by Doyle (2005) and pantoporate aperture configuration was not considered in the character matrix of later phylogenetic discussions by Doyle (e.g. Doyle & Endress 2014).

We here describe a new fossil flower, *Paisia pantoporata* sp. nov., from the Early Cretaceous Catefica mesofossil flora, Portugal, with pantoporate *in situ* pollen. It shares the actinomorphic flower arrangement and free floral parts with many other Early Cretaceous floral structures such as *Kajanthus* and *Kenilanthus* (Mendes et al. 2014; Friis et al. 2017) and *Paisia* adds to the diversity of Early Cretaceous floral structures with an apocarpous gynoecium. It is, however, distinguished from all other Early Cretaceous flowers recorded so far by its pantoporate pollen and provides the first information of a flower producing pantoporate pollen in the Early Cretaceous. *Paisia pantoporata* is restricted to the Catefica mesofossil flora and is another unique taxon for this flora.

The systematic position of *Paisia pantoporata* is uncertain. It may represent an extinct lineage close to the base of the eudicot angiosperms, most likely in the Ranunculales or among other early diverging eudicots. This position is inferred from the pentamerous and isomerous organisation of the flower, stamens with a massive filament and an apocarpous gynoecium with plicate carpels, as well as the common occurrence of pantoaperturate pollen at this grade.

## Material and methods

The fossil floral structures described here are from the Lusitanian Basin, western Portugal, and were collected at the Catefica locality (39° 3' 16" N; 09° 14' 24" W) situated near Torres Vedras on the western margin of the Runa Basin. The plant bearing strata at the Catefica locality were previously assigned to the 'Grés de Torres Vedras' (Carta Geológica de Portugal, Folha 30-D Alenquer; Zbyszewski & Torre de Assunção 1965) that is now included in the Almargem Formation (Rey 1992, 1993). The Almargem Formation is of Early Cretac-

eous (late Barremian–Albian) age, but the exact stratigraphic position of the Catefica deposits within the Almargem Formation is not yet established. According to Jacques Rey (personal communication, June 2012) the Almargem Formation at the Catefica locality may be equivalent to the basal part of the Figueira da Foz Formation and of late Aptian–early Albian age, but although the Catefica mesofossil flora does share some elements with the mesofossil floras of the Figueira da Foz Formation, there are many taxa that are unique to the Catefica plant assemblages, both among the mesofossils (EMF and KRP, own observation) and the microfossils (MMM, own observation). There are also elements in the Catefica mesofossil flora that are shared with the probably older Torres Vedras mesofossil flora (EMF; KRP, P. R. Crane, own observation) and that are not known for the slightly younger mesofossil floras of the Figueira da Foz Formation.

Plant mesofossils were first reported from the Catefica locality by Friis et al. (1994). They are typically small and three-dimensionally preserved either as charcoalifications or lignitised. The fossils were extracted from the sediments and prepared for examination following standard methods for Cretaceous mesofossils (Friis et al. 2011). The mesofossil assemblages are rich in angiosperm flowers and inflorescences as well as isolated fruits, seeds and stamens of angiosperms, in addition to a diversity of seeds related to the Bennettitales–Erdtmanithecales–Gnetales complex, conifer seeds and twigs of Cheirolepidiaceae as well as many fern fragments and megaspores (e.g. Friis et al. 1994, 2009, 2010, 2013, 2014b, 2015a, 2015b; Friis & Pedersen 2014).

About 60 specimens were studied. For scanning electron microscopy (SEM), fossil specimens were mounted on aluminium stubs with nail polish, sputter coated with gold and examined using a Hitachi Field S-4300 FE-SEM at 2 kV. Organisation and internal details of 15 fossils (accession numbers: S101214, S118680, S171514, S171515, S171519, S171523–S171526, S171529, S171530, S174439, S174743, P0298, P0338) were studied using synchrotron radiation X-ray tomographic microscopy (SRXTM) at the TOMCAT Beamline, Swiss Light Source, at the Paul Scherrer Institute, Villigen, Switzerland (Stampanoni et al. 2006). The fossils were mounted with nail polish on brass stubs and measured at 10 keV using a 10× objective with isotropic pixel size of 0.65 µm, a sCMOS detector and a 20 µm thick LAG:Ce scintillator screen (for details on SRXTM work on Cretaceous plant mesofossils at TOMCAT see Friis et al. 2014a). Virtual slices and reconstructions based on the SRXTM data were made using Avizo software (versions 5–9.1.1). The specimens are housed in the palaeobotanical collec-

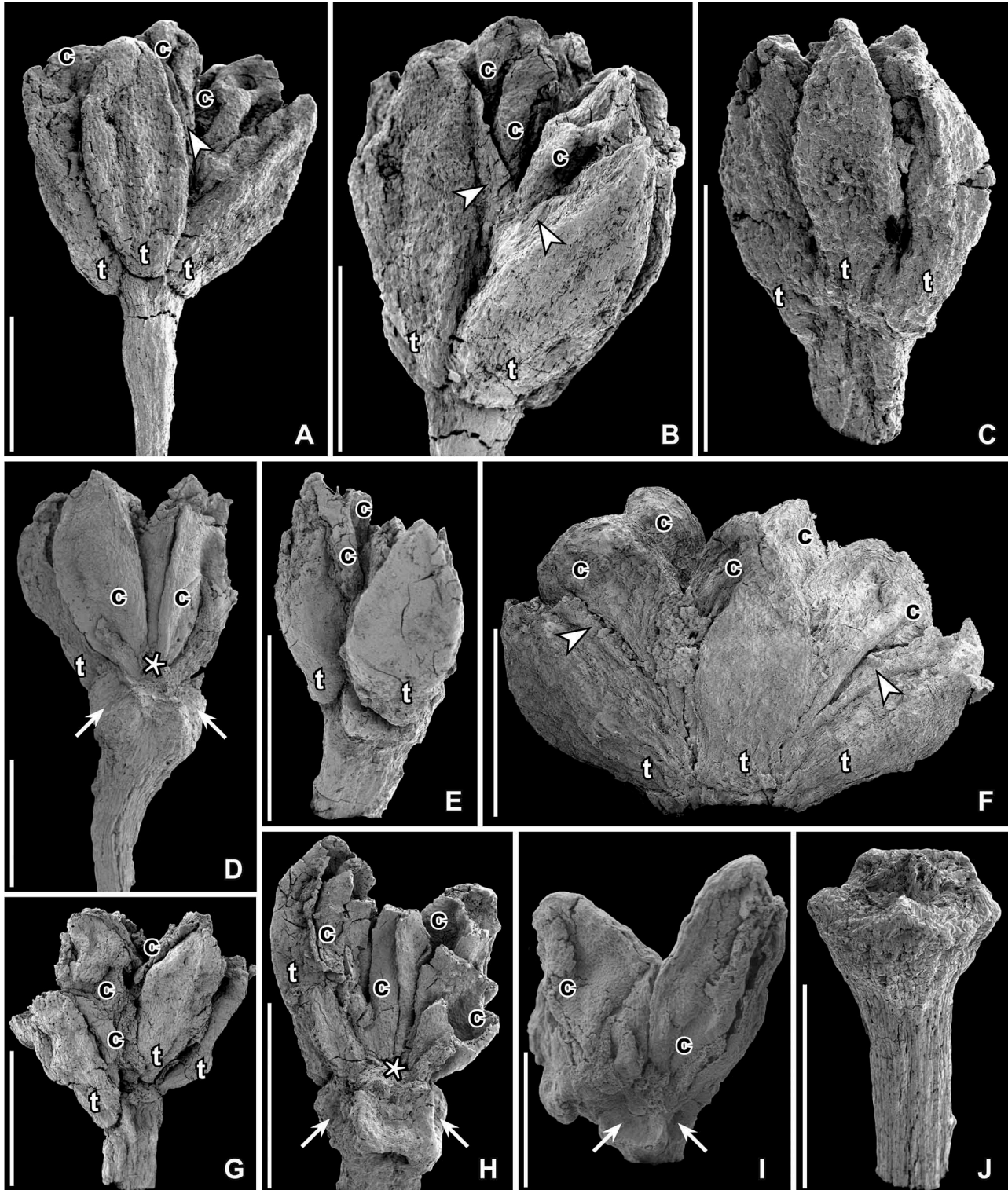


Figure 1. SEM images of *Paisia pantoporata* gen. et sp. nov., flowers from the Early Cretaceous Catefica locality, Portugal. **A, B.** Holotype; anthetic flower with pedicel, tepals (t) and carpels (c) preserved; margins of tepals are incurved at base and very thin (arrow heads) further up (S101214; sample Catefica 49). **C.** Floral bud with all floral parts and part of pedicel preserved; tepals (t) cover stamens and carpels (S118680; sample Catefica 49). **D.** Fragmentary anthetic flower with pedicel preserved; one tepal (t) and two carpels (c) are exposed and the ventral suture of one carpel is visible; asterisk marks base of slit; facets on receptacle (arrows) show scars from tepals and stamens (S174739; sample Catefica 50). **E.** Anthetic flower with pedicel preserved showing tepals (t) with incurved margins and carpels (c) (S170429; sample Catefica 342). **F.** Anthetic flower showing tepals (t) and carpels (c); note the thin margins of tepals (arrowheads) (S174302; sample Catefica 242). **G.** Anthetic flower with tepals (t) and carpels (c) preserved; base of tepals incurved; note downwards expanded base of tepals (S171519; sample Catefica 342). **H.** Same specimen as in (E) from opposite side showing receptacle with scars from tepals and stamens (arrows); tepals (t) and carpels (c) only partly preserved; asterisk shows base of ventral slit (S170429; sample Catefica 342). **I.** Anthetic flower with two carpels (c) preserved and scars from tepals and stamens (arrow) (S118679; sample Catefica 49). **J.** Isolated pedicel with swollen, angular receptacle (S171530; sample Catefica 151). Scale bars – 500  $\mu$ m.

tions of the Palaeobiology Department of the Swedish Museum of Natural History, Stockholm (S) and the Geological Museum of Lisbon, Portugal (P).

### Systematic palaeontology

*Angiospermae*  
*Eudicots*  
*Paisia gen. nov.*

*Derivation of generic name.* — In honour of Professor João Pais (1949–2016) for his contribution to the palaeobotany and geology of Portugal.

*Generic and specific diagnosis.* — Flower small, pedicellate, actinomorphic, pentamerous and isomerous and functional bisexual with one whorl of five tepals, one whorl of five stamens and one whorl of five free carpels, all opposite on the same radii. Receptacle distinctly five-angled. Perianth of a single whorl of five tepals; aestivation involute-valvate. Tepal base extended downwards and margins incurved, clasping the stamens. Stamens with a single massive bundle extending from base to apex. Stamens differentiated into a short, stout filament and an elongated, basifixed anther. Anthers dithecate and tetrasporangiate; sporangia minute, separated by a massive connective. Anther dehiscence latrorse by longitudinal slits. Pollen pantoporate, tectate-punctate, spiny. Gynoecium superior; carpels free, sessile, elongate, and plicate. Ovules many, borne in two longitudinal rows on either side of the ventral suture. Stigma sessile, decurrent, indistinct.

*Type species designated here.* — *Paisia pantoporata* sp. nov.

*Paisia pantoporata* sp. nov.  
(Figures 1–6, 8)

*Derivation of specific name.* — From the pantoporate pollen observed *in situ* in the stamens.

*Specific diagnosis.* — See combined generic and specific diagnosis.

*Dimensions.* — Mature flowers without pedicel about 1 mm long and up to 1.2 mm wide.

*Holotype.* — S101214 (Catefica sample 49; illustrated here on Figures 1A, B, 2A–G).

*Paratypes.* — S118679, S118680, S118682, S171526, S174746, S174747 (Catefica 49); S174739, S174740, S174742 (Catefica 50);

S171530 (Catefica 151); S174302 (Catefica 242); S170429, S171519 (Catefica 342); S171514, S171515 (Catefica 343); S174743, S174344 (Catefica 361). Totally, about 60 specimens; several specimens may be stored in box slides under the same number.

*Type locality.* — Catefica (39° 03' 30" N; 09° 14' 30" W), between the villages of Catefica and Mugideira, about 4 km south of Torres Vedras, Portugal.

*Type horizon and age.* — Almargem Formation, Early Cretaceous (late Barremian–early Albian).

*Description and remarks.* — The material includes several complete flowers (Figures 1A–C, F, G, 2A–G) or partly preserved flowers (Figures 1D, E, H, I, 3A–D, H–J, 4A–C) as well as isolated floral parts, such as tepals either empty or enclosing a single stamen (Figure 5A), pedicels where all floral parts are shed (Figures 1J, 6A–D), young carpels and stamens (Figure 3E–G) and mature follicles. Most flowers are preserved in the anthetic or post-anthetic stage, while a few are preserved in the pre-anthetic stage.

Flowers are pedicellate, small, about 1 mm long without pedicel and up to 1.2 mm in diameter, actinomorphic, pentamerous and isomerous with an apocarpous and superior gynoecium (see floral reconstruction and floral diagram Figure 8). Tepals and the enclosed stamens and carpels are inserted on a five-angled receptacle with faceted sides with tepals and stamens borne on the receptacle facets. The floral organs are apparently arranged in whorls. The perianth consists of a single whorl of parts, described here as tepals. Tepals are elliptical to ovate in dorsal view (Figure 1A–C, E–H) with pointed apex and rounded base that is distinctly separated from the pedicel and curving slightly downwards forming a dorsal extension that is sometimes prominent (Figures 1A, B, E, G, 2C). In cross-section, the tepals are more or less M-shaped with a broad base and incurved, thinner margins (Figures 2F–G, 3H–J). In young flowers, the tepal margins are incurved along the full length of the tepals (Figures 3B, H–J, C), while in more mature flowers the margins are incurved only at the base (Figures 1B, 2A, G) and in all specimens the tepal margins are thinner than the middle part of the tepals (Figures 1A, B, F, 2A, E, F). The tepals are fleshy composed of equiaxial, rounded parenchyma cells (Figures 2C, 3H–J). There are three bundles extending almost for the full length of the tepals (Figure 3I). The inner surface of the tepals has densely spaced bulging papillae (Figure 3C, H).

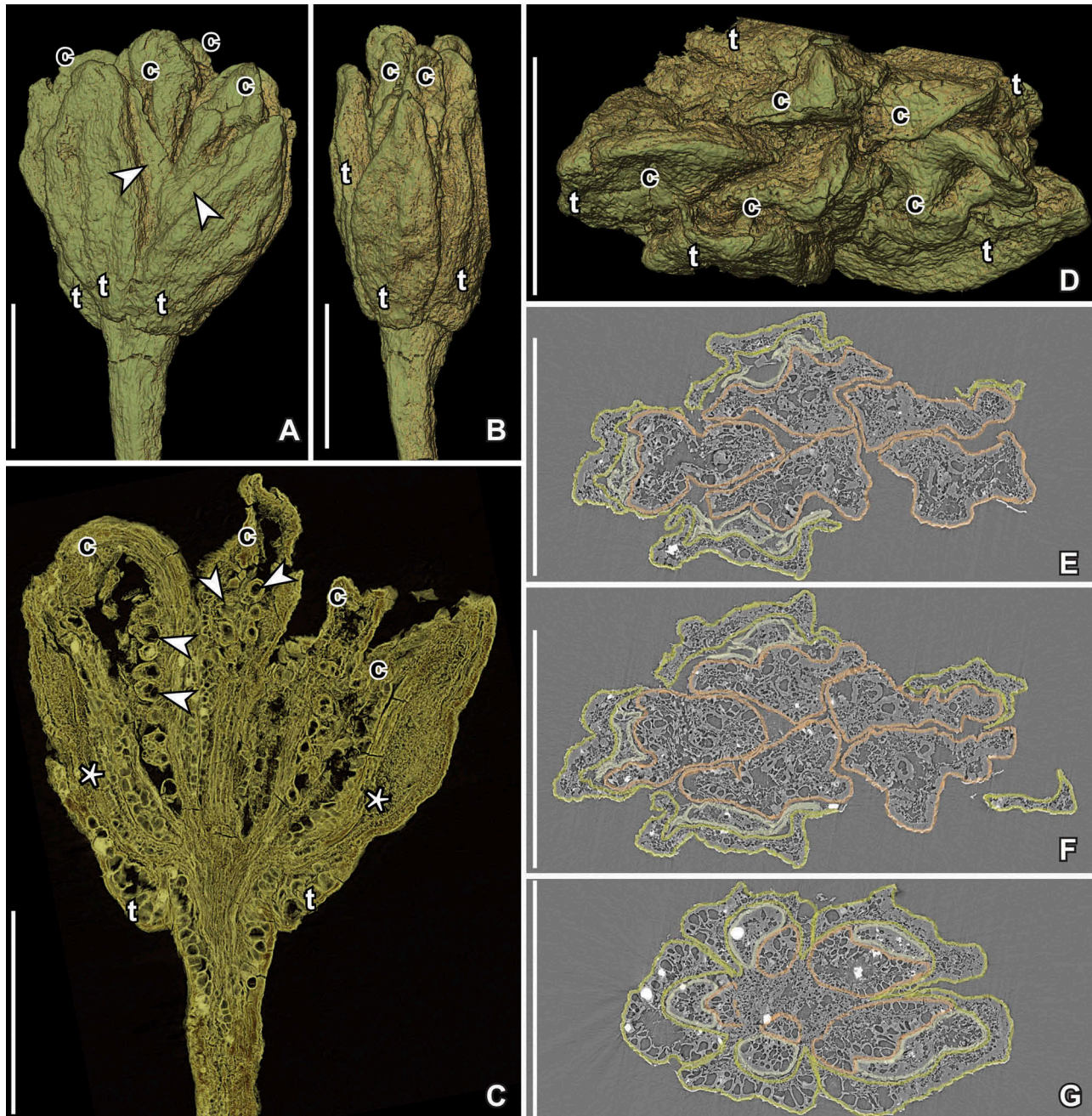


Figure 2. SRXTM volume renderings (A–D) and reconstructed transverse orthoslices (E–G) of *Paisia pantoporata* gen. et sp. nov., anthetic flower from the Early Cretaceous Catefica locality, Portugal (holotype, S101214; sample Catefica 49). **A, B.** Lateral views of flower at different angles showing well-preserved tepals (t) with thin margins (arrowheads) surrounding the carpels (c). **C.** Cut longitudinal volume rendering of flower (orthoslices yz500–520) showing sections of carpels with numerous small ovules/seeds (arrowheads) that do not fill out the ovary cavity; stamens (asterisk) are preserved between the tepals (t) and carpels. **D.** Apical view of flower showing the five tepals (t) and five carpels (c). **E–G.** Sections through flower at different levels from close to apex (E) to the base of the flower (G) showing the five tepals (light green) claspings the five stamens (light yellow) and surrounding the five carpels (orange); tepal margins at base incurved, further up extended outwards. Scale bars – 500 μm.

The androecium consists of five stamens opposite the tepals and the carpels. Stamens are elongate, about 0.5–0.8 mm long, embraced by the incurved margins of the tepals. In young flowers, they consist of a short, stout filament, about 0.25 mm long that

grades without a joint into the basally attached, elongate anther (Figures 3B, E, 4A, B). Anthers in young flowers are about 0.35 mm long, dithecate and tetrasporangiate with small pollen sacs (Figures 3G, I, 4A–C). The two thecae are separated by a broad

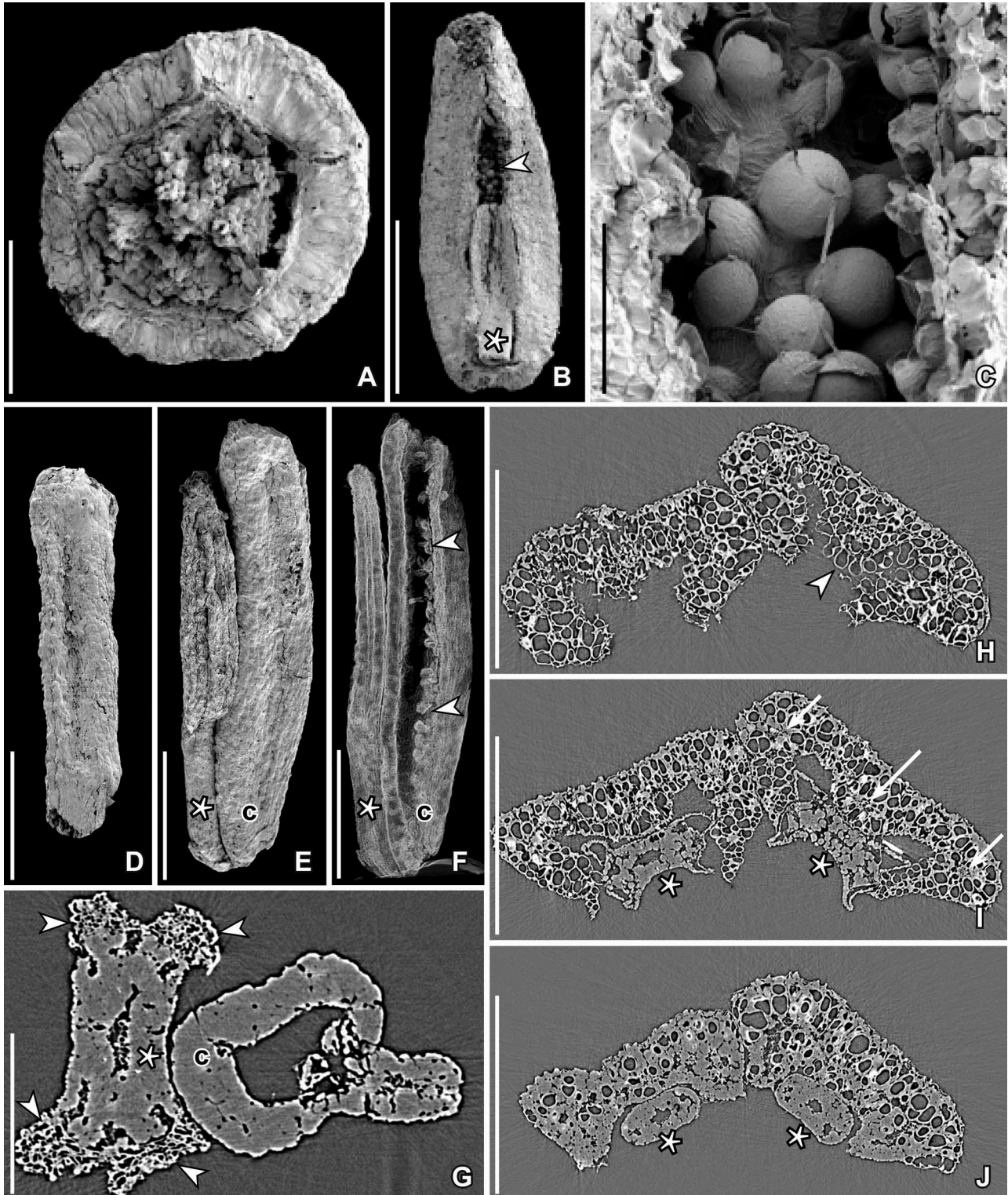


Figure 3. SEM images (A–F) and SRXTM reconstructed transverse orthoslices (G–J) of *Paisia pantoporata* gen. et sp. nov., floral organs from the Early Cretaceous Catefica locality, Portugal. A–D, H–J. Pedicel and floral organs isolated from the same floral bud (S171526; sample Catefica 49). **A.** Pedicel in apical view showing swollen, slightly five-angled receptacle with scars from the floral organs. **B.** Single tepal clasping a stamen (*asterisk*); inner surface of tepal above stamen is papillate (*arrowhead*). **C.** Papillate inner surface of tepal enlarged. **D.** Young carpel with almost straight and parallel dorsal and ventral faces. **H–J.** Transverse orthoslices at different levels through two tepals; each tepal clasping a stamen; tepals fleshy with three vascular bundles (*arrows* in **I**); large, isodiametric parenchyma cells and incurved margins from apical part (**H**) to the base (**J**); stamens (*asterisks*) show massive connective and tiny pollen sacs (**I**) and a massive filament with a single central strand (**J**). **E.** Isolated stamen (*asterisk*) and adhering carpel (*c*) in lateral view showing longitudinal dehiscence line of anther (S171514; sample Catefica 343). **F.** Cut longitudinal volume rendering of same specimen as shown in **E** (cut through median part of carpel and stamen) showing numerous, tiny ovules not filling the ovary cavity. **G.** Transverse orthoslice (orthoslice xy1300) of the same specimen as shown in (**E**) showing stamen (*asterisk*) with massive connective with a single bundle and the four tiny, lateral pollen sacs (*arrowheads*) and section through middle part of carpel (*c*) with tiny ovules on both side of the ventral suture. Scale bars – 500  $\mu$ m (**B**), 250  $\mu$ m (**H–J**), 200  $\mu$ m (**A–F**), 100  $\mu$ m (**G**), 50  $\mu$ m (**C**).

connective (Figures 3G, I, 4C). There is a single bundle extending from base almost to apex. The pollen sacs protrude and are laterally oriented with lateral dehiscence by longitudinal slits.

Pollen grains are found *in situ* in the anthers of several flowers and in isolated fragments (Figure 5A–I). They are pantoporate, spheroidal and minute, about 11–14  $\mu\text{m}$  in diameter, with tectate-punctate pollen wall and a supracteal ornamentation of spiny, conical elements, 0.7–1.0  $\mu\text{m}$  long, constricted at the base, with a pointed or blunt tip, and with longitudinal ridges that give the elements an appearance of being compound of elongated elements (Figure 5I). The elements form a dense ring around each aperture, but are otherwise more irregularly scattered over the tectum surface (Figure 5C, F–I). In some specimens the pollen grains appear immature with supracteal elements of adjacent grains coalesced (Figure 5F, G). There are about six to eight pores, about 3  $\mu\text{m}$  in diameter, and globally distributed over the grain. The aperture membrane is covered by irregular sculptural elements (Figure 5C, H) that are sometimes completely concealed by the surrounding spiny elements (Figure 5I). Orbicules were not observed.

There are five free carpels (Figures 1F, 2D–G). Carpels are sessile and elongated, interpreted as plicate. In young flowers they are narrow and of almost the same width from base to apex and with almost straight ventral and dorsal margins (Figures 3D–F). In more mature floral structures they are elliptical to obovate with slightly convex ventral margin and rounded dorsal margin (Figures 1D, F, I, 2C). The ventral slit extends for the full length of the carpel. This is obvious on broken specimens (Figure 1D, H) as well as in some of the specimens studied using SRXTM. There is no indication of an ascidiate zone in any of the specimen studied. The stigma is sessile and indistinct. The carpel wall is smooth and consists of almost equiaxial, rounded parenchyma cells. There are one dorsal and two ventral bundles. The outer epidermis is composed of tiny, equiaxial cells, apparently without stomata.

Ovules are numerous per carpel (about 20–30) and tiny, apparently anatropous and both in young stages (Figure 3E, F) and more mature flowers (Figure 2C) ovules do not fill the ovary cavity. They are borne in two longitudinal rows, one on each side of the ventral suture extending from the carpel base to the apex.

The pedicel is about 0.2 mm in diameter below the receptacle. The preservation does not allow a detailed description of the stem anatomy and comparison with extant plants, but in all specimens studied by SRXTM it is clear that there are five or more vascular bundles close to the centre of the pedicel

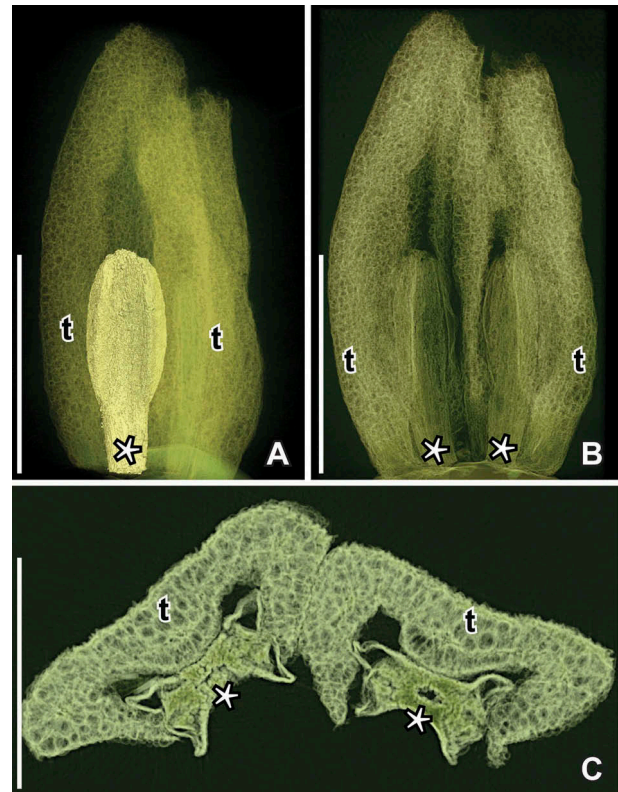


Figure 4. SRXTM reconstructions of two tepals and two stamens of *Paisia pantoporata* gen. et sp. nov., from the Early Cretaceous Catefica locality, Portugal; floral organs from the same floral bud as in Figure 3A–D, H–J (S171526; sample Catefica 49). **A.** Longitudinal voltex of tepals (t) and stamens (asterisk) and surface rendering (yellow) of one stamen showing filament, massive connective and tiny pollen sacs. **B.** Transparent voltex showing thick parenchyma tissue of tepals and stamens enclosed in the tepals. **C.** Cut transverse voltex reconstruction at the level of the pollen sacs showing the two tepals with incurved margins clasp the stamens (asterisks); note massive connective with one central bundle and the two lateral thecae with tiny pollen sacs. Scale bars – 500  $\mu\text{m}$  (A, B); 250  $\mu\text{m}$  (C).

surrounding a small pith and surrounded by a broader zone of thick-walled parenchyma cells and a thick epidermis (Figure 6A–D).

?*Paisia* sp.  
(Figure 7)

One specimen (P0292) from the Catefica locality (Figure 7A–E) consists of a small axis, about 3.2 mm long, with a terminal apocarpous gynoecium and a lateral bract further down the axis supporting a bud. The bud is in an early developmental stage and it is unknown whether it is vegetative or a floral bud. The axis is more or less circular in transection, about 0.2 mm in diameter. Vascular bundles are arranged in a ring around the small central pit and are surrounded by a tissue of thick-walled parenchyma cells.



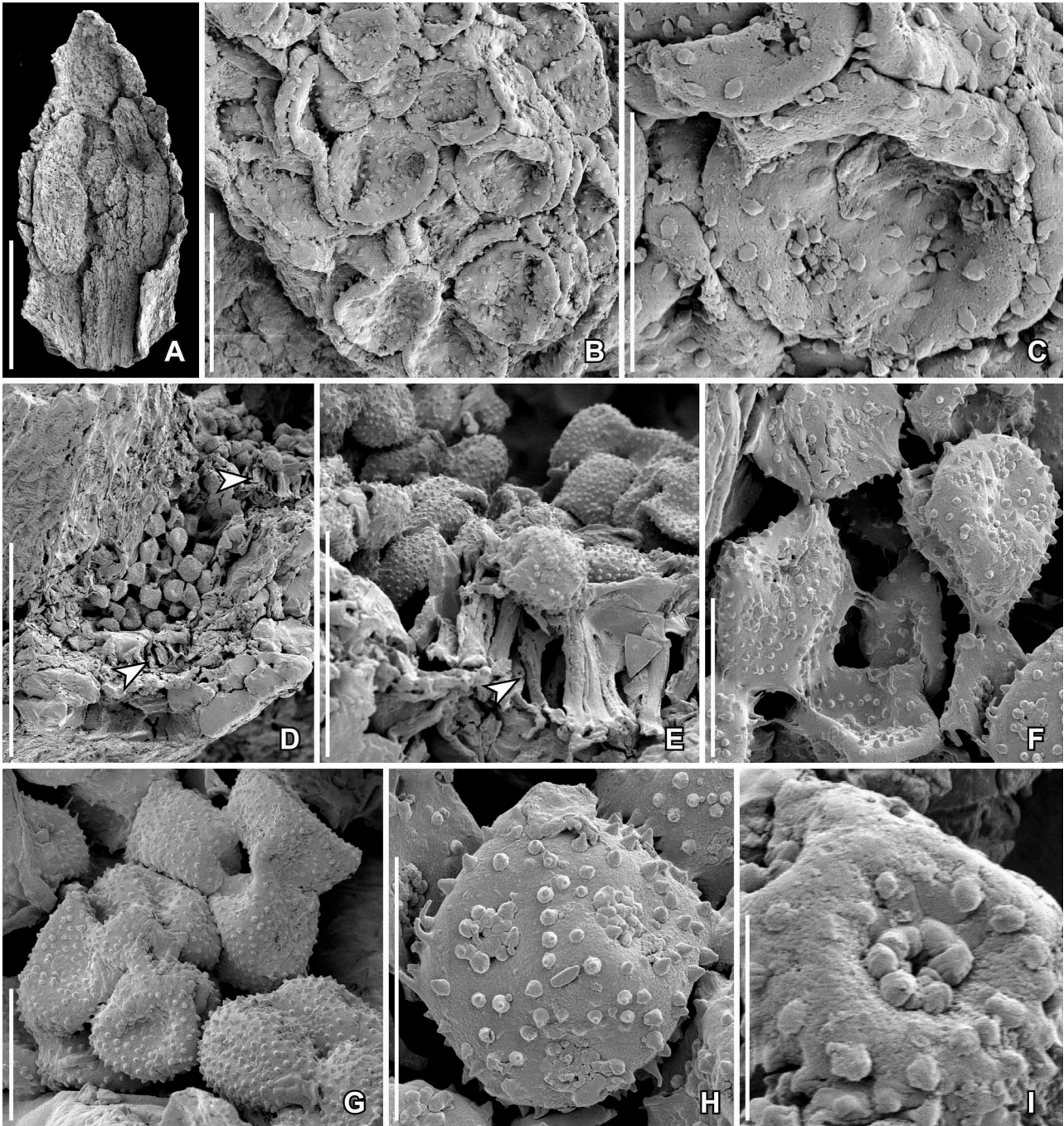


Figure 5. SEM images of stamens and pollen *in situ* of *Paisia pantoporata* gen. et sp. nov., from the Early Cretaceous Catefica locality, Portugal. **A.** Isolated tepal and enclosed stamen with pollen *in situ* (S170388; sample Catefica 50). **B, C.** Pantoporate pollen from stamen shown in **(A)**; note the scattered suprategal elements on the pollen body and the concentration of elements around the apertures (S170388; sample Catefica 50). **D–H.** Fragment of tepal enclosing stamen with pantoporate pollen *in situ* from floral structure shown in Figure 1I; cell wall thickenings of anther wall are seen in **(D)** and **(E)** (*arrowheads*); the pollen grains appear to be immature, sometimes grouped in tetrads and sometimes with suprategal elements of adjacent grains coalesced (**F, G**); suprategal elements with blunt or spiny apex (**H**) (S118679; sample Catefica 49). **I.** Detail of pollen grain from floral structure in Figure 1G showing apparent compound suprategal elements; note concentration of elements around the aperture (S171519; sample Catefica 342). Scale bars: 250  $\mu\text{m}$  (**A**), 100  $\mu\text{m}$  (**D**), 25  $\mu\text{m}$  (**E**), 20  $\mu\text{m}$  (**B**), 10  $\mu\text{m}$  (**C, F–H**), 5  $\mu\text{m}$  (**I**).

The terminal gynoecium appears to be in a post-anthetic stage. There are no perianth parts or stamens preserved. The receptacle below the carpels is

faceted with a number of scars (Figure 7A, B) indicating that other floral organs were originally present in the flower, but shed after anthesis. The gynoecium

consists of three free carpels (Figure 7A–C, E), about 0.52 mm long and 0.34 mm wide, ovoid to elliptic in shape, each with a distinct ventral suture and an indistinct, sessile stigma (Figure 7C). No pollen grains were observed in the stigmatic area. There are about ten ovules/seeds borne in two longitudinal rows along the entire ventral suture (Figure 7D, E). The ovules/seeds do not fill in the ovary cavity. The epidermal cells of the carpels are polygonal and more or less isodiametric in surface view.

The fossil specimen is similar to *Paisia pantoporata* in the faceted receptacle, large parenchymatic cells in pedicel, receptacle and carpels, and a ring of vascular bundles near the centre of the pedicel. The fossil is, however, distinguished from *Paisia pantoporata* by its trimerous gynoecium. It is possible that the specimen represents an aberrant tricarpellate form of the otherwise pentacarpellate *Paisia pantoporata*, but it is more likely that the specimen represents a new species, either of *Paisia* or a new fossil genus. With the material currently available, a definite assignment of the specimen to *Paisia* is not possible and we therefore refer to the specimen as ?*Paisia* sp.

## Discussion

### *Comparison of Paisia pantoporata with Early Cretaceous flowers and pollen*

A number of isolated plicate carpels apparently from apocarpous gynoecia co-occur with *Paisia pantoporata* and ?*Paisia* sp. in the Catefica mesofossil flora and may represent related forms. A diversity of fossils with apocarpous gynoecia is also known from other Early Cretaceous mesofossil floras in Portugal and eastern North America (for Late Cretaceous follicular fruitlets see later). Some of them are known from flowers and have been assigned to eudicots based on their organisation and *in situ* tricolpate pollen. *Kajanthus lusitanicus* E.M.Friis, M.M.Mendes et K.R.Pedersen (Mendes et al. 2014) from the Chicalhão locality (late Aptian–early Albian) of Portugal, and *Kenilanthus marylandensis* E.M.Friis, K.R.Pedersen et P.R.Crane from early–middle Albian strata of the Kenilworth locality, Maryland, USA (Friis et al. 2017), both have structurally bisexual flowers and an apocarpous gynoecium of three to five plicate carpels. *Kajanthus* is closely related to the extant *Sinofranchetia* of the ranunculalean family Lardizabalaceae (Mendes et al. 2014) and is distinguished from *Paisia pantoporata* by its trimerous flowers and tricolpate, reticulate pollen. *Kenilanthus* is similar to *Paisia* in having a pentamerous and isomerous organisation with five free carpels and numerous ovules that do

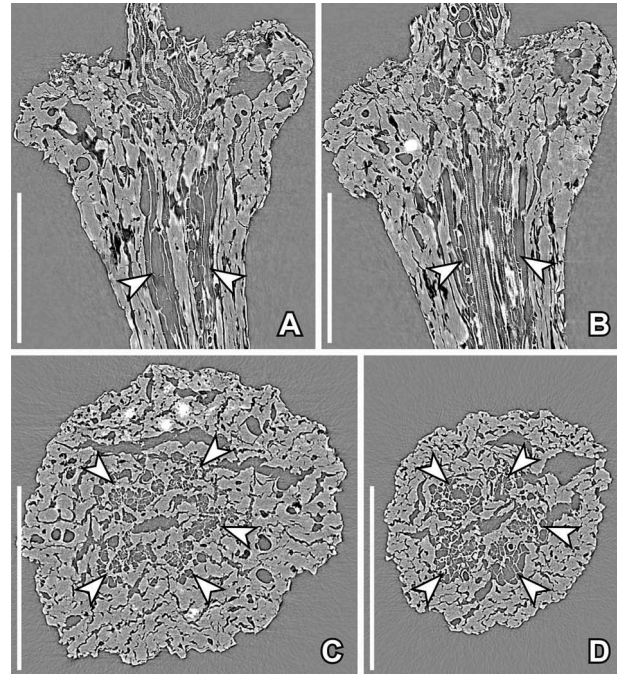


Figure 6. SRXTM reconstructions of pedicel and receptacle anatomy in *Paisia pantoporata* gen. et sp. nov., from the Early Cretaceous Catefica locality, Portugal, same specimen as in Figure 1J (S171530; sample Catefica 151). A–D. Longitudinal (A, B) and transverse (C, D) orthoslices showing thick-walled cells towards the periphery and ring of bundles (arrowheads) around the narrow central pith (A, orthoslice xz470; B, orthoslice xz640; C, orthoslice xy700; D, orthoslice 1015). Scale bars – 200 µm.

not fill out the ovary space. *Kenilanthus* may also have a single whorl of tepals as in *Paisia pantoporata*, but the nature of the perianth is not fully documented for *Kenilanthus*. *Kenilanthus* differs in many other respects from *Paisia* and they are probably not closely related. It has two whorls of apparently extrorse stamens and pollen grains are tricolpate-reticulate. Also, the epidermis of the *Kenilanthus* carpels have scattered stomata not observed for the carpels of *Paisia*.

*Teixeiraea lusitanica* K.R.Pedersen et E.M.Friis is another early eudicot flower with *in situ* pollen from the Early Cretaceous Vale de Água locality (late Aptian–early Albian) of Portugal. It is distinguished from *Paisia* in the multiparted nature of the androecium and the reticulate, tricolpate pollen. Further, *Teixeiraea lusitanica* is apparently unisexual and currently only the staminate flower is known (von Balthazar et al. 2005). Specimens with an apocarpous gynoecium from the Early Cretaceous (late Barremian–early Aptian?) Torres Vedras locality are multicarpellate, apparently with carpels in a helical arrangement (e.g. Friis et al. 2011).

Two pentacarpellate and apocarpous structures with free plicate carpels were reported from the Early Cretaceous (early–middle Albian) Puddledock locality,

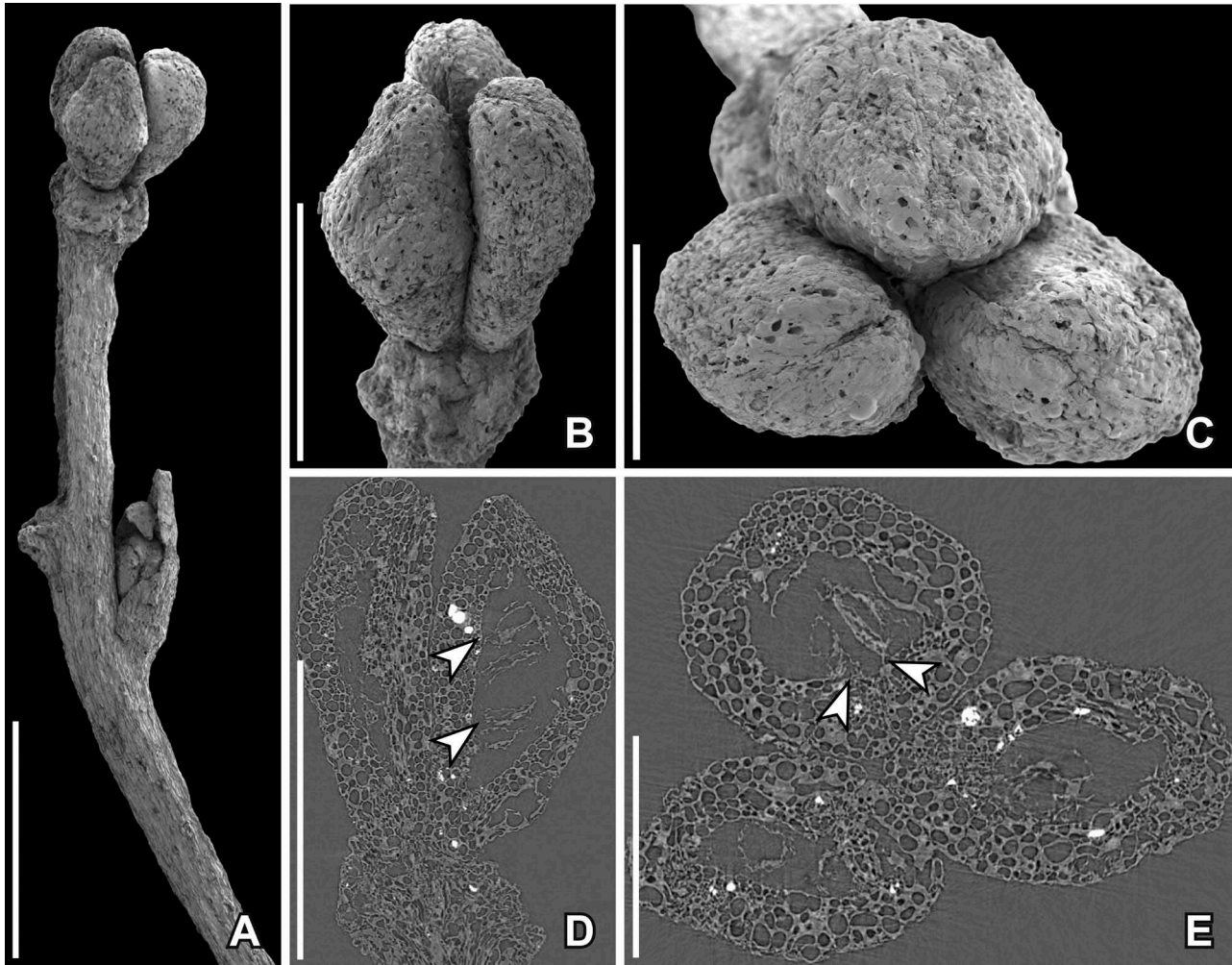


Figure 7. SEM illustrations (A–C) and SRXTM reconstructions (D–E) of *?Paisia* sp., axis with tricarpellate gynoecium, from the Early Cretaceous Catefica locality, Portugal (P0292; sample Catefica Mendes 125). **A.** Axis with terminal floral structures and two lateral buds. **B.** Close up of terminal floral structure consisting of a tricarpellate, apocarpous gynoecium and the angular, swollen receptacle with scars from other floral organs. **C.** Apical view of gynoecium showing the three free carpels and the ventral sutures; stigmatic area indistinct. **D, E.** Longitudinal (**D**) and transverse (**E**) orthoslices of gynoecium showing two rows of ovules along the ventral margins of the carpels (arrowheads); note ovules do not fill ovary cavity; fruit wall and receptacle with large isodiametric parenchyma cells (**D**, orthoslice; **E**, orthoslice xy). Scale bars – 1 mm (A), 500  $\mu$ m (B, D), 250  $\mu$ m (C, E).

Virginia, USA (unnamed pistillate flower of Crane et al. [1994, figure 6a, 6b]). They may both be related to *Paisia* and particularly the specimen shown in Crane et al. (1994, figure 6a); has a comparable expanded receptacle. The other specimen is distinguished by its scattered stomata. In both specimens only the pistillate organs are preserved and it is uncertain whether the flowers were unisexual or bisexual.

Flowers with an apocarpous gynoecium are also known from several Early Cretaceous macrofossil floras including *Sinocarpus decussatus* Leng et E.M. Friis from the Aptian Yixian Formation of Liaoning, China (Leng & Friis 2003, 2006), *Hyracantha karatscheensis* (Vakhram.) Krassilov, Shilin et Vakhram. from the Albian of Kazakhstan (Vakhrameev 1952; Krassilov et al. 1983), *Ranunculaecarpus quinquecarpel-*

*latus* Samylina from the Albian of eastern Siberia, Russia (Samylina 1960), and *Ternariocarpus floribundus* Krassilov et Volynets from the Albian of the Primorye Region, Russia (Krassilov & Volynets 2008). These fossils are all preserved in the post-anthetic stage and none of them show details of floral organisation (see Friis et al. 2011).

*In situ* pantoporate pollen grains have also been discovered in stamens and coprolites from two Early Cretaceous mesofossil floras. The spiny pantoporate grains from the Torres Vedras locality (Friis et al. 2010, plate 5, figures 1–2) are similar to those of *Paisia pantoporata* in the spiny supracteal ornamentation and aperture configuration, but details of the pollen wall is distinctly different from that of *Paisia* and the plants producing these two pollen types may

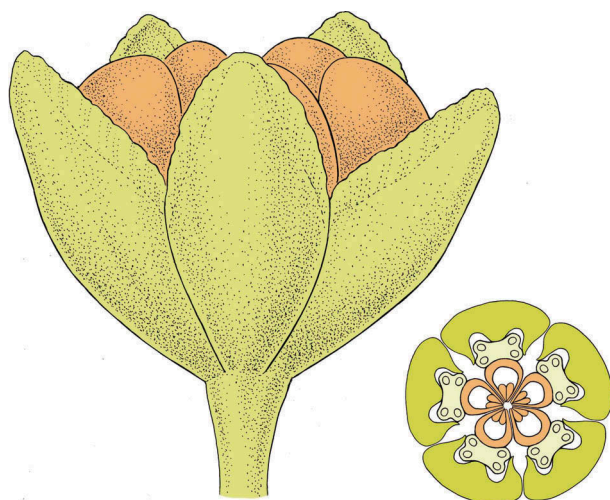


Figure 8. Reconstruction of open flower and floral diagram of *Paisia pantoporata*; light green, tepals and pedicel; light yellow, stamens; orange, carpels.

not be closely related. Pantoporate pollen from the Famalicão flora (Friis et al. 1999, figures 75–77) is reticulate with small, indistinct apertures and without supracteal ornamentation. They are very similar to pollen of extant *Sarcandra* (Chloranthaceae) and clearly distinct from the pollen of *Paisia*.

Dispersed pantoporate grains similar to those observed in *Paisia pantoporata* have also been found in the Catefica palynoflora, but are so far unknown from other dispersed palynological assemblages associated with the Early Cretaceous mesofossil floras of Portugal. The *Paisia* flowers and pollen are not common in the Catefica assemblages suggesting that the plant was not abundant in the vegetation. Pollen sacs are tiny comprising only a small part of the total stamen suggesting low pollen production for each flower. This together with an herbaceous habit suggested by the stem anatomy and possible insect pollination suggested by the spiny pollen would result in low pollen dispersal with no or only little pollen transported to the depositional basin.

Dispersed pantoporate or polyporate grains from the Cretaceous are typically assigned to the pollen genera *Australopollis*, *Bochemiperiporis*, *Cretacaeiporites*, *Erdtmanipollis*, *Penetetrapites*, *Periporopollenites* and *Polyporites* (e.g. Chlonova 1986). None of them have spiny supracteal ornamentation similar to that of *Paisia pantoporata*, but detailed comparison with the dispersed grains is typically impeded by lack of SEM images that shows details of pollen wall. The several species of *Cretacaeiporites* reported from the dispersed palynological assemblages of the São Julião shallow marine section near Ericeira, western Portugal (Horikx et al. 2016), are all different from the *in situ* pollen of *Paisia* in the lack of spines. Other reports of panto-

porate pollen from the Iberian Peninsula include rare occurrences of *Penetetrapites* from the late Albian of north-eastern Spain (Sender et al. 2012). Early Cretaceous reports from other regions shows that although pantoporate pollen are not common they were already geographically widespread in the Aptian with occurrences in Egypt and Columbia (Ibrahim et al. 2017) and by the Albian pantoporate pollen grains are diverse and almost global in distribution with occurrences in areas such as the former SSSR, Portugal, Egypt, Qatar, Sudan, Morocco, Tanzania, western Equatorial Africa, eastern North America, Brazil, Peru, and western China (e.g. Hengreen 1973; Chlonova 1986; Ibrahim et al. 2017; Zhang et al. 2015; Ferreira et al. 2016; Horikx et al. 2016).

#### *Systematic assessment of Paisia pantoporata*

The arrangement of tepals, stamens and carpels in the same radii is unusual among extant angiosperms. Further, tepals, stamens and carpels of each radius appear almost as a separate synorganised unit with the tepal margin enveloping not only the stamens, but also part of the carpel base. An intriguing possibility is that the floral structure represents an inflorescence of five simple flowers consisting of a bract, a stamen and a carpel instead of a single pentamerous flower (J. Schönenberger, personal communication, January 2017). Unfortunately, the fossil material currently available does not allow for developmental studies and we therefore maintain the interpretation of the floral structure as a single flower. Uncertainties regarding floral organisation make comparison with flowers of extant plants difficult. For instance, it is unknown whether *Paisia pantoporata* is primitively monochlamydous or whether the single whorl of perianth parts is secondarily derived from a typical heterochlamydous eudicot flower with two sets of perianth parts by reduction of either the inner or outer whorl. This together with the relatively few morphological features impedes a precise phylogenetic analysis of *Paisia pantoporata*.

Testing the position of *Paisia* using the morphological dataset and backbone constraint tree of Doyle and Endress (2010) by adding the pantoporate/pantocolpate aperture state resulted in a most parsimonious position between the Chloranthaceae and the remaining angiosperms, but most other positions were only a few steps less parsimonious. Using the Wang et al. (2009) dataset and backbone tree (Wang et al. 2009: figure 3: Strict consensus tree of eight most parsimonious trees, MPTs) suggested a position in the Ranunculales close to Berberidaceae and Ranunculaceae. The following characters of Wang et al. (2009) were scored for *Paisia*: 1–20: ?; 21, inflorescence: ?; 22, sex: 0 = monoclinal; 23,

calyx: ?; 24, perianth phyllotaxis: 1 = whorled; 25, perianth whorls: 2 = one; 26, perianth arrangement: 3 = 5; 27, nectary petals: ?; 28, androecium phyllotaxis: 1 = whorled; 29, stamen arrangement: 2 = in fives; 30, stamen fusion: 0 = free; 31, connective apex: 1 = truncate or smoothly rounded; 32, orientation of dehiscence: 1 = latrorse; 33, pollen aperture type: 2 = porate; 34, pollen aperture number: 2 = more than three; 35, exine sculpturing: 3 = spinose; 36, pollen exine: ?; 37, pollen endexine: ?; 38, gynoecium phyllotaxis: 1 = whorled; 39, carpel number: 0 = more than 3; 40, carpel form: 0 = plicate; 41, carpel fusion: 0 = apocarpous; 42, pollen transmitting tissue: ?; 43, tanniferous tissue in carpel: 0 = absent; 44, stylar scar: ?; 45, placentation type: 0 = marginal; 46, ovule number: 0 = more than 2; 47–65: ? (for method, see Friis et al. [2017]). None of the signals were very strong and the analysis was not conclusive.

Pantoporate pollen occurs scattered among all major groups of angiosperms and is reported both among early diverging lineages as well as in more derived groups. Among monocots, members of Alismataceae and Limnocharitaceae are characterised by having pantoporate pollen (Argue 1973, 1974, 1976; Chanda et al. 1988; Furness & Banks 2010) and pollen in some genera such as *Sagittaria* and *Hydrocleys* has spiny supracteal elements scattered over the tectum and surrounding the apertures in a similar way as seen in the pollen of *Paisia*. However, in *Paisia*, the elements appear compound and constricted at the base, while the microechinate-echinate pollen of Alismataceae and Limnocharitaceae has more conical and non-constricted supracteal elements. A position of *Paisia* among monocots is highly unlikely due to the pentamerous arrangement of the floral parts. Instead the pentamerous arrangement of perianth, androecium and gynoecium suggests that *Paisia* is related to eudicot angiosperms.

Pantoporate pollen together with most floral features of *Paisia* including the massive stamen filaments, basifixed anthers with broad connective between the thecae, longitudinal anther dehiscence, apocarpous gynoecium with plicate carpels and many small ovules, occur commonly among members of the earliest diverging eudicot order Ranunculales (see discussion in Friis et al. [2017]). In Ranunculales, flowers with a single series of perianth parts are not common, but do occur in several taxa, sometime the outer set and sometimes the inner set are lost. Whether the single set of perianth parts in *Paisia* is a result of a secondary loss is unknown. The apparent presence of three vascular bundles might suggest that the tepals represents an outer set of perianth parts, but there is also some resemblance in the downwards extended base of the tepals to

young petals in certain Ranunculaceae such as *Semiaquilegia* (Tucker & Hodges 2005) and the petals of *Sabia* (Sabiaceae, see later), although the hollow spurs of *Semiaquilegia* are clearly distinct from the solid tepal bases of *Paisia*. The isomerous floral organisation also occur among Ranunculales, but are more common among rosoid angiosperms (see discussion in Friis et al. [2017]). However, none of these isomerous rosoids have pantoporate pollen and core eudicots with pantoporate pollen and spiny supracteal ornamentation such as members of the Caryophyllales, Malvales and Cucurbitales are all clearly distinct from *Paisia*.

In the Ranunculales, pantoaperturate (pantoporate and pantocolpate) pollen occurs in the Eupteleaceae, Papaveraceae, Berberidaceae and Ranunculaceae. The position of Eupteleaceae as sister to all other Ranunculales and the position of Ranunculales as sister to all other eudicots (Stevens 2001 onwards) make the occurrence of pantoaperturate pollen in Eupteleaceae particularly interesting. In most species of *Euptelea* the grains are pantocolpate, but partially pantoporate grains occur in *Euptelea polyandra* Siebold et Zucc., while tricolpate pollen is less common in *Euptelea* (Pragowski 1974) and the scoring of *Euptelea* pollen as basically tricolpate as in the analysis of pollen evolution by Doyle (2005) could be misleading. In Papaveraceae, pantoporate pollen is known in Fumarioideae (*Rupicapnos*, *Fumaria*) and Papaveroideae (*Bocconia*, *Eomecon*, *Macleaya*, *Meconopsis*, *Papaver*, *Roemeria*, *Sanguinaria*) (Kadereit 1993; Blackmore et al. 1995; Wang et al. 2009) and in Berberidaceae, pantoporate pollen is reported for *Ranzania* (Nowicke & Skvarla 1981). In the Ranunculaceae, pantoporate pollen is known for species of *Caltha* (Smit & Punt 1969), *Thalictrum* (Wodehouse 1936; Blackmore et al. 1995; Tatlidil et al. 2005), *Clematis* (Wang & Xie 2007; Xie & Li 2012), *Coptis* (Wodehouse 1936), *Ranunculus* (Nowicke & Skvarla 1979; Blackmore et al. 1995; Emadzade et al. 2010), *Krafia* and *Laccopetalum* (Emadzade et al. 2010) and pantocolpate pollen is known for *Hepatica* (Nowicke & Skvarla 1981). Many of the pantoporate grains in Ranunculaceae have a punctate-perforate tectum with microechinate-echinate supracteal ornamentation that in some species is superficially similar to the ornamentation in *Paisia*, but as for the alismatalean pollen, the supracteal elements are not constricted at their bases, do not appear compound, and are typically more densely distributed.

Flowers of modern *Sabia* (Sabiaceae), another early diverging eudicot, have some floral structures that are similar to those of *Paisia pantoporata*. Particularly the shape and structure of the inner set of perianth parts (petals) in the flower buds of *Sabia limoniacea* Wall.

are M-shaped at the base embracing the massive stamen filament as in *Paisia*. Also the inner surfaces of the petals of *Sabia* are papillate comparable to the tepal surface of *Paisia* (Ronse de Craene et al. 2015). However, in the preliminary phylogenetic analysis using the Wang et al. (2009) dataset *Paisia* is not resolved as close to *Sabia* or *Sabiaceae*. Critical differences are the two sets of perianth whorls, dithecal and disporangiate anthers, bicarpellate, syncarpous or sometimes monocarpellate gynoecium and the presence of a nectary disk (Ronse de Craene et al. 2015) as well as tricolporate pollen in *Sabia* and other *Sabiaceae* (Furness et al. 2007).

Apocarpous gynoecia occur in other early diverging eudicot lineages such as Proteales, but members of Proteaceae and Platanaceae all have triaperturate, or sometimes biaperturate, pollen. Five free carpels are common in fossil platanoid flowers, but flowers of Platanaceae are unisexual, the carpels uniovulate and the associated pollen tricolpate. In Proteaceae, the flowers are typically tetramerous, sometimes borne in pairs, with a monocarpellate or sometimes bicarpellate gynoecium, and porate or more rarely colporoidate pollen (Weston 2007). The follicular fruitlets of *Agapitocarpus*, *Chontrocarpus*, *Maiandrocarpus*, *Mallicarpus*, *Mitocarpus*, *Xylocarpus* and *Zeugarocarpus* from the Late Cretaceous Åsen mesofossil flora (Leng et al. 2005) show superficial resemblance to the fruitlets of *Paisia* and were compared to extant Proteaceae, although they could not be included in the family. Some of these Late Cretaceous fossils are among the most abundant plant remains in the Åsen mesofossil assemblages. They are commonly found isolated, but those that are found attached to the inflorescence/infructescence axis are borne either single or in pairs and probably not closely related to *Paisia*.

Pantoporate pollen also occurs among basal grade angiosperms in two species of *Trimenia* (Trimeniaceae, Austrobaileyales) and in *Sarcandra* (Chloranthaceae; Sampson & Endress 1984; Endress 1986). Floral structures in these taxa are distinctly different from the flowers of *Paisia* and *Trimenia* and *Sarcandra* also differ from *Paisia* in their tectum ornamentation. The pantoporate pollen of *Trimenia* is weakly rugulose, while the pollen of *Sarcandra* is reticulate (Sampson & Endress 1984; Endress 1986).

Suprathecal sculptural elements similar to those of *Paisia* have not been observed in any of the pantoporate pollen of extant angiosperms that we have observed, but this kind of compound spines are known for inaperturate pollen of the two extant genera *Peumus* and *Palmeria* of the Monimiaceae in the Laurales (Sampson & Foreman 1990), but floral morphology of *Peumus* and *Palmeria* are distinct from that of *Paisia* in most features including their

unisexual organisation, cup-shaped receptacle, and irregular numbers of floral parts.

## Conclusion

*Paisia pantoporata* described here from the Catefica locality, Portugal, is the first Early Cretaceous flower to be described with pantoporate *in situ* pollen. The combined floral and palynological features indicate that *Paisia* most probably belongs to an extinct lineage close to the base of the eudicot angiosperms, most likely close to the Ranunculales, but the exact position has not been established. Two other kinds of pantoporate pollen were reported from stamens and coprolites of the Early Cretaceous mesofossil floras of Torres Vedras and Famalicão, Portugal, and pantoporate pollen are also recorded from other parts of the Lusitanian Basin (Horikx et al. 2016). The occurrence of pantoporate pollen in Early Cretaceous (Aptian–Albian) palynological assemblages from other regions documents that plants producing this kind of pollen occur early in the history of angiosperms with dispersed grains geographically widespread already in the Aptian (Ibrahim et al. 2017) and diverse and almost globally distributed by the Albian (Chlonova 1986; Ibrahim et al. 2017). The Early Cretaceous record of pantoporate pollen in the Portuguese mesofossil floras suggests that plants producing this kind of pollen may have been much more diverse and widespread in the Early Cretaceous than is apparent from the palynological record.

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