THE EARLY CRETACEOUS MESOFOSSIL FLORA OF CATEFICA, PORTUGAL:
ANGIOSPERMS

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Friis, E. M., Crane, P. R., Pedersen, K. R., Mendes, M. M., Kvaček, J. (2022): The Early Cretaceous mesofossil flora of Catefica, Portugal: angiosperms. – Fossil Imprint, 78(2): 341–424, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Angiosperm mesofossils are described from the Lower Cretaceous Almargem Formation exposed near the village of Catefica, Portugal, and are thought to be of Aptian-early Albian age. The mesofossil assemblage from Catefica is diverse and, in addition to the angiosperms described here, also contains a rich assemblage of non-angiosperm fossils, including leafy axes of bryophytes and lycopsids, lycopsid and salvinialean megaspores, and sporangia, sori and leaf fragments of ferns. There are also twigs, cones, cone scales, seeds and sporangia of several kinds of conifers. Other seed plants include 11 species of chlamydospermous seeds and vegetative axes related to the BEG group (Bennettiales-Erdtmanithecales-Gnetales). In terms of the number of plant fragments identified, angiosperms are most abundant in the Catefica assemblage and account for more than half of all specimens. Angiosperms also dominate in number of species, but because the non-angiosperm fossils have not been studied in detail the total number of species in the flora is not yet established. Sixty-seven species of angiosperms are recognized. Angiosperm diversity is mainly at the level of non-eudicots, including ANA-grade angiosperms, Chloranthaceae and magnoliids. Remains of chloranthoid angiosperms are especially common, both in the number of specimens and in number of species recognized. About 40 % of the specimens, and more than 25 % of the species are chloranthoids. Remains of magnoliid angiosperms (Magnoliidae, Laurales, Canellales, Piperales) are also prominent among the angiosperms. Eudicots are subordinate: only 3–4 % of all angiosperm specimens can be assigned confidently to eudicot angiosperms. Five new genera and six new species of angiosperms are established (Canrightia foveolata sp. nov., Elasmostemon paisii gen. et sp. nov., Endressistemum cateficensis gen. et sp. nov., Ibericarpus cuneiformis gen. et sp. nov., Proencistemon portugallicus gen. et sp. nov., Valvidistemon globiferus gen. et sp. nov.). Several other new taxa are also described, but not formally named.

Key words: Almargem Formation, angiosperms, Early Cretaceous, fossil flowers, mesofossils, pollen, SRXTM, synchrotron radiation X-ray tomographic microscopy

Received: February 3, 2022 | Accepted: June 13, 2022 | Issued: December 20, 2022

Introduction

Plant fossils preserved in Cretaceous sediments of the Lusitanian Basin in western Portugal have been studied since the late nineteenth century (Heer 1881, Saporta 1894) and later research by Teixeira (1945, 1946, 1947, 1948, 1950, 1952) highlighted their importance for documenting a marked floristic change from plant assemblages dominated by ferns and conifers in the earliest Cretaceous to younger floras, especially from the Late Cretaceous, dominated by angiosperms. These pioneering studies, which were based mainly on leaf impressions or thin compressions, have since been supplemented by investigations of Cretaceous pollen and spores from Portugal, including from the Early Cretaceous (e.g., Groot and Groot 1962, Médus and Berthou 1980, Hasenboehler 1981, Pais and Reyre 1981, Trincão 1985, 1990, Heimhofer et al. 2005, 2007, Mendes et al. 2011, 2014, 2017, 2018a, 2019, 2022, Horikxx et al. 2016,
Mendes and Friis 2018), and together with evidence from fossil leaves have become an important point of reference against which floristic changes in other parts of the world (e.g., Hughes 1976, Crane 1987, Lidgard and Crane 1990), including the Potomac Group in eastern North America, can be compared.

While studies of fossil leaves and pollen from Portugal, eastern North America (particularly the Potomac Group, e.g., Fontaine 1889, Brenner 1963, Doyle 1969, Doyle and Hickey 1976, Hickey and Doyle 1977, Doyle and Robbins 1977) and elsewhere (Hughes 1976) have revealed important aspects of Cretaceous vegetational change, studies of fossil leaves and pollen grains generally provide only a limited suite of features for assessing the relationships of early angiosperms with their living counterparts. In particular, so far, there are no detailed studies of fossil leaves from the Early Cretaceous of Portugal using modern techniques, and most palynological investigations have been limited to standard light microscopy, which is insufficient to resolve critical features in pollen grains that are often very small.

Beginning in the late 1980s, extensive fieldwork by E. M. Friis, K. R. Pedersen and P. R. Crane in the Lusitanian Basin, which re-collected several classic sites and also discovered new Early and Late Cretaceous localities, identified numerous mesofossil assemblages containing abundant and well-preserved angiosperm flowers, fruits, and seeds. Subsequent studies of mesofossils from localities of Early Cretaceous age at Arazede, Buarcos, Catcica, Chicalhão, Famalicão, Juncal, Nossa Senhora da Luz, Torres Vedras, Vale de água, and Vila Verde have provided a previously unimagined variety of exquisitely well-preserved angiosperm fossils (Friis et al. 1997, 1999, 2000, 2009a, 2010a, b, 2011, 2015a, 2017, 2018a–c, 2019a–d, 2020a, 2021, Friis and Pedersen 2011, Pedersen et al. 2007, Mendes et al. 2011, 2014, Mendes and Friis 2018). This material gives detailed structural information on the flowers, fruits, and seeds of early angiosperms, which permits detailed comparison with their potential living relatives. In particular, so far, there are no detailed studies of fossil leaves from the Early Cretaceous of Portugal using modern techniques, and most palynological investigations have been limited to standard light microscopy, which is insufficient to resolve critical features in pollen grains that are often very small.

In this paper, we provide a comprehensive account of the angiosperm component of a second Early Cretaceous mesofossil flora based on material collected from a road cut close to the small village of Catcica in western Portugal, ca. 40 km north of Lisbon. Several angiosperm and non-angiosperm taxa based on mesofossils have been described previously from Catcica (e.g., Friis et al. 1999, 2011, 2015a, b, 2017, 2018a, 2020a, 2021, Friis and Pedersen 2011, Mendes et al. 2017, 2018b, Kvaček and Mendes 2020, 2021, Mendes and Kvaček 2020, Tekleva et al. 2021). A complete description of the non-angiosperm seed plants from the Catcica mesofossil flora, together with the bryophytes and pteridophytes, will be provided in later accounts.

Like the slightly older Torres Vedras mesofossil flora, the Catcica mesofossil flora is dominated by well-preserved fossils of early angiosperms, among which, ANA-grade and magnoliid angiosperms, with a small number of monocots (Friis et al. 2019a). In contrast, eudicots are not well represented and account for only three of the 39 pollen types recorded among the mesofossils from Torres Vedras based on critical scanning electron microscope studies (Friis et al. 2019a).

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Material and methods

The Catcica mesofossil flora (39° 03’ 30” N; 09°14’ 30” W) was discovered in 1989 by K. R. Pedersen, E. M. Friis and P. R. Crane exposed in a road cut along Rua General Humberto Delgado between the villages of Catcica and Mugideira, about 4 km south of Torres Vedras, western Portugal (Text-fig. 1). The outcrop consists of cross-bedded sands with subordinate horizons of clay and silt that contain lenses rich in small plant fragments. The plant bearing sequence belongs to the Almargem Formation (Rey 1992, 1993), previously assigned to the “Grés de Torres Vedras” (Carta Geológica de Portugal, Folha 30-D Alenquer; Zbyszewski and Torre de Assunção 1965). While the precise stratigraphic position of the Catcica deposits within the Almargem Formation is not certain, they are thought to be either in the upper part of the Lower Almargem Formation, and of late Aptian age, or in the basal part of the Upper Almargem Formation, correlative with the basal part of the Figueira da Foz Formation, which is regarded as of late Aptian-early Albian age (Dinis et al. 2008, 2010). The age of the Catcica mesofossil flora is thus most likely late Aptian-early Albian or perhaps slightly older (see Friis et al. 2018a for further discussion). Further information on the locality, including geological maps, illustrations of the Catcica exposure, and consideration of its sedimentological setting is provided in several previous studies of fossils from the Catcica locality (e.g., Friis et al. 2011, Mendes et al. 2017, 2018b, Kvaček and Mendes 2020, 2021, Mendes and Kvaček 2020, Tekleva et al. 2021).
The sediments exposed at the Catefica locality are rich in plant mesofossils. The sediments are unconsolidated and easily disintegrated in water. The plant fossils, preserved as slightly compressed coalifications or three-dimensional charcoalifications, were floated over a 125 µm mesh sieve, cleaned of adhering mineral matrix using 40% HF, followed by 10% HCl and thorough rinsing in water. The cleaned organic material was then air-dried and sorted under binocular microscope.

All sediment samples collected throughout the exposure, vertically as well as laterally, contained well-preserved plant fossils. The most productive sample, Catefica sample 49, was collected in 1989 from the basal part of the exposed sequence from a dark, organic rich lens (Text-fig. 1). In this paper, we consider the angiosperm component of the Catefica mesofossil flora based on the information currently available. Some of the angiosperms are already described and formally named, including *Canrightia resinifera* E.M.Friis et K.R.Pedersen, *Canrightiopsis crassitesta* E.M.Friis, G.W.Grimm, M.M.Mendes et K.R.Pedersen, *C. intermedia* E.M.Friis, G.W.Grimm, M.M.Mendes et K.R.Pedersen, *Catanthus dolichostemon* E.M.Friis, P.R.Crane et K.R.Pedersen, *Goczania rugosa* E.M.Friis, P.R.Crane et K.R.Pedersen, *Hedyflora crystallifera* E.M.Friis, P.R.Crane et K.R.Pedersen, *Kempia longicolpites* E.M.Friis, P.R.Crane et K.R.Pedersen, *Mugideiriflora portugallica* E.M.Friis, P.R.Crane et K.R.Pedersen, *Saportanthus parvus* E.M.Friis, P.R.Crane et K.R.Pedersen, *Serialis communis* E.M.Friis, P.R.Crane et K.R.Pedersen and *Serialis crassitesta* E.M.Friis, P.R.Crane et K.R.Pedersen (for references see Systematic palaeobotany). Several taxa related to the Bennettitales-Erdtmanithecales-Gnetales (BEG) group and to conifers have also been formally described and will be discussed in detail in a separate account of the non-angiosperm component of the Catefica mesofossil flora (J. Kvaček, M. M. Mendes, E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress). Because only the angiosperm mesofossils are described here, an analysis of the total species diversity is not possible. However, we provide an analysis and discussion of the angiosperms in the Catefica mesofossil flora based on the extensive collections housed in the Swedish Museum of Natural History (Catefica samples 49, 50, 150–154, 242, 342, 343, 358–362, 381, 382). These samples were collected by K. R. Pedersen, E.
Text-fig. 2. Scanning electron microscope (SEM, a, c–f) and synchrotron radiation X-ray tomographic microscopy (SRXTM, b, g) images of the flower of *Mugideiriflora portugallica* (a, b) and fruits, seeds and pollen of *Canrightia resinifera* (c–g); Catefica locality, Portugal. a) Oblique, apical view of flower showing multiparted organization with numerous laminar tepals, stamens that are rhomboidal and flattened in transverse section and carpels that are borne on the short conical apex of the receptacle; b) Transverse section (orthoslice xy0800) through basal part of flower showing the elongate bases of the laminar tepals and the flattened rhomboidal bases of the stamens; c) Fruit in lateral view showing irregular surface resulting from the abundant resin bodies in the fruit and hypanthium wall, scars from stamens on the rim of the hypanthium (arrowheads) and the lobed apical stigmatic region (st); d) Broken fruit with one or two seeds missing but showing three pendant, orthotropous seeds with pointed micropylar regions (mi) and a finely pitted crystalliferous endotesta; e) Single seed isolated from a fruit showing two distinct bundles (vb) still attached apically to the chalazal region of the seed, the pointed micropyle (mi) and the finely pitted surface of the crystalliferous endotesta; f) Monocolpate pollen from stigmatic region of fruit
M. Friis and P. R. Crane, who also sorted, examined and counted the specimens. Additional specimens collected by M. M. Mendes and colleagues, which are stored in Portugal at the University of Coimbra and the Geological Museum of Lisbon, were not included in the counts to ensure reasonably consistent sampling. These fossils are, however, included in the systematic accounts when they provide additional information so that the systematic coverage and angiosperm species list is as complete as possible. For the most productive sample (Catefica sample 49), angiosperm specimens with recognizable botanical features were separated and counted with great care. Other samples were sorted in less detail (see Discussion).

The specimens were studied using scanning electron microscopy (SEM) and synchrotron radiation X-ray tomographic microscopy (SRXTM). For both, fossils were mounted on metal stubs using nail polish. Specimens for SEM were coated with gold or platinum and studied using a Hitachi S-4300 field emission, Phillips 515 and Jehol SEM were coated with gold or platinum and studied using a Hitachi S-4300 field emission microscope at the Swedish Museum of Natural History, and a Versa 3D FIB-SEM at the iNano Institute, Aarhus University, Denmark. Specimens for SRXTM were mounted without further treatment and analyzed at the TOMCAT beamline of the Swiss Light Source of the Paul Scherrer Institute, Villigen, Switzerland (Stampakoni et al. 2006, Friis et al. 2014). More than 160 specimens were analyzed at TOMCAT, mostly using a 10× or 20× objective over 180° (App. I). Reconstructions of SRXTM data were made using Avizo software and an even black background for the SEM images was made using Photoshop. For terminology, see Friis et al. 2019a.

Specimens described in this paper are housed in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm (S numbers) and in the Geological Museum of Lisbon (P numbers). All raw data from the SRXTM measurements, including that for specimens with S and P numbers are stored at the Swedish Museum of Natural History, Stockholm.

The generic and specific names of the new taxa described here are registered in the Plant Fossil Names Registry (PFNR), each with a unique registry number. PFNR is hosted and operated by the National Museum, Prague, for the International Organisation of Palaeobotany (IOP).

**Systematic palaeobotany**

**Subdivision Angiospermae Lindl., 1830**  
**Order Nymphaeales Salisb. ex Bercht. et J.Presl., 1820**  
**or Austrobaileyales Takht. ex Reveal, 1992**

**Remarks.** Only floral material of *Mugideiriflora portugallica* is treated here under Nymphaeales-Austrobaileyales. Several exotestal seeds in the Catefica mesofossil flora are closely similar to those of extant taxa in the orders Nymphaeales and Austrobaileyales, indicating the probable presence of one or both of these two extant clades, or extinct forms related to them, among the Catefica early angiosperms. However, because these seeds have not yet been investigated in detail, they are treated here under the heading “Angiosperms of uncertain affinity”. Other fossils from Catefica that are possibly related to extant Nymphaeales-Austrobaileyales are treated as “Angiosperms of uncertain position at the level of ANA-grade angiosperms-Chloranthaceae-magnoliids.”

**Genus Mugideiriflora E.M.Friis, P.R.Crane et K.R.Pedersen, 2020**

*Mugideiriflora portugallica* E.M.Friis, P.R.Crane et K.R.Pedersen, 2020  
Text-fig. 2a, b

**Description and remarks.** *Mugideiriflora portugallica* is based on a single small, partly abraded, early anthetic flower (Text-fig. 2a) that has a multiparted perianth, androecium and gynoecium and was recovered from the Catefica mesofossil flora (for a full description and discussion of the species see Friis et al. 2020a). Additional specimens are preserved at very early developmental stages. The receptacle is slightly concave, but with a short conical apex in the gynoecial region (Text-fig. 2a). There are about 50 laminar tepals, 50 stamens and more than 50 carpels, all apparently in a spiral arrangement (Text-fig. 2b).

**Affinity and other occurrences.** Phylogenetic assessment suggests that *Mugideiriflora portugallica* is closely related to members of extant Austrobaileyales, although a possible affinity with members of extant Magnoliales cannot be excluded (Friis et al. 2020a).

*Mugideiriflora portugallica* is currently known only from the Catefica mesofossil flora where it is recorded from samples collected near the base of the exposure.

**Order Chloranthales R.Br. ex Sims, 1821**

**Remarks.** Chloranthoid fossils are the most diverse group of angiosperms in the Catefica mesofossil flora. Eighteen taxa are recognized based on inflorescences and flowers as well as isolated fruits, seeds and stamens (Text-figs 2–16, Tab. 1).

**Genus Canrightia E.M.Friis et K.R.Pedersen, 2011**

*Canrightia resinifera* E.M.Friis et K.R.Pedersen, 2011  
Text-fig. 2c–g

**Description and remarks.** Fruits and seeds of *Canrightia resinifera* are the most common angiosperm fossils in the Catefica mesofossil flora. Several hundred specimens recorded so far including the type material on which the genus was established (Friis and Pedersen 2011). The fruits are elliptical to spherical in outline, contain two to five seeds, and have abundant resin-bodies in the fruit wall.
The fruits are interpreted as berries (Text-fig. 2c, d). The fruits develop from bisexual flowers with a semi-inferior ovary and about four staminal scars in a radially symmetrical arrangement on the rim of the hypanthium (Text-fig. 2c). The many resin bodies in the fruit wall, combined with the often-wrinkled fruit surface, sometimes make the precise position of the hypanthium and the staminal scars difficult to distinguish. The stigma at the apex of the fruit is lobed. The seeds are orthotropous, pendent and endotestal, with a distinct, finely crystalliferous, endotesta (Text-fig. 2d, e) and with the inner epidermis of the tegmen developed as a distinct endothelium (Text-fig. 2g).

Pollen grains are common in the stigmatic region. They are monocolpate, 15.8–21.0 μm with a long extended colpus, and a coarsely reticulate tectum. Muri are smooth, with a high and sharp profile, and are supported by long and scattered columellae (Text-fig. 2f). The grains are similar to pollen assigned to the extinct genus *Piercipollis* E.M.Friis, P.R.Crane et K.R.Pedersen (Friis et al. 2019a). Dispersed pollen of this type has traditionally been assigned to the extinct genus *Retimonocolpites* R.L.Pierce, but in the type species, *Retimonocolpites dividuus* R.L.Pierce, the colpus extends from the distal surface over to the proximal surface of the grain dividing the grain in two halves (Pierce 1961). In contrast, in *Piercipollis* the colpus is restricted to the distal half of the grain (Friis et al. 2019a).

A second species of *Canrightia*, *Canrightia foveolata* sp. nov., is formally described below from the Catefica mesofossil flora. It is distinguished from *C. resinifera* by its finely pitted endotesta. *Canrightia elongata* E.M.Friis, P.R.Crane et K.R.Pedersen described from the Torres Vedras mesofossil flora (Friis et al. 2019a) is distinguished from both of the Catefica species by its more elongated fruits that have a shorter hypanthium.

**Affinity and other occurrences.** The original phylogenetic analysis of *Canrightia* placed the genus close to the base of the Chloranthaceae (Frii and

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**Table 1. Chloranthoid taxa recognized in the Catefica mesofossil flora based on inflorescences and flowers as well as isolated fruits, seeds and stamens with pollen characters added for those taxa where pollen are known.**

| Taxon              | Text-figs | Organ                  | Stamen, length | Diameter of pollen | Aperture configuration | Aperturediametre grain | Muri, ornamentation | Muri, width |
|--------------------|-----------|------------------------|----------------|--------------------|------------------------|------------------------|---------------------|-------------|
| *Canrightia resinifera* | 2c–g      | flower/fruit/seed      | ?             | 15.8–21.0 μm       | monocolate             | 1:1                    | smooth              |             |
| *Canrightia foveolata* | 3a–f, 4a–i| flower/fruit/seed      | ?             | ?                  | ?                      | ?                     | ?                   |             |
| *Canrightia sp.*     | 5a, b     | flower/fruit/seed      | ?             | ?                  | ?                      | ?                     | ?                   |             |
| *Canrightiopsis crassitesta* | 6a–c, g, h| flower/fruit/seed      | ?             | 12–14 μm           | monocolate             | 1:1                    | beaded, 1 row      | 0.25 μm    |
| *Canrightiopsis intermedia* | 6d–f    | flower/fruit/seed      | ?             | ?                  | ?                      | ?                     | ?                   |             |
| *Canrightiopsis sp.*  |           | flower/fruit/seed      | ?             | ?                  | ?                      | ?                     | ?                   |             |
| *Hedyflora crystallifera* | 7a–f      | flower/fruit/seed      | ?             | 22 μm              | tetrachotomocolpate    | 2:3                   | beaded, 2 rows     | 0.3 μm     |
| *Proencistemon portugalis* | 8a–f, 9a–g| inflorescence/stamen  | 0.55 mm       | 12.5–16 μm         | trichotomocolpate      | 2:3                   | beaded, 2–3 rows   | 0.2 μm     |
| *Proencistemon sp.*   | 9b–j      | inflorescence/stamen  | 0.8 mm        | 16 μm              | trichotomocolpate      | 2:3                   | beaded, 2 rows     | 0.3 μm     |
| *Clavatipollenites type pollen sp. 1* | 10a–d | stamen                 | 1.3 mm        | 17–20 μm           | monocolate             | 2:3                   | beaded, 1 row      | 0.2–0.4 μm |
| *Clavatipollenites type pollen sp. 2* | 11a–e | stamen                 | 1.3 mm        | 24–26 μm           | monocolate             | 1:3                   | beaded, 1–2 rows   | 0.5 μm     |
| *Clavatipollenites type pollen sp. 3* | 12a–e | stamen                 | 0.5 mm        | 15–17 μm           | monocolate             | ?                     | beaded, 1–2 rows   | 0.4 μm     |
| *Clavatipollenites type pollen sp. 4* | 13a–d | stamen                 | 0.5 mm        | 14–17 μm           | monocolate             | 2:3                   | beaded, 1–2 rows   | 0.3 μm     |
| *Asteropollis type pollen sp. 1* | 14a–e | stamen                 | 0.4 mm        | 20–24 μm           | tetrachotomocolpate    | 2:3                   | beaded, 2 rows     | 0.5 μm     |
| *Asteropollis type pollen sp. 2* | 15a–e | stamen                 | 0.9 mm        | 15–18 μm           | pentachotomocolpate    | 2:3                   | beaded, 2 rows     | 0.4 μm     |
| *Asteropollis/Clavatipollenites sp. 1* | 16a–c | stamen                 | 1 mm          | 17–20 μm           | ?                      | ?                     | beaded-perforated, beaded, 1–2 rows | 0.3 μm       |
| *Asteropollis/Clavatipollenites sp. 2* | 16d–f | stamen                 | 1.4 mm        | 22 μm              | ?                      | ?                     | beaded, 2 rows     | 0.5 μm     |
| *Asteropollis/Clavatipollenites sp. 3* | 16g–i | stamen                 | 0.8 mm        | 16 μm              | ?                      | ?                     | beaded, 2 rows     | 0.8 μm     |
Pedersen 2011), a position that has been corroborated by several subsequent analyses (Doyle and Endress 2014, Friis et al. 2015a).

Canrightia resinifera is one of the most common angiosperm fossils in the Early Cretaceous floras of Portugal with numerous specimens recorded from the Arazede, Buarcos, Catetica, Famalicão and Vale de Água mesofossil floras (Friis and Pedersen 2011), as well as from the Chicalhão and Nossa Senhora da Luz mesofossil floras (Mendes et al. 2014, Mendes and Friis 2018). In the Catetica mesofossil flora Canrightia resinifera is recorded from all samples.

Pollen similar to that associated with Canrightia resinifera has not been observed in situ in any of the dispersed stamens from the Catetica mesofossil flora (Tab. 1). Pollen grains similar to those observed on the Canrightia fruits are present, however, in palynological samples analyzed from the Catetica locality and in other palarctic floras from the Early Cretaceous of Lusitanian Basin in western Portugal.

Canrightia foveolata E.M.Friis, P.R.Crane, K.R.Pedersen, M.M.Mendes et J.Kvacek sp. nov.

Text-figs 3a–f, 4a–i

Holotype. S174249 (Catetica sample 49; figured Text-fig. 3a–f).

Plant Fossil Names Registry Number. PFN002785 (for new species).

Paratypes. S175179, S265998, S266057, S266107 (Catetica sample 49), S266042 (Catetica sample 154), S175178 (Catetica sample 242).

Repository. Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.

Etymology. From Latin: fovea (pit) referring to the densely pitted surface of the endotesta.

Type locality. Catetica (39°03’30ʺ N; 09°14’30ʺ W), between the villages of Catetica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almargem Formation, Early Cretaceous (Aptian-early Albian).

Diagnosis. Fruit obovoid with a broad hypanthium and two pendent seeds. Perianth of six tepals. Contact surface between the two seeds flat; external surface rounded. Crystals evenly distributed in the cells of the endotesta. Surface of endotesta foveolate with shallow foveae arranged in more than 30 closely packed longitudinal rows. Fruit wall particularly thick apically over the seeds.

Distinguishing features. The new species is assigned to the extinct genus Canrightia based on the berry-like fruit with pendent, orthotropous seeds that have an endotestal-endotegmic seed coat and a crystalliferous endotesta. Canrightia foveolata is distinguished from C. resinifera (see above), and from C. elongata from the Torres Vedras mesofossil flora (Friis et al. 2019a), mainly by the densely pitted and grooved surface of the endotesta. Seeds of C. foveolata also have crystals that are of more or less of similar size and that are evenly distributed in the endotestal cells, whereas in C. resinifera and C. elongata larger crystals are concentrated close to the outer surface of endotesta. Canrightia foveolata is also two-seeded, as are most specimens of C. resinifera from the Famalício locality, while fruits of C. resinifera from the Catetica locality typically have three to five seeds and C. elongata has three seeds.

Canrightia foveolata is further distinguished from the two other species of Canrightia by the well-developed soft tissue of the fruit wall above the seeds. Canrightia foveolata may also be distinguished from the two other species by the larger number of perianth parts, but as the perianth is known for only one specimen of C. foveolata, and only a few specimens of C. resinifera, the range of tepal numbers in Canrightia is not fully established.

A pitted surface of the endotesta is also present in seeds of Canrightiopsis E.M.Friis, G.W.Grimm, M.M.Mendes et K.R.Pedersen and Kvacekspermum E.M.Friis, P.R.Crane et K.R.Pedersen, two other extinct genera of chloranthoid affinity (Friis et al. 2015a, 2018b), but both of these genera have one-seeded fruits and a much thicker endotestal seed coat.

Dimensions. Length of fruit: 1.7 mm; maximum width of fruit: 1.6 mm; length of seed: 0.85–1.05 mm; maximum width of seed: 0.6–0.9 mm.

Description and remarks. The new species is based on a single fruit, containing two seeds (Text-fig. 3a–f). There are also several isolated seeds (Text-fig. 4a–i). The fruit and two of the isolated seeds were studied using SRXTM. The fruit is partly abraded, and although the stigmatic region is missing, the fruit is otherwise well preserved in its apical part. There is a swollen rim about halfway up the fruit with six, small poorly developed tepals that are best preserved on one side of the fruit (Text-fig. 3a). Five vascular bundles are preserved in the hypanthium, each extending to a tepal and their symmetry indicates that a sixth bundle has been lost where the fruit wall is abraded (Text-fig. 3d). The fruit wall is particularly thick in the region above the seeds and consists mainly of isodiametric cells (Text-fig. 3a–c).

The seeds are broadly elliptical, crescent-shaped in lateral view, slightly pointed at the micropylar end and rounded at the chalazal end (Text-figs 3b, 4a–d, f). Where the two seeds meet, their faces are flattened, but with a prominent chalaza that projects towards the face where the seeds meet (Text-fig. 4b, d). The opposite faces are rounded (Text-figs 3c, d, 4b, e, c). In the isolated seeds, the outer cells of the seed coat are abraded exposing the surface of the endotesta, which is characterized by numerous small pits arranged in more than 30 shallow, closely-spaced, longitudinal grooves (Text-fig. 4a–d).

In the fruit the exotesta of the seeds is partly preserved and consists of thick-walled, isodiametric cells. The endotesta is thin (about 30 μm) in the region between the two seeds, but thicker (about 55 μm) in the chalazal region and toward the outer surfaces (Text-fig. 3c, e, f). The exotesta is so tightly appressed to the tissue of the fruit wall that the two tissues are sometimes difficult to delimit. The endotesta consists of palisade-shaped cells that are infilled with fibrous material in which there are abundant casts of cubic crystals. The casts of these crystals are distributed more or less evenly within
Text-fig. 3. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images of fruits of *Canrightia foveolata* sp. nov.; Catefica locality, Portugal. a) Volume rendering of fruit showing prominent rim around the middle of the fruit with reduced tepals (arrowheads) and partly abraded fruit wall exposing the pitted endotesta surface of one of two seeds (arrow); note two of the vascular bundles (vb) extending from the base of the fruit to the tepals; b) Voltex of fruit showing prominent rim around the fruit (arrowhead) and dense precipitation of crystals in the endothelium cells of one of the two seeds in the fruit; c) Longitudinal section of fruit (orthoslice yz0520) showing the inferred hypanthium rim (arrow head) and two seeds, one with a dense precipitation of crystals; note the prominent endothelium cells (asterisks) of the inner integument and the well-developed fruit wall above the seeds; d) Transverse section through basal part of fruit and seeds close to the micropyle (orthoslice xy0312) showing partly abraded fruit wall with five vascular bundles (vb) and details of the seed coat with endotesta (oi-end) surrounding the tegmen consisting of an outer epidermis (ii-o), middle layer (ii-m) and a distinct inner epidermis (endothelium) consisting of radially elongated cells (asterisk); e) Transverse section (orthoslice xy1680) through apical part of the fruit close to chalaza showing the tips of two seeds; note the endotesta (oi-end) surrounded by thick-walled cells of the exotesta (oi-o); f) Transverse section (orthoslice
the cells (Text-figs 3f, 4e–i).

The inner integument is three cell layers thick. It consists of an outer epidermis, a middle layer of thick-walled and slightly longitudinally elongated cells, and an inner epidermis that develops into an endothelium of thin-walled and radially elongated cells (Text-figs 3c, d, 4e, f, h).

The stigmatic area is not preserved and no pollen was observed on the surface of the fruit.

Affinity and other occurrences. The relationships of Canrightia foveolata, as for Canrightia resinifera, are likely close to the base of extant Chloranthaceae (see above). Canrightia foveolata is currently known only from the Catefica locality.

Canrightia sp.
Text-fig. 5a, b

Description and remarks. A single isolated seed that closely resembles isolated seeds of Canrightia foveolata in general morphology (above) is not assigned to any of the species of Canrightia. The seed is broadly elliptical in shape, about 1.05 mm long and 0.75 mm wide, with a slightly pointed micropylar region and a rounded chalazal region. One face is flattened and the opposite face is slightly convex (Text-fig. 5a). The chalaza protrudes slightly to the flattened face (Text-fig. 5a). The flattened surface suggests that the seed is from a two-seeded fruit similar to that of Canrightia foveolata. The outer tissues of the seed coat and fruit wall are abraded and the exposed part of the seed is the hard, finely crystalliferous, endotesta. The surface of the endotesta is pitted with many larger pits arranged in about 20 shallow, longitudinal rows and also by smaller cavities formed by angular crystals (Text-fig. 5a, b). There is no information on internal features.

Affinity and other occurrences. The seed is assigned to Canrightia based on its close similarity to Canrightia foveolata in general morphology (above) is not assigned to any of the species of Canrightia. Both have one flattened face, prominent pits arranged in longitudinal rows on the outer surface, and a distinctly crystalliferous endotesta. However, the seed of Canrightia sp. is larger than that of C. foveolata and also has the pits arranged in fewer longitudinal rows (about 20 in Canrightia sp. compared to more than 30 in C. foveolata). Similar seeds have not yet been encountered in other Early Cretaceous mesofossil floras from Portugal.

Genus Canrightiopsis E.M. Friis, G.W. Grimm, M.M. Mendes et K.R. Pedersen, 2015

Canrightiopsis crassitesta E.M. Friis, G.W. Grimm, M.M. Mendes et K.R. Pedersen, 2015
Text-fig. 6a–c, g, h

Description and remarks. Canrightiopsis crassitesta was established based on fruits, seeds and adhering pollen from the Catifica mesofossil flora (Friis et al. 2015a). The fruits are elliptical to spherical in outline and are interpreted as berries with a single seed (Text-fig. 6a, b). They are derived from bisexual flowers and remains of a hypanthium, as well as scars from stamens, are present on the probable abaxial face of the fruit, about one third to two thirds of the distance from the base (Text-fig. 6a, d). The seeds are orthotropous, pendent and endotestal with a distinct, thick and finely crystalliferous endotesta (Text-fig. 6b, c). The outer surface of endotesta is characterized by relatively large pits arranged in longitudinal rows that are also visible where the fruit wall is compressed or poorly preserved (Text-fig. 6a). The tegmen is three cell layers thick. In some specimens, remains of an endothelium are seen as slightly elongated cells, but the distinct endotestal seen in other species of Canrightiopsis has not been observed. Pollen grains attached to the fruits are similar to dispersed pollen assigned to the extinct pollen genus Clavatipollenites Couper (Text-fig. 6g, h). Grains are 12–14 µm in equatorial diameter, monocolpate, semitectate-reticulate with a long, extended colpus with an irregular margin. The reticulum is composed of narrow, beaded muri supported by long, scattered columellae (Text-fig. 6g, h). The embryo is minute and surrounded by a nutritive tissue of thin-walled, isodiametric cells (Text-fig. 6b, c).

Affinity and other occurrences. Analysis of the phylogenetic relationships of Canrightiopsis placed the genus in the Chloranthaceae as part of the Ascarina J.R. Forst. et G.Forst.-Sarcandra Gardn.-Chloranthus Sw. clade, particularly close to Sarcandra and Chloranthus (Friis et al. 2015a), a result also supported by a subsequent analysis (Doyle and Endress 2018).

Fruits and seeds of Canrightiopsis are common in Early Cretaceous mesofossil floras from Portugal. In addition to C. crassitesta, two other species have been recognized including C. intermedia and C. dinisi/E.M. Friis, G.W. Grimm, M.M. Mendes et K.R. Pedersen. Only C. crassitesta and C. intermedia are present in the Catifica mesofossil flora. C. crassitesta is distinguished from C. intermedia by its much thicker endotesta, but the two species are similar in fruit morphology and without internal details, the fossils are difficult to separate. All Canrightiopsis specimens from Catifica studied using SEM are typical C. crassitesta, while only one specimen is a distinct C. intermedia. Other specimens from Catifica for which internal features are unknown are referred to as Canrightiopsis sp. (Friis et al. 2015a).

Fruits and seeds of Canrightiopsis are particularly common in the mesofossil flora from Famalicão, but are also reported from the Arazede, Buarcos, Chicalhão, Vale de Água and Vila Verde mesofossil floras (Friis et al. 2015a). Currently C. crassitesta is reported only from the Catifica mesofossil flora.

Pollen grains found on fruits of Canrightiopsis crassitesta are similar in size and general morphology to those found in situ in isolated stamens and inflorescence fragments from Catifica with Clavatipollenites-type pollen (Text-figs 10–13, Tab. 1), but the reticulum of the pollen associated with

xy1485) through fruit in the region of the hypanthium rim showing sections through the two seeds close to the chalazal region; note endotesta (oi-end) surrounded by larger cells of exotesta (oi-σ) and fruit wall (fr). Specimen, Catifica 49-S174249 (holotype, a–f).
Scale bars = 300 µm (a–c, e, f), 100 µm (d).

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Text-fig. 4. Synchrotron radiation X-ray tomographic microscopy (SRXTM) images of seeds of Canrightia foveolata sp. nov.; Catefica locality, Portugal. a–d) Volume renderings of abraded seeds in ventral (a), lateral (b, d) and apical (c) views showing the slightly protruding chalaza (arrows) and dense longitudinal grooves with shallow pits in the surface of the endotesta; e) Transverse section of seed (orthoslice xy0665) showing the irregular grooved surface of the endotesta (oi-en) and the tegmen comprised of two layers of thick-walled cells that surround the cells of the prominent endothelium (asterisk); f) Longitudinal section (orthoslice xz1195) through seed showing the thin-walled endothelium cells (asterisk) surrounded by the thicker cells of the outer tegmen and endotesta; g) Longitudinal section (orthoslice yz0727) through seed showing outlines of angular crystals evenly distributed in cells of the endotesta (oi-en); note the outer epidermis of the tegmen (ii-o) composed of thick-walled cells; h) Longitudinal section (orthoslice xz0940) of seed showing details of the chalazal region with course of the vascular bundle (vb), cells of the prominent endothelium (asterisk), crystalliferous endotesta of the outer integument (oi-en) and the distinct thick walled cells of the outer cells of the tegmen (ii-o); i) Longitudinal and tangential section (orthoslice yz0542) through the endotesta (oi-en) showing the outlines of densely spaced crystals. Specimens, Catefica 242-S175178 (a–c, e–h), Catefica 49-S175179 (d, i). Scale bars = 300 μm (a–d), 100 μm (e, f, h, i), 50 μm (g).
Canrightiopsis crassitesta is more open and the grains are smaller.

**Canrightiopsis intermedia** E.M.Friis, G.W.Grimm, M.M.Mendes et K.R.PederSEN, 2015

*Text-fig. 6d–f*

**Description and remarks.** A single specimen from the Catefica mesofossil flora can be assigned with confidence to *Canrightiopsis intermedia*. It is a small, single-seeded berry with remains of a hypanthium and scars from three stamens on the probable abaxial side of the fruit (*Text-fig. 6d*). In this respect the specimen is closely similar to *Canrightiopsis crassitesta* (see above) as also is the seed in being orthotropous, pendent and endotestal with a pitted outer surface of the endotesta. However, the Catefica specimen of *C. intermedia* differs from *C. crassitesta* in its much thinner endotesta (*Text-fig. 6e, f*). Pollen grains have not been observed attached to the *C. intermedia* specimen from Catefica, but *Clavatipollenites*-type pollen grains were reported on specimens of *C. intermedia* from Famalicão (Friis et al. 2015a).

**Affinity and other occurrences.** *Canrightiopsis* is placed in the Chloranthaceae close to *Ascarina*, *Sarcandra* and *Chloranthus* clade (see above). *Canrightiopsis intermedia* is based on fruits and seeds from the Famalicão mesofossil flora where the species is very common (Friis et al. 2015a) and is also reported from the Buarcos and Vale de Água localities. The species is distinguished from *C. crassitesta* mainly by its much thinner endotesta.

**Canrightiopsis sp.**

**Remarks.** The three species of *Canrightiopsis* described from the Early Cretaceous of Portugal are closely similar to each other in morphology and in the organization of the fruits and seeds. The three species are mainly distinguished by details of their seed coat (Friis et al. 2015a). The Catefica mesofossil flora includes several *Canrightiopsis* fruits that cannot be placed securely in any of the existing species due to the lack of information on their internal structure. These seeds are collectively referred to here as *Canrightiopsis* sp.

**Genus Hedyflora** E.M.Friis, P.R.Crane et K.R.PederSEN, 2019

*Hedyflora crystallifera* E.M.Friis, P.R.Crane et K.R.PederSEN, 2019

*Text-fig. 7a–f*

**Description and remarks.** *Hedyflora crystallifera* was established based on floral structures with adhering pollen from the Buarcos mesofossil flora (Friis et al. 2019b). The specimens from Catefica are often strongly compressed and lignitised. Internal details are known from only a few specimens. It is possible that the material represents more than one species, but the information currently available does not warrant recognition of several taxa. Differences in size may be attributed to differences in maturity as the floral structures appear to be preserved at different post-anthetic stages. The fruits/ovaries are obovate in longitudinal view, triangular in transverse section with rounded to sharp edges (*Text-fig. 7a, b, d*), and have the remains of three apical tepals (*Text-fig. 7a, b*). The hypanthium is thickened over the edges of the fruits with lateral depressions between the angles (*Text-fig. 7a, b*). The outer surface of the hypanthium over the lateral depressions shows polygonal cells each with a central papilla (*Text-fig. 7c*).

Fruits of *Hedyflora* are one-seeded with an orthotropous, pendent and endotestal seed. The endotesta is distinctly crystalliferous and the outer tegmen is sclerified (*Text-fig. 7d*).
Text-fig. 6. Scanning electron microscope (SEM, a, g, h) and synchrotron radiation X-ray tomographic microscopy (SRXTM, b–f) images of fruits and pollen grains of Canrightiopsis crassistesta (a–c, g, h) and fruit of Canrightiopsis intermedia (d–f); Catéfica locality, Portugal. a) Dorsal view of fruit showing rim of hypanthium (arrowheads); b) Surface rendering of longitudinal section in the median plane of fruit (cut between orthoslices yz0440-0510) showing the thin fruit wall, thick endotesta of the seed coat (en, dark blue) and the orthotropous, pendent seed with the chalaza (ch) near the fruit apex and the micropyle (mi) at the fruit base; note the tiny embryo (emb) adjacent to the micropyle at the base of the fruit; c) Longitudinal section (orthoslice xz0511) through the seed wall showing the thick, finely crystalliferous endotesta (en) surrounding the nutritive tissue of the seed; d) Surface rendering of fruit in dorsal view showing rim of the hypanthium (arrowheads) and apical stigmatic region (st); e) Surface rendering of
Pollen grains attached to the surface of several fruits are circular in equatorial view, about 22 µm in diameter, and have an irregular branched polar aperture. The aperture is typically tetrachotomocolpate with a poorly defined aperture membrane that has irregular verrucate ornamentation (Text-fig. 7e). The tectum is reticulate with narrow muri, about 0.3 µm wide, ornamented by two poorly defined rows of minute verrucae and supported by long, scattered columellae (Text-fig. 7f).

Affinity and other occurrences. *Hedyflora* is closely similar to the pistillate flowers and fruits of extant *Hedyosmum* Sw. (Chloranthaceae) from which it is mainly distinguished by the more elaborate seed coat in the fossil material. Extant *Hedyosmum* has an unspecialized seed coat that lacks a crystalliferous endotesta and also lacks sclerified cells in the tegmen, both features that are shared by *Hedyflora* and other extinct and extant Chloranthaceae (Friis et al. 2019b). Fossils assigned to *Hedyflora* are known from several mesofossil floras from Portugal, including Arazede, Buarcos, Torres Vedras and Vale de Água (Friis et al. 2019a, b). Pollen grains are similar to dispersed fossil grains typically assigned to the pollen genus *Asteropollis* R.W.Hedl. et G.Norris. Closely similar grains are also found in situ in an isolated stamen from Catefica (*“Stamen with Asteropollis-type pollen sp. 1”; Text-fig. 14) and similar grains also occur in situ in stamens from the Vale de Água locality (Friis et al. 2019b). Dispersed pollen grains of the *Hedyflora* type are also present in the Catefica palynoflora, but are rare.

**Genus Proencistemon** E.M.Friis, P.R.Crane, K.R.Pedersen, M.M.Mendes et J.Kvaček gen. nov.

Type. *Proencistemon portugallicus* E.M.Friis, P.R.Crane, K.R.Pedersen, M.M.Mendes et J.Kvaček gen. et sp. nov.

Plant Fossil Names Registry Number. PFN002788 (for new genus).

Etymology. In honor of Pedro Proença e Cunha for his contributions to understanding the stratigraphy and geology of the Early Cretaceous of Portugal and stemon (Greek for stamen).

Generic diagnosis. Stamine inflorescences spherical with closely packed, unisexual flowers radiating from the central axis. Each flower delimited by a bract subtending one or two stamens. Anthers sessile, or almost sessile, narrowly elongate, dithecate and tetrasporangiate, lacking a well-developed filament but with a short flattened apical connective. Anther dehiscence lateral by longitudinal slits. Pollen small, trichotomocolpate, circular in outline, semitectate-reticulate, columellate, with long, scattered columellae and a homobrochate reticulum. Muri with a rounded profile and supratectal ornamentation composed of minute verrucae aligned in two to three longitudinal rows that create poorly defined transverse ridges over the muri. Aperture margin indistinct. Aperture membrane irregularly verrucate. Orbicules spherical with fine verrucose-spiny ornamentation.

Distinguishing features. Among extant angiosperms, species of *Ascarina* (Chloranthaceae) are comparable to *Proencistemon* in having stamine inflorescences consisting of simple flowers with one to three stamens. Pollen grains of extant *Ascarina*, as well as extant *Hedyosmum*, are also closely similar to those found in situ in *Proencistemon*. The grains have an indistinctly delimited polar aperture with poorly defined aperture margins, an aperture membrane covered by irregular verrucae, and a semitectate-reticulate pollen wall with finely beaded supratectal ornamentation. The trichotomocolpate pollen of *Proencistemon* is most similar to the monocolpate or sometimes trichotomocolpate pollen of *Ascarina*. Pollen of *Hedyosmum* is pentachotomocolpate or more rarely tetra- or hexachotomocolpate. *Proencistemon* flowers also differ from those of *Hedyosmum* in being delimited by a bract. In extant *Hedyosmum* the flowers are ebracteate and presumed to be unistaminate.

There are several records of stamine inflorescences, inflorescence fragments and isolated stamens from the Early Cretaceous of Portugal that are similar to *Proencistemon* and that also contain chloranthoid pollen, but so far none of them has been named. *Hedyosmum*-like stamine inflorescences from the Torres Vedras locality (Friis et al. 2019a: text-fig. 20h ) and from the Vale de Água locality (Friis et al. 2011: figs 8.13D, E, 16.2B ) that have five whorls of staminate flowers differ in being ebracteate with smaller stamens, and have a larger number of stamens in each whorl than in *Proencistemon*. In addition, while the form of the pollen aperture in the single Torres Vedras specimen of a *Hedyosmum*-like stamine inflorescence is unknown, it is tetra- to pentachotomocolpate in the Vale de Água specimen. The tetra- to pentachotomocolpate pollen grains of the Vale de Água specimen are comparable to grains of *Hedyosmum* and to dispersed grains assigned to the extinct pollen genus *Asteropollis*. In contrast, *Proencistemon* has trichotomocolpate pollen. Although trichotomocolpate pollen grains are sometimes assigned to *Asteropollis*, the type material for *Asteropollis asteroides* R.W.Hedl. et G.Norris from the Early Cretaceous (Albian) of Oklahoma, USA, only includes forms with pentachotomocolpate, or rarely tetrahoto- or hexachotomocolpate apertures. Trichotomocolpate grains are not recorded from the type locality (Hedlund and Norris 1968).

Fossil pollen grains with a trichotomocolpate aperture similar to that of *Proencistemon* have sometimes been assigned to the extinct pollen genus *Clavatipollenites*.
Text-fig. 7. Scanning electron microscope (SEM, a–c, e, f) and synchrotron radiation X-ray tomographic microscopy (SRXTM, d) images of fruits and pollen grains of *Hedyphora crystallifera*; Catefica locality, Portugal. a, b) Lateral view of fruits showing the remains of apical tepals and remains of the hypanthium, which is thicker on the edges of the fruit in (b) (arrows); c) Detail of hypanthium surface between the thickenings on the edges of the fruit showing polygonal cells with a central papilla; d) Transverse section (orthoslice xy0600) of fruit and seed showing the finely crystalliferous endotesta (arrowhead) and sclerified outer tegmen (asterisk); e) Distal view of pollen grain from surface of fruit showing the poorly defined tetrachotomocolpate aperture (daggers indicating the four arms of the aperture) and semi-tectate, reticulate tectum; f) Detail of pollen wall showing narrow muri with indistinctly beaded surface ornamentation of minute verrucae in poorly defined rows and supported by long columellae. Specimens, Catefica 49-S172313 (a), Catefica 49-S153159 (b), Catefica 49-S172324 (c), Catefica 49-S172325 (d), Catefica 50-S170453 (e, f). Scale bars = 300 μm (a, b), 100 μm (d), 50 μm (c), 6 μm (e), 1.5 μm (f).
Proencistemon portugallicus E.M. Friis, P.R. Crane, K.R. Pedersen, M.M. Mendes et J. Kvaček sp. nov.

Text-figs 8a–f, 9a–g

Holotype. P0341 (Catėfica sample MM282; figured Text-fig. 8a, c, d).

Plant Fossil Names Registry Number. PFN002789 (for new species).

Paratypes. S266015, S266016 (Catėfica sample 49), S170393, S170394 (Catėfica sample 50), S174257 (Catėfica sample 150), S122086 (Catėfica sample 342).

Repository. Holotype: Geological Museum of Lisbon, Portugal (P).

Paratypes: Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden (S).

Etymology. From Portugal where the fossils were recovered.

Type locality. Catėfica (39° 03ʹ 30ʺ N; 09°14ʹ 30ʺ W), between the villages of Catėfica and Mugideira, about 4 km south of Torres Vedras, Portugal.

Type stratum and age. Almargem Formation, Early Cretaceous (Aptian-early Albian).

Specific diagnosis. As for the genus with the following addition: anthers very narrowly elliptical and of the same width from base to apex.

Distinguishing features. Proencistemon portugallicus is distinguished from the staminate inflorescence fragment from Catėfica described here as Proencistemon sp., in having shorter stamens in which the pollen sacs are of equal width from base to apex. In Proencistemon sp. the pollen sacs are broader towards the apex.

Dimensions. Staminate structure (measured on holotype) about 1.5 mm in diameter; stamens 0.55 mm long and 0.25 mm broad; pollen diameter 12.5–16 µm.

Description and remarks. The material includes two spherical staminate inflorescences that are three dimensionally preserved and have several series of stamens radiating from the central axis (Text-fig. 8a, b). There are also strongly compressed, lignitised inflorescence fragments (Text-fig. 9a, b), isolated stamens and pollen clumps. The inflorescences are unisexual, about 1.5 mm in diameter and appear to be more or less spherical. They consist of up to 30 densely packed stamens. Bracts observed on the abaxial surface of an inflorescence fragment are poorly preserved (Text-fig. 9a) and it is unclear whether each bract subtends one or several stamens. The arrangement of the stamens in the three-dimensionally preserved specimens is also not conclusive. In specimen P0341 stamens appear to be arranged singly (Text-fig. 8a), while in specimen S174257 some of the stamens appear to occur in pairs (Text-fig. 8b). This is also the case for several of the compressed specimens (Text-fig. 9a, b).

Stamens are narrowly elongate, elliptical to rectangular in shape, about 0.55 mm long, 0.25 mm broad, and lack a well-developed filament. Anthers are sessile or almost sessile, dithecate, tetrasporangiate and with a short flattened apical connective that is mostly abraded (Text-fig. 8a, b). Stamens in the lignitised specimens are flattened and elliptical (Text-fig. 9b). They are slightly longer than those in the charcoalified stamens, but are treated here as the same species based on the identical pollen. Pollen grains are small, circular in outline, 12.5–16 µm in diameter and have a trichotomocolpate aperture in which the arms are short and do not reach to the equator (Text-figs 8c, e, 9c–f). The aperture margin is indistinct and the aperture membrane is irregularly verrucate (Text-figs 8c, e, 9c–f). The pollen wall is semitectate-reticulate with a homobrochate reticulum (Text-figs 8c–f, 9c–f). Muri are about 0.2 µm broad with a rounded profile and a supratectal ornamentation of minute verrucae that are aligned in two to three longitudinal rows and form poorly defined transverse ridges over the muri (Text-figs 8e, f, 9g). Muri are supported by medium sized and widely spaced columellae (Text-figs 8d, 9g). Lumina are irregular in shape and up to about 0.8 µm in diameter. Tiny, spherical orbicules, about 0.5 µm in diameter, which are ornamented by fine verrucae-spinules, are present on the surface of some pollen grains (Text-fig. 8f). Pollen morphology and ultrastructure was described in detail for specimen P0341 (Tekleva et al. 2021), which we designate here as the holotype of Proencistemon portugallicus.

Affinity and other occurrences. For comments on the relationships to extant chloranthoids see discussion of the new genus above. A phylogenetic analysis was performed by Tekleva et al. (2021) based on specimen P0341, which suggested that “despite some uncertainty … phylogenetic analyses are most consistent with a position attached to the stem lineage of Hedyosmum.” This conclusion may be correct, but because other relevant specimens were not considered, the full significance of the material requires further analysis. In specimen P0341 the bracts are not obvious and the stamens appear to be borne singly. The flowers were therefore interpreted as ebracteate and unistaminate (Tekleva et al. 2021). However, in another specimen bracts are clearly present (Text-fig. 9a), and in several inflorescence fragments stamens appear to occur in pairs (Text-figs 8b, 9a). Together with the trichotomocolpate pollen, these points of similarity with extant Ascarina, rather than with extant Hedyosmum, need to be considered.
Text-fig. 8. Scanning electron microscope (SEM) images of staminate inflorescences and pollen of Proencistemon portugallicus gen. et sp. nov.; Catefica locality, Portugal. a, b) Staminate inflorescences composed of numerous tetrasporangiate stamens; each stamen lacks a filament and there is no clear indication of other floral organs; note apparently paired arrangement of stamens in (b) (asterisks); c) Pollen in situ in anther from specimen in (a) showing poorly defined trichotomocolpate aperture and semitectate-reticulate tectum; d) Detail of pollen from specimen in (a) showing narrow muri with beaded surface ornamentation; e) Distal and proximal views of pollen in situ in an anther fragment; f) Orbicules attached to surface of in situ pollen from anther fragment. Specimens, Catefica M282-P0341 (holotype, a, c, d), Catefica 150-S174257 (b), Catefica 50-S170393 (e, f). Scale bars = 600 μm (a, b), 6 μm (c, e), 1.5 μm (d, f).
Densely crowded stamens very similar to those of *Proencistemon portugalicus*, and also with similar in situ trichotomocolpate pollen, have been described from the Torres Vedras mesofossil flora (Friis et al. 2019a: text-fig. 21). The two taxa are clearly closely related, but stamens of the Torres Vedras specimens are larger and more crowded and also have larger pollen grains (about 18–22 µm in diameter compared to 12.5–16 µm in diameter in *Proencistemon portugalicus*). Whether the stamens in the Torres Vedras specimens are in pairs, and whether the flowers were bracteate or ebracteate is unknown.

In the Catefica palynoflora similar trichotomocolpate pollen grains are rare, but have been reported from coastal exposures in Portugal that are of Early Cretaceous age as *Asteropollis cf. asteroides, Asteropollis sp. 3 and Asteropollis sp. 4* (Heimhofer et al. 2007). These trichotomocolpate grains are similar to those of *Proencistemon portugalicus* in general morphology, but are larger. The specimen illustrated and assigned to *Asteropollis as Asteropollis cf. asteroides* (Heimhofer et al. 2007: pl. III, figs 1, 2) differs more significantly in being tetrachotomocolpate.

**Proencistemon sp.**

*Description and remarks.* The material includes a single staminate inflorescence fragment consisting of about seven tightly packed, stamens that lack a well-developed filament and have anthers that are almost sessile (Text-fig. 9h). Anthers are elongate, narrowly obtriangular, and 0.45 mm broad. Their full length is not preserved, but they are more than 0.8 mm long. Pollen grains are trichotomocolpate, about 16 µm in diameter, and semitectate-reticulate (Text-fig. 9i, j). These grains are very similar to pollen found in situ in the stamens of *Proencistemon portugalicus*.

**Affinity and other occurrences.** Pollen grains of *Proencistemon sp* are closely similar in size, shape, aperture configuration and details of pollen wall to those found in situ in *Proencistemon portugalicus*, but the anthers are longer and differ in their narrow obtriangular shape. More material is needed to determine if a new species should be recognized formally. We have not observed similar stamens and pollen in other Early Cretaceous mesofossil floras from Portugal.

**Stamens with monocolpate Clavatipollenites-type pollen sp. 1**

*Description and remarks.* The material comprises two stamen fragments that have a long, narrow, elongated tetrасosporangiate anther (Text-fig. 10a) with in situ *Clavatipollenites*-type pollen (Text-fig. 10b–d). The anther is about 1.3 mm long and about 0.2 mm broad. Pollen is monoaperturate, almost circular in equatorial outline and about 17–20 µm in diameter. The aperture is about 12 µm long, with an irregular, indistinctly delimited margin and a colpus membrane covered by irregular verrucae that grade into the non-apertural reticulum (Text-fig. 10b, c). The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 10b–d). Lumina are irregular, up to about 1.4 µm in diameter. Muri are narrow, 0.2–0.4 µm wide, and ornamented with minute verrucae arranged in a single longitudinal row. Columellae are long, about 0.6 µm, and widely spaced (Text-fig. 10d). Orbicules observed on the inner surface of the anther wall are tiny, spherical and with fine spines.

**Affinity and other occurrences.** The general shape of the pollen grains, as well as their semitectate reticulate pollen wall, indistinctly delimited aperture, and aperture membrane covered by irregular verrucae, is closely similar to dispersed pollen assigned to the extinct pollen genus *Clavatipollenites* and pollen of extant *Ascarina* (Walker and Walker 1984). Based on these similarities these fossils are included here in the Chloranthales.

The four staminate structures described here from Catefica that have monocolpate *Clavatipollenites*-type pollen differ from each other in size and shape of anthers and in details of the pollen wall (Tab. 1). Similar *Clavatipollenites*-type pollen grains are also present in the palynological preparations from Catefica. *Clavatipollenites*-type pollen observed on *Canrightiopsis crassitesta* from Catefica is much smaller and with a more open reticulum (see above).

**Stamens with monocolpate Clavatipollenites-type pollen sp. 2**

*Description and remarks.* The material comprises a single stamen that has in situ *Clavatipollenites*-type pollen. The anther is tetrасosporangiate, elongate and narrow, about 1.3 mm long and 0.3 mm broad (Text-fig. 11a). Pollen is monocolpate and almost circular in equatorial outline, about 24–26 µm in diameter. The aperture is short, about 14 µm long, and has an irregular, indistinctly delimited margin. The colpus membrane is covered by irregular verrucae that grade into the reticulum in the non-apertural regions of the grains (Text-fig. 11b, c). The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 11b, c). Lumina are irregular and up to about 3 µm in diameter. Muri are narrow, 0.5 µm wide, ornamented with minute verrucae arranged in a single longitudinal row, or sometimes in two rows. The verrucae are sometimes laterally expanded and form poorly defined transverse ridges. Columellae are long, about 1.5 µm, and widely spaced (Text-fig. 11e). Orbicules are tiny, spherical with finely verrucate to spiny surface ornamentation (Text-fig. 11d).

**Affinity and other occurrences.** The pollen grains in this specimen are larger than any of the other *Clavatipollenites*-type pollen observed in the Catefica mesofossil flora. They are also larger than the pollen grains in situ within anthers of *Proencistemon* (Tab. 1). See also comments on “Stamens with monocolpate *Clavatipollenites*-type pollen sp. 1” above.

**Stamens with monocolpate Clavatipollenites-type pollen sp. 3**

*Description and remarks.* The material comprises a single stamen with an elongated, elliptical and tetrасosporangiate anther (Text-fig. 12a) that has in situ
Text-fig. 9. Scanning electron microscope (SEM) images of stamens and pollen of *Proencistemon portugalicus* gen. et sp. nov. (a–g) and *Proencistemon* sp. (h–j); Catefica locality, Portugal. a) Fragment of stamen whorl from staminate inflorescence showing almost sessile anthers; note short bracts at the base of the stamen whorl (arrow) and apparent paired arrangement of the stamens; b) Fragment of stamen whorl showing almost sessile anthers and apparent paired arrangement of the stamens; c) Pollen in situ from stamen whorl in (b) showing poorly defined trichotomocolpate aperture and semitectate-reticulate tectum; d–g) Distal views of pollen in situ from
Clavatipollenites-type pollen (Text-fig. 12b–e). The anther is about 0.5 mm long and about 0.25 mm broad. Pollen is monoaperturate, but the grains are typically folded and the aperture is not fully exposed in any of the specimens. The grains are about 15–17 µm in diameter. The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 12b–e). Lumina are irregular and up to about 1.5 µm in diameter. Muri are narrow, about 0.4 µm wide and ornamented with verrucae or spines arranged in one to two rows. Columellae are long, about 0.7 µm, and widely
orbicules (Text-fig. 12d). Orbicules on the inner surface of the anther wall and on the surface of the pollen grains are tiny, spherical and with fine spines (Text-fig. 12e).

Affinity and other occurrences. See comments on “Stamens with monocolpate Clavatipollenites-type pollen sp. 1” above.

Stamens with monocolpate Clavatipollenites-type pollen sp. 4

Text-fig. 13a–d

Description and remarks. The material comprises a fragment of a staminate structure with more than ten closely packed stamens that have in situ Clavatipollenites-
type pollen. There are no well-developed filaments. The shape of the fragment indicates that the anthers were sessile or almost sessile and that the stamens were originally borne in whorls in a multistaminate inflorescence (Text-fig. 13a). The anthers are strongly compressed, obovate in outline, about 0.5 mm long and 0.2 mm broad. Pollen is monoparturate with a poorly delimited aperture (Text-fig. 13b, c). The grains are about 14–17 µm in diameter. The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 13b–d). Lumina are irregular, up to about 1 µm in diameter. Muri are narrow, about 0.3 µm wide ornamented with minute verrucae arranged in one to two rows. Columellae are long, about 0.7 µm, and widely spaced (Text-fig. 13d). Orbicules were not observed.

**Affinity and other occurrences.** See comments on “Stamens with monocolpate Clavatipollenites-type pollen sp. 1” above. The pollen is closely similar to dispersed fossil grains assigned to the extinct genus Clavatipollenites, as well as pollen of extant Ascarina. The stamens are similar to those in the staminate inflorescences of Proencistemon portugallicus and Proencistemon sp. from Cattefa (above) in being arranged in dense whorls and having sessile or almost sessile anthers. However, pollen in situ within stamens of Proencistemon differs in having a trichotomocolpate aperture, and stamens of Proencistemon are longer than those of the staminate structure described here. The estimated number of stamens per whorl is also fewer than in Proencistemon.

**Stamen with Asteropollis-type pollen sp. 1**

Text-fig. 14a–e

**Description and remarks.** The species is based on a single stamen with numerous Asteropollis-type pollen grains in situ. The stamen is slightly abraded, both apically and also at the base, but is estimated to have been about 1 mm long. The anther is about 0.4 mm broad, tetrasporangiate with two pairs of pollen sacs (Text-fig. 14a). Pollen is tetrachotomocolpate, circular in equatorial outline.
and about 20–23 µm in diameter (Text-fig. 14b–d). The arms of the aperture are short and do not reach the equator. The aperture margins are poorly defined and the aperture membrane is covered by irregular verrucae (Text-fig. 14c, d). The exine is semitectate-reticulate, columellate, with long, scattered columellae about 0.9 µm long that become thinner toward the base (Text-fig. 14e). Lumina are irregular in shape, up to about 1.5 µm in diameter. Muri are about 0.5 µm wide with a rounded profile and are ornamented by minute verrucae aligned in two rows along the margins of the muri (Text-fig. 14e).

Affinity and other occurrences. The in situ pollen grains are closely similar in size, shape and aperture configuration to pollen found attached to the surface of specimens of Hedyflora crystallifera from Catefica (above), and also specimens from Buarcos, the type locality for Hedyflora (Friis et al. 2019b). We consider it likely that this stamen, and the pistillate structures assigned to H. crystallifera, are from the unisexual flowers of the same plant species. In the size of the pollen grains, pollen shape, aperture configuration and details of the pollen wall the fossil stamen is also closely similar to material from the Torres Vedras locality described as “Stamen with in situ Asteropollis sp. pollen” (Friis et al. 2019a). Pollen grains associated with H. crystallifera from the Buarcos locality include tetrachotomocolpate as well as trichotomocolpate forms, while in the Catefica mesofossil flora stamens with both tri- and tetrachotomocolpate pollen have not been found. Dispersed pollen grains assigned to Asteropollis cf. asteroides that are reported from early Aptian to middle Albian strata from coastal sections in Portugal are closely similar to the in situ grains from Catefica in both size and their tetrachotomocolpate aperture (Heimhofer et al. 2007).

Stamen with Asteropollis-type pollen sp. 2
Text-fig. 15a–e

Description and remarks. The species is based on a single stamen with numerous Asteropollis-type pollen grains in situ. The stamen is about 0.9 mm long and 0.4 mm broad, obovate in shape, with a pointed base and a dome-shaped sterile extension of the connective with short, stiff trichomes at the apex (Text-fig. 15a). There are no remains of a filament and the anthers may have been sessile or almost sessile. The anther is tetrasporangiate with two pairs of pollen sacs (Text-fig. 15a). Pollen is pentachotomocolpate, rarely tetrachotomocolpate, circular in equatorial outline and about 15–18 µm in diameter (Text-fig. 15b–d). The arms of the aperture are short and do not reach to the equator. The aperture margins are poorly defined and the aperture membrane is covered by irregular verrucae (Text-fig. 15b–
The exine is semitectate-reticulate, columnellate, with short, densely spaced columnellae, about 0.8 µm long that diminish in thickness towards the thick foot layer (Text-fig. 15b–e). Lumina are irregular in shape, up to about 1.2 µm in diameter. Muri are about 0.4 µm wide with a rounded profile and are ornamented by minute verrucae aligned in two longitudinal rows that form poorly defined transverse ridges.

Affinity and other occurrences. The in situ pollen grains of Asteropollis-type pollen sp. 2 differ from the pollen associated with Hedyflora crystallifera, and also pollen of Asteropollis-type pollen sp. 1 (above), in their smaller size and in having a mainly pentachotomocolpate aperture configuration in contrast to the typical tetrachotomocolpate, or sometimes trichotomocolpate, pollen of Hedyflora crystallifera. Stamens producing the two Asteropollis pollen types (sp. 1 and sp. 2) are also distinct in shape and size.

In aperture configuration the pentachotomocolpate grains are more comparable to pollen of Asteropollis asteroides and pollen of extant Hedyosmum (e.g., Walker and Walker 1984).

Stamens with Asteropollis- or Clavatipollenites-type pollen sp. 1

Description and remarks. The material consists of a single tetrasporangiate stamen with Asteropollis- or Clavatipollenites-type pollen in situ (Text-fig. 16a–c). The filament is lacking, and the anther was probably sessile or almost sessile. The anther is elongate elliptical, about 1 mm long and 0.3 mm broad. None of the grains shows the aperture clearly exposed, which creates the uncertainty about their generic assignment, but the grains were probably

Text-fig. 14. Scanning electron microscope (SEM) images of “Stamen with Asteropollis-type pollen sp. 1”; Catefica locality, Portugal. a) Stamen with pollen in situ; b–d) Pollen in situ in stamen in (a) showing poorly defined tetrachotomocolpate aperture and semitectate-reticulate tectum; e) Detail of pollen wall showing semitectate-reticulate tectum with long, scattered columnellae supporting the narrow muri; note two irregular rows of minute verrucae ornamenting surface of muri. Specimen, Catefica 50-S170385 (a–e). Scale bars = 600 µm (a), 20 µm (b), 6 µm (c, d), 1.5 µm (e).
monoaperturate. Pollen is circular in equatorial view, about 17–20 µm in diameter (Text-fig. 16b). The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 16b, c). Lumina are irregular and up to about 0.9 µm in diameter. Muri are narrow, about 0.3 µm wide, ornamented with minute verrucae arranged in one row, or sometimes in two longitudinal rows, separated by a line of fine perforations (Text-fig. 16c). Columellae are short, about 0.4 µm, and widely spaced (Text-fig. 16c). Orbicules are tiny, spherical with a verrucate to spiny surface ornamentation (Text-fig. 16c).

Affinity and other occurrences. The pollen wall is closely similar to that of pollen in situ in Proencistemon portugallicus, and also pollen in situ in the unnamed stamens and inflorescence fragments with Clavatipollenites- and Asteropollis-type pollen. The pollen is typically chloranthoid, but is distinct from all other chloranthoid pollen from Catefica, as well as from chloranthoid pollen recorded from other mesofossil floras from Portugal, in the line of fine perforations on top of the muri. The distinctiveness of this feature would support the recognition of a separate species, but the lack of information on the aperture configuration precludes closer comparison with pollen of extant Chloranthaceae and also the relevant genera of fossil pollen.

Stamens with Asteropollis- or Clavatipollenites-type pollen sp. 2
Text-fig. 16d–f

Description and remarks. The material comprises a single, well-preserved, tetrasporangiate stamen with in situ Asteropollis- or Clavatipollenites-type pollen. The filament is very short and the anther was probably almost sessile (Text-fig. 16d). The stamen is obovate in outline, about 1.4 mm long and 0.5 mm broad, with a dome shape apical extension of the connective. The aperture is...
Text-fig. 16. Scanning electron microscope (SEM) images of “Stamen fragments with in situ Clavatipollenites- or Asteropollis-type pollen” (sp. 1: a–c; sp. 2: d–f; sp. 3: g–i); Catefica locality, Portugal. a) Stamen fragment showing pollen sacs; b) Distal view of pollen grain from (a) showing semitectate-reticulate tectum; c) Detail of pollen wall showing the semitectate-reticulate tectum and long, scattered, columellae supporting muri with fine pits and rounded supratectal ornamentation; note orbiculae with a finely spiny surface (arrows); d) Stamen showing very short filament, lateral pollen sacs and short apical extension of the narrow connective; e) Folded pollen grain from (d) showing semitectate-reticulate tectum; f) Detail of pollen wall from (d) showing the semitectate-reticulate tectum and muri with fine rounded ornamentation; g) Stamen fragment; h, i) Detail of pollen grains from (g) showing the semitectate-reticulate tectum with smooth muri, long scattered columnellae and tiny scattered orbicules (arrow). Specimens, Catefica 50-S170395 (a–c), Catefica 49-S172561 (d–f), Catefica 50-S170390 (g–i). Scale bars = 600 μm (a, d, g), 6 μm (b, e, h), 1.5 μm (c, f, i).
not exposed in any of the grains, which creates uncertainty about their generic assignment, but they were probably monoaperturate. The pollen grains are circular in equatorial view, about 22 µm in diameter (Text-fig. 16e). The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 16e, f). Lumina are irregular and up to about 1.8 µm in diameter. Muri are narrow, about 0.5 µm wide and ornamented with minute verrucae arranged in two rows. Columellae are short and widely spaced. Orbicules were not observed.

**Affinity and other occurrences.** The specimen is very similar to the “Stamen with Asteropollis-type pollen sp. 2” also from Catefica (see above), but both the stamen and the in situ pollen are larger. As only the proximal side of the grains is exposed, it is unknown whether the supposed single aperture is branched as in “Stamen with Asteropollis-type pollen sp. 2” or monocolpate/trichotomocolpate as in other chloranthoid stamens from Catefica. The stamen is currently the largest of the chloranthoid stamens from Catefica that we have encountered and clearly belongs to a separate species.

**Stamens with Asteropollis- or Clavatipollenites-type pollen sp. 3**

**Description and remarks.** The material comprises a single poorly preserved stamen with in situ Asteropollis- or Clavatipollenites-type pollen (Text-fig. 16g). The apical and basal parts of the stamen are missing but the anther is clearly tetrarugangulate. The stamen is rectangular in outline, about 0.8 mm long and 0.45 mm broad. The pollen grains are not well exposed, although one appears to be monocolpate (Text-fig. 16h). Lack of clarity about the form of the aperture creates uncertainty about their generic assignment. The pollen appears circular in equatorial view, about 16 µm in diameter. The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 16h, i). Lumina are irregular and up to about 4 µm in diameter. Muri are narrow, about 0.8 µm wide, with very faint surface ornamentation comprising minute verrucae arranged in two longitudinal rows. Columellae are short and widely spaced. Orbicules are tiny and spherical with a fine verrucate-spiny ornamentation (Text-fig. 16h, i).

**Affinity and other occurrences.** The stamen differs from the other chloranthoid stamens known from Catefica and other Early Cretaceous mesofossil floras from Portugal in its broad rectangular shape. The in situ pollen also differs from the other chloranthoid pollen described from Catefica and other mesofossil floras from Portugal, in its more open reticulum, the very faint supratexcal ornamentation and the much smaller orbicules. Among the stamens and pollen recovered from the Early Cretaceous mesofossil floras from Portugal the specimen is unique.

**Order Magnoliales**

**Genus Serialis**

**Description and remarks.** The material includes several fruits with to five permanently adhering seeds assignable to *Serialis communis* (Text-fig. 17a). The fruit wall is thin and typically almost entirely lost by abrasion. The seeds are anatropous, and bitegmic with a thick mesotestal-endotestal seed coat. The micropyle is formed from the inner integument and the micropylar region is seen on the seed surface as a transverse slit in the testa (Text-fig. 17a). In all details the seeds are comparable to the type material from the Famalicão mesofossil flora (Friis et al. 2019c).

**Serialis communis**

**Description and remarks.** The material includes several fruits with five permanently adhering seeds assignable to *Serialis communis* (Text-fig. 17a). The fruit wall is thin and typically almost entirely lost by abrasion. The seeds are anatropous, and bitegmic with a thick mesotestal-endotestal seed coat. The micropyle is formed from the inner integument and the micropylar region is seen on the seed surface as a transverse slit in the testa (Text-fig. 17a). In all details the seeds are comparable to the type material from the Famalicão mesofossil flora (Friis et al. 2019c).

**Serialis crassitesta**

**Description and remarks.** The material includes several fruits with permanently adhering seeds that are assignable to *Serialis crassitesta* (Text-fig. 17b). Conclusions on the relationships of *Serialis crassitesta* are similar to those on *Serialis communis* (see above). *Serialis crassitesta* is common in the Famalicão mesofossil flora with about 250 specimens, but less common than *S. communis*. *Serialis crassitesta* is also common in the Vale de Água mesofossil flora (Friis et al. 2019c) and is also present in the Chicalhão mesofossil flora (“Fruits with co-adhering seeds in row type 1”; Mendes et al. 2014).

**Serialis spp.**

**Description and remarks.** The Catefica mesofossil flora includes other seeds and fruits that can be assigned to the genus *Serialis*, but that do not show the critical features needed to assign them to one of the existing species. There are more than 250 such specimens, which are housed separately or several together (S105279, S105280, S174256, S266050, S265983, S265984, S266118, S266137, S266152, S266157, S266162, S266169, S266181, S266200; see also Tab. 2).
Order Canellales Cronq., 1957 or Magnoliales Juss. ex Bercht. et J. Presl., 1820

Genus Catanthus E.M. Friis, P. R. Crane et K. R. Pedersen, 2020

Catanthus dolichostemon E.M. Friis, P. R. Crane et K. R. Pedersen, 2020

Text-fig. 18a, b

Description and remarks. The species was described based on several flower buds and open flowers preserved as charcoalified or lignitic specimens from the Catefica mesofossil flora (for a full description see Friis et al. 2021; taxon names valid from effectively published online version in 2020, see Friis et al. 2020c). The flowers are whorled with nine tepals in three whorls of three and many stamens in several successive whorls. The stamens have long, broad and fleshy bases that continue into the short anthers without a joint. In lignitised specimens, the stamens are flattened, but their original bulky, three-dimensional shape is particularly well-preserved in charcoalified specimens (Text-fig. 18a, b). The pollen is circular in polar view, about 12 µm in diameter, monoaperturate and trichotomocolpate (Friis et al. 2021: fig. 4A–C). The gynoecium is superior, apocarpous and consists of six, or rarely five, carpels.

Affinity and other occurrences. A phylogenetic assessment of Catanthus dolichostemon suggests a relationship to extant members of Canellales and Magnoliales (Friis et al. 2021). The species is currently known only from the Catefica and Vale de Água mesofossil floras.

Pollen grains of Catanthus dolichostemon have also been observed in palynological strew preparations from the Catefica microfossil assemblages.

Order Laurales Juss. ex Bercht. et J. Presl., 1820

Genus Saportanthus E.M. Friis, P. R. Crane et K. R. Pedersen, 2017

Saportanthus parvus E.M. Friis, P. R. Crane et K. R. Pedersen, 2017

Text-fig. 18c, d

Description and remarks. The species was described based on well-preserved flowers from the Catefica mesofossil flora (for a full description see Friis et al. 2017). The flowers are small, actinomorphic, with six to eight broadly ovate tepals, five to seven stamens, and a unicarpellate, uniovulate, semi-inferior ovary (Text-fig. 18c, d). The pollen is 8–12 µm in diameter. The aperture configuration of the pollen is not securely established for the material from Catefica, but the tectum ornamentation is finely striate and forms a fingerprint-like pattern (Friis et al. 2017: fig. 13A–C) similar to that known for the trichotomocolpate and dicolpate pollen of the two other species of Saportanthus recorded from other Early Cretaceous mesofossil floras from Portugal.

Affinity and other occurrences. A phylogenetic assessment of Saportanthus suggests that the genus is sister to, or embedded within, core Laurales (Friis et al. 2017). The genus is widely distributed among the Early Cretaceous mesofossil floras from Portugal. Three species are currently recognized; S. brachystemon E.M. Friis, P. R. Crane et K. R. Pedersen, S. dolichostemon E.M. Friis, P. R. Crane et K. R. Pedersen and S. parvus. Currently, S. parvus is known only from Catefica. “Flower sp. 2” from the Chicalhão site near Juncal is closely similar and may also belong to this species, but only one specimen is known and there are no details of internal features (Friis et al. 2017).
Flowers of *Saportanthus parvus* are common in the Catefica mesofossil flora, but the characteristic, finely striate pollen grains produced by these flowers have so far not been observed in the Catefica dispersed palynoflora, probably due to their very thin and poorly preserved pollen wall.

**Order Piperales Bercht. et J.Presl, 1820**

**Family Aristolochiaceae Juss., 1789 nom. cons.**

**Genus Aristospermum E.M.Friis, P.R.Crane et K.R.Pedersen, 2022**

* Aristospermum huberi E.M.Friis, P.R.Crane et K.R.Pedersen, 2022  
  Text-fig. 19a–c

**Description and remarks.** Seeds strongly flattened, triangular in outline, about 1.9 mm long and 1.65 mm broad (Text-fig. 19a). The seeds are anatropous and flattened, triangular in outline, about 1.9 mm long and 1.65 mm broad (Text-fig. 19a). The endosperm is one cell layer deep and each cell has one, or more rarely two, large crystals, which are seen as one or two angular imprints in the center of the cell (Text-fig. 19a–c). The inner integument (tegmen) has two layers of elongated fiber cells that are arranged perpendicular to each other (Text-fig. 19c) and an inner layer of small cubic cells. The micropyle is formed from the inner integument. A narrow funicle extends along one margin of the seeds, but it is often only partly preserved (Text-fig. 19a).

**Affinity and other occurrences.** The anatomy of the seed coat of these seeds strongly suggests a relationship to extant Aristolochiaceae, including *Aristolochia* L., which has very similar triangular and flattened seeds with a bitegmic seed coat. In extant Aristolochiaceae the testa, which forms from the outer integument, consists of an outer layer of thin-walled cells and an inner layer of crystalliferous inner cells. The tegmen, which forms from the inner integument, consists of two layers of fibrous cells that are more or less perpendicular to each other and an inner layer of cubic cells (Corner 1976). These details of the seed coat are unique for the family (Corner 1976, González and Rudall 2003) and justify the conclusion of a close relationship between these fossils and extant Aristolochiaceae. However, the combination of features seen in the fossil material, including the course of the raphe, exclude assignment of the fossil seeds to any extant genus of the Aristolochiaceae (Friis et al. 2022).

Similar aristolochiaceous seeds are also present in other Early Cretaceous mesofossil floras from Portugal and North America including specimens in which the outer tissues are better preserved. The formal description of the species is based on an assessment of that broader suite of specimens, including the type material from the Buarcos mesofossil flora (Friis et al. 2022).

**Genus Appomattoxia E.M.Friis, K.R.Pedersen et P.R.Crane, 1995**

*Appomattoxia* sp.  
  Text-fig. 20a–d

**Description and remarks.** The material comprises three strongly compressed and lignitised fruits. SRXTM of one of the specimens did not provide any information on internal structure and there is no information on how the fruits were attached to the plant. The fruits are minute, elliptical to ovate in outline, 0.5–0.6 mm long and 0.3–0.35 mm wide (Text-fig. 20a, b). The fruit wall is thin with its surface covered by a thick cuticle bearing densely arranged, short, sometimes hooked trichomes, each with a broad base (Text-fig. 20c, d). The stigmatic area is indistinct, sessile and lacks trichomes. No pollen grains have been observed on the stigmatic region or on the fruit surface.

**Affinity and other occurrences.** The fossils are similar to fruits assigned to the fossil genus *Appomattoxia* in general shape, nature of the stigmatic region, thin fruit wall and the prominent trichomes that are sometimes coiled. The type species, *A. ancistrophora* E.M.Friis, K.R.Pedersen et P.R.Crane from the Early Cretaceous mesofossil flora from Puddledock, Virginia, USA, has much larger fruits with trichomes that are longer and more distinctly and more regularly hooked (Friis et al. 1995). The fruits from Catefica are more similar to fruits of *Appomattoxia minuta* E.M.Friis, P.R.Crane et K.R.Pedersen from the Torres Vedras mesofossil flora (Friis et al. 2019a), but the trichomes are shorter, less prominently hooked and more densely arranged.

Pollen grains associated with *Appomattoxia ancistrophora* and *A. minuta* are identical to pollen of *Goczania* E.M.Friis, P.R.Crane et K.R.Pedersen. No pollen was found attached to the *Appomattoxia* fruits from Catefica, but *Goczania* stamens and pollen occur with the fruits in the Catefica mesofossil flora (see below). A piperalean affinity is inferred for *Appomattoxia* based on the combined pollen, fruit and seed characters (Friis et al. 1995, for further discussion see also Friis et al. 2019a).

**Genus Goczania E.M.Friis, P.R.Crane et K.R.Pedersen, 2019**

*Goczania* rugosa E.M.Friis, P.R.Crane et K.R.Pedersen, 2019  
  Text-fig. 20e–h

**Description and remarks.** *Goczania rugosa* is represented in the Catefica mesofossil flora by two anthers and an isolated pollen sac with pollen grains in situ (Text-fig. 20e–h). Identical pollen also occurs in pollen clumps and coprolites. The anther is short and broad, about 0.6 mm long and 0.55 mm wide, dithecate and tetrasporangiate (Text-fig. 20e). As in the type material from Torres Vedras, the inner wall of the anthers of the Catefica specimen and the in situ pollen grains show numerous small, spherical orbicules with a finely spiny surface ornamentation (Text-fig. 20f).
The pollen grains are oblate, circular to elliptical in equatorial outline, about 17 µm in diameter and monocolpate (Text-fig. 20f–h). The colpus is short with an irregular margin (Text-fig. 20h). The exine is tectate with the tectum covered with densely spaced microechinae that occur singly without merging with their neighbors (Text-fig. 20f–h).

Affinity and other occurrences. Pollen of the Goczania type has been found on the stigma and surface of Appomattoxia fruits in the Torres Vedras mesofossil flora and also on fruits of Appostractus E.M.FRIS, P.R.CRANE et K.R.PEDERSEN from Torres Vedras (Friis et al. 2019a). Goczania-type pollen has also been found on the stigma.
and surface of *Appomattoxia* fruits from the Puddledock mesofossil flora of eastern North America. *Appomattoxia* and *Approfructus* are both thought to be related to Piperales (Fris et al. 1995, 2019a).

*Goczania rugosa* was first described from the Torres Vedras mesofossil flora (Fris et al. 2019a) and the anthers with in situ pollen from Catefica are closely similar to the type material. Small differences, such as the slightly larger size of the pollen grains and slightly smoother pollen wall in the Catefica specimens, may be related to differences in preservation, with the Torres Vedras material being slightly more shrunken.

Two other species of *Goczania* occur with *Goczania rugosa* at Torres Vedras, but they differ in details of the supratectal ornamentation of the pollen wall (Friis et al. 2019a).

Pollen grains of *Goczania rugosa* have also been observed in palynological strew preparations of the Catefica microfossil assemblages.

### Angiosperms of uncertain position at the level of ANA-grade angiosperms-Chloranthaceae-magnoliids

**Genus Anacostia E.M.FRIS, P.R.CRANE et K.R.PEDERSEN, 1997**

*Anacostia* sp.

**Description and remarks.** Three specimens (S266205, S266208, S266218) assignable to *Anacostia* (not figured) were recovered from the Catefica mesofossil flora. Cells of seed and fruit surface are distinctive for *Anacostia*, but the preservation does not allow a species level assignment.

**Affinity and other occurrences.** *Anacostia* was first described based on fruits, seeds and associated pollen from the Early Cretaceous of Maryland and Virginia, USA (*Anacostia marylandensis* E.M.FRIS, P.R.CRANE et K.R.PEDERSEN, *A. virginiensis* E.M.FRIS, P.R.CRANE et K.R.PEDERSEN) and from Portugal (*Anacostia portugallica* E.M.FRIS, P.R.CRANE et K.R.PEDERSEN, *Anacostia teixeirae* E.M.FRIS, P.R.CRANE et K.R.PEDERSEN) (Friis et al. 1997). The genus is characterized by its one-seed fruits and exotesta seeds that have a crystalliferous seed coat and the inner layer of testa with strongly undulate walls. The four species also share the regular occurrence of trichotomocolpate, and occasionally monocolpate, pollen on the stigma and fruit surface. The monocolpate pollen indicates a relationship to non-eudicot angiosperms and the presence of an embryo with two cotyledons allows a monocot affinity to be rejected (Fris et al. 2015b). A possible affinity with Austrobaileyales was suggested by Friis et al. (1997) and has also been inferred based on several phylogenetic analyses by Doyle and Endress (e.g., Doyle and Endress 2014). However, there are critical features of *Anacostia*, such as the crystalliferous exotesta and the trichotomocolpate pollen, that are not consistent with the characters of extant taxa of Austrobaileyales, and relationship to other early diverging angiosperm lineages, for example among magnoliids (e.g., Canellales) cannot be ruled out.

Only three specimens of *Anacostia* have been recovered in the Catefica mesofossil flora, so far. This relative rarity contrasts with occurrences of the genus in the Buarcoes, Famalicão and Vale de Água mesofossil floras where fruits and seeds of *Anacostia* are abundant.

**Genus Choffaticarpus E.M.FRIS, P.R.CRANE et K.R.PEDERSEN, 1999**

*Choffaticarpus compactus* E.M.FRIS, P.R.CRANE et K.R.PEDERSEN, 1999

**Description and remarks.** The material comprises a fragment of an apocarpous, multicarpellate fruiting structure with tightly packed, helically arranged fruitlets (Text-fig. 19d), as well as several isolated fruitlets (Text-fig. 19e). The fruitlets are strongly compressed laterally with a small attachment scar on the adaxial face, and a distinctive deep furrow on the diamond-shaped abaxial face (Text-fig. 19d, e). Each fruitlet contains a single seed. The large circular, sunken regions seen in many fruitlets (Text-fig. 19e) may be collapsed oil cells, but details of the outer cell layers of the fruit wall are not clear from SRXMT analyses.

**Affinity and other occurrences.** *Choffaticarpus* compactus was formally described from the Torres Vedras mesofossil flora (Fris et al. 2019a) and compared to pistillate structures of extinct Kadsura KAESPP. ex Juss. and Schisandra Michx. (Schisandraceae, Austrobaileyales). However, *Choffaticarpus* differs in seed coat structure and the systematic relationships of the fossil are currently unresolved (Friis et al. 2019a). A complete *Choffaticarpus* fruiting structure, as well as fragments of fruiting structures and isolated fruitlets, are also known from the Buarcoes mesofossil flora (see comments in Friis et al. 2019a) and will be the subject of future studies (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress).

**Genus Ibericarpus E.M.FRIS, P.R.CRANE, K.R.PEDERSEN, M.M.MENDES et J.KVAČEK gen. nov.**

*Type. Ibericarpus cuneiformis* E.M.FRIS, P.R.CRANE, K.R.PEDERSEN, M.M.MENDES et J.KVAČEK gen. et sp. nov.

**Plant Fossil Names Registry Number.** PFN0002790 (for new genus).

**Etymology.** From the Iberian Peninsula where the fossil was collected.

**Generic diagnosis.** Pistillate structure with numerous, densely spaced carpels borne in a spiral arrangement along a slender axis, with no remains of perianth parts or stamens. Carpels obconical to pyriform, sessile, uniovulate. Style lacking, stigmatic region slightly bulging. Fruit indehiscent. Epidermal cells of fruit with isodiametric facets. Ovule/seed obovate with micropyle pointing towards the base of the carpel. Embryo tiny. Seed coat unspecialized.

**Comments on the genus.** There are no scars from bracts, perianth parts or stamens on the axis below the carpels, and there are no traces of a perianth or stamens associated with the individual carpels. The structure of the carpel is uncertain, but its shape and the lack of an obvious suture suggests that it is ascidiate.

Interpreting the floral structure is not straightforward. One possibility is that the carpel-bearing axis of *Ibericarpus cuneiformis* is a simple, unbranched inflorescence bearing numerous ebracteate pistillate flowers, each consisting of
only a single carpel. Under this interpretation, *Ibericarpus cuneiformis* shows some similarity to floral structures of Chloranthaceae. Flowers of Chloranthaceae have simple, typically naked flowers, that are borne in elongated inflorescences and the carpels are asciadate and uniovulate without a style. Among extant Chloranthaceae, *Hedyosmum* and *Ascarina* also have unisexual flowers. However, in extant Chloranthaceae the flowers are typically in the axil of

Text-fig. 19. Synchrotron radiation X-ray tomographic microscopy (SRXTM, a–c) of *Aristospermum huberi* and scanning electron microscope (SEM, d, e) images of *Choffaticarpus compactus*; Catefica locality, Portugal. a) Volume rendering of strongly flattened, triangular seed with pointed micropylar region; note thin-walled cells of outer integument preserved along the margins of the seed and pitted surface of the crystalliferous inner cells of outer integument where the outer cells are abraded and the narrow, lateral funicle/raphe; b) Volume rendering of seed showing surface of inner integument (endotesta) with cells showing clear imprints of crystals (arrows); c) Longitudinal section (orthoslice yz0241) of seed showing crystalliferous cells of endotesta (white arrows) and the two fiber layers of the tegmen that are perpendicular to each other (inner integument, ii-f, black arrows); d) Fragment of multiparted, apocarpous fruiting structure showing several helically-arranged, laterally flattened, fruitlets; e) Fruitlet in lateral view showing the prominent ventral face with its lateral groove, short attachment scar, and sunken regions of the fruit wall that indicate the probable presence of oil cells. Specimens, Catefica 49-S266049 (a–c), Catefica 49-S172558 (d), Catefica 49-S118675 (e). Scale bars = 300 μm (a, c–e), 100 μm (b).
a distinct bract and only the staminate flowers of *Hedyosmum* are ebracteate. Because no bracts are present associated with the individual carpels in *Ibericarpus cuneiformis*, we regard the inflorescence interpretation as unlikely. This conclusion is also supported by the unspecialized seed coat of *Ibericarpus*. In all chloranthoid seeds so far described from the Cretaceous, the seed coat is endotestal with crystaliferous endotestal cells.
An alternative interpretation of Ibericarpus is that the fruiting structure is derived from a pistillate, perhaps naked, flower with an apocarpous gynoecium of numerous free carpels. Among extant angiosperms, taxa with an apocarpous gynoecium of many carpels arranged spirally along a long, slender floral axis occur in Kadsura and Schisandra (Schisandraceae, Austrobaileyales), in Magnoliaceae (Magnoliales), and also in Galbulimima F.M.Bailey (Himantandraceae, Magnoliales).

Flowers of Magnoliaceae differ from those of Ibericarpus cuneiformis in being bisexual, and typically with well developed, often leathery, perianth parts that leave distinct scars after flowering. The carpels also have a distinct style, and each contains two or more ovules. Flowers of Galbulimima also differ from those of I. cuneiformis in being bisexual, but they are more like the fossils in being naked and in having uniovulate carpels that lack a style. Fruits of Galbulimima are drupes, while those of Ibericarpus are nuts or one-seeded berries. Carpels in both Magnoliaceae and Himantandraceae are plicate or intermediate plicate-ascidiate.

If the carpels of Ibericarpus cuneiformis are correctly interpreted as ascidiate then in this feature they are more similar to the carpels of Austrobaileyales. Flowers of Kadsura and Schisandra are similar to Ibericarpus cuneiformis in their unisexual organization as well as having carpels that lack a style, but flowers of both extant genera have a distinct perianth and also have one to several ovules per carpel.

Against this background, while we think that Ibericarpus cuneiformis is most likely an elongated receptacle bearing numerous fruitlets, and while a relationship to extant Austrobaileyales seems the most likely possibility, I. cuneiformis cannot be included securely in any extant angiosperm family or order.

Among the fossil floral structures that have a multicarpellate and apocarpous gynoecium, species of Atlantocarpus E.M.Friis, P.R.Crane et K.R.Pedersen from the Early Cretaceous floras of Puddledock, Virginia, USA, and also Buarcos and Vale de Água, Portugal (Friis et al. 2020a), are the most similar to Ibericarpus cuneiformis in their uniovulate carpels that lack a style. However, fossils of Atlantocarpus have distinct remains of floral organs below the carpels and the receptacle is obconical, rather than slender and stalk-like as in Ibericarpus.

Floral structures of Choffaticarpus compactus E.M.Friis, P.R.Crane et K.R.Pedersen first described from the Torres Vedras mesofossil flora (Friis et al. 2019a), and Anacostia? sp. from the Puddledock flora of eastern North America (Friis et al. 2020a), are also similar to Ibericarpus in having tightly packed carpels spirally arranged along an elongated receptacle. However, Anacostia? sp. differs in having a distinct joint between pedicel and flower with remains of other floral parts below the carpels and Choffaticarpus compactus differs having strongly compressed carpels with a distinct ventral depression (see above).

Ibericarpus cuneiformis E.M.Friis, P.R.Crane, K.R.Pedersen, M.M.Mendes et J.Kváček sp. nov.

Text-figs 21–23

Holotype. S115851 (Catefica sample 49; figured Text-fig. 21a–c).

Plant Fossil Names Registry Number. PFF002791 (for new species).

Paratypes. S115852–S115856, S118683–S118685, S265996, S266012 (Catefica sample 49), S170413–S170417, S174907, S266037, S266135 (Catefica sample 50); P0477 (Catefica sample MM75).

Repository. Holotype: Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden (S).

Paratypes: Palaeobotanical Collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden (S) and Geological Museum of Lisbon, Lisbon, Portugal (P).

Etymology. From the wedge-shaped fruits.

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 stratum and age. Almargem Formation, Early Cretaceous (Aptian-early Albian).

Specific diagnosis. As for the genus.

Dimensions. Carpels bearing axis up to about 1.7 mm long and 1.1 mm in diameter; individual carpels up to 0.65 mm long and 0.4 mm broad.

Description and remarks. The species is known from two pistillate structures bearing carpels (Text-figs 21a–c, 22a, b) as well as detached fruits that occur either isolated (Text-fig. 22c) or in groups (Text-figs 22d, 23a–c). One group of detached fruits (S174907; Text-fig. 22d) was studied for internal details using SRXTM.

The holotype consists of a central axis with numerous carpels borne in a spiral arrangement (Text-fig. 21a–c). Although the specimen has lost some of its carpels the total original number is estimated to have been about 70, based on those still attached to the axis and the scars from the detached carpels. This specimen was probably preserved early in development before the carpels were shed. Another carpel-bearing specimen is thought to be at fruiting stage and the few carpels still attached to the axis when it was recovered were only loosely attached and fell off as the axis was mounted for SEM (Text-fig. 22a, b). The infructescence axis of this second specimen is about 1.9 mm long and based on the scars on the axis, there were about 70 carpels as also in the holotype. The diameter of the axis (ca. 0.3 mm) is more or less uniform from base to apex (Text-fig. 22a). There are no traces of other floral organs or bracts associated with the individual carpels or with the carpel-bearing axis. Specifically, there is no distinct joint between the infructescence stalk and the portion of the inflorescence axis that has the carpel scars. There are also no scars from bracts, perianth parts or stamens associated with the carpel scars.

The carpels are densely spaced on the axis. Each carpel is about 0.35 mm long and 0.25 mm wide, with the carpels of the second specimen (Text-fig. 22) larger than those of the
holotype. Carpels are obconical to pyriform in lateral view, and angular in transverse section as a result of their dense packing on the axis. Each carpel contains a single ovate ovule/seed with micropyle pointing towards the base and in one specimen with remains of embryo preserved (Text-fig. 23a–c).

The epidermis of the carpel wall consists of small, bulging, isodiametric cells covered by a thick cuticle (Text-figs 21a, 22b–d, 23a–c). The cell outlines are particularly distinct in the protected regions where adjacent carpels meet, but less so in the apical portion of the carpel that is free (Text-figs 21c, 22b–d). The stigmatic area of each carpel is seen as a small apical swelling (Text-figs 21c, 22b–d).

No pollen grains have been observed in the stigmatic region or on other parts of the structure.

Affinity and other occurrences. For comments on the possible relationships of Ibericarpus see comments on the genus (above). Ibericarpus cuneiformis is common in the Catefica mesofossil flora, where it is characteristic for the basalmost layers of the outcrop. There are also fruitlets of Ibericarpus cuneiformis in the Buarcos mesofossil flora.

Stamen with zona-aperturate pollen

Text-fig. 24a–i

Description and remarks. The material comprises a single stamen. The anther is basifixed, and there is no trace of the filament indicating that the anther may have been sessile (Text-fig. 24a, b). The anther is tetrasporangiate, dithecate and narrowly elongate. It is about 2.2 mm long, 0.3 mm broad in abaxial-adaxial view and about 0.45 mm broad in lateral view. The anther is curved, most likely towards the centre of the flower, indicating that the pollen sacs are in a lateral to abaxial position (Text-fig. 24a, b). The four pollen sacs are arranged in two pairs separated by a broad connective with the connective more prominent and bulging on the probable adaxial side (Text-fig. 24a–c).

The pollen sacs dehisced longitudinally along their entire length and in dehisced pollen sacs the valves are curled back to expose their inner surface and the pollen (Text-fig. 24d). Most grains are concealed by folds in the anther wall, but a few grains are fully exposed.

Pollen grains are zona-aperturate with a ring-like aperture that apparently encircles the entire grain, dividing it into two equal halves. Grains are elliptical in outline, about 17–20 µm long, and with their longest axes perpendicular to the aperture (Text-fig. 24e, f, h). All grains are isolated and whether the aperture is equatorial or runs through the poles of the grain is uncertain. The pollen wall is semitectate-reticulate with a heterobrochate reticulum (Text-fig. 24e–i). Lumina are irregular in size and shape, with the smaller lumina about 0.2 µm in diameter and the larger lumina up to about 1 µm in diameter. Muri are narrow and tall with a sharp pointed profile and a smooth surface. Columellae are irregular, mostly long and closely spaced (Text-fig. 24g, i). The reticulum is loosely attached to the foot layer (Text-fig. 24h). The aperture margin is well-defined and the aperture membrane is seen as a band, about 1–1.5 µm wide, that forms a zone encircling the grains (Text-fig. 24e) and that becomes detached with separation of the grains into two halves (Text-fig. 24f, h). There are apparently no constrictions in the width of the apertural band, which is the same width over all the exposed surfaces. We interpret this as indicating a fully encircling (zona-aperturate) aperture. Orbicules are tiny and spherical, with a smooth surface (Text-fig. 24e).

Affinity and other occurrences. The pollen grains are similar to dispersed grains assigned to the extinct pollen genus Dichastopollenites F.E.May, which is characterized by zona-aperturate grains that separate in two equal halves and have a coarse, heterobrochate reticulum (May 1975). The type species of the genus, Dichastopollenites reticulatus F.E.May, from the Cenomanian of Utah and Arizona, differs from the Catefica in situ pollen in being slightly larger (24–29 µm in D. reticulatus, 17–20 µm in the Catefica material) and also in having a specialized apertural structure. In D. reticulatus a ridge on the exine of one half of the grain interlocks with a furrow on the other half of the grain, until the grain splits at germination. The absence of this feature in the Catefica material precludes assignment to Dichastopollenites. The robust band-like aperture membrane that separates the Catefica pollen grains into two halves has also not been observed in Dichastopollenites.

Other dispersed zona-aperturate pollen with a semitectate-reticulate pollen wall include species assigned to Afropollis J.A.DOYLE, S.JARDINÉ et DOREN. (Doyle et al. 1982), Schrankipollis J.A.DOYLE, HOTTON et J.V.WARD (Doyle et al. 1990) and Pararisteapollis M.HESSE et ZETTER (Hesse and Zetter 2005). Pollen grains of Afropollis and Schrankipollis were compared by Doyle et al. (1990) to pollen of extant Winteraceae and are distinguished from the Catefica pollen by their segmented muri. In the zona-aperturate pollen of Afropollis and Pararisteapollis, the two halves of the grain are also of unequal size (Doyle et al. 1990, Hesse and Zetter 2005) unlike the Catefica grains that are divided into equal halves by the encircling aperture membrane.

Zona-aperturate pollen is rare among extant angiosperms but occurs scattered in the Nymphaeaceae (Nymphaeaceae), Magnoliaceae (Eupomatiaceae, Annonaceae), Laurales (Atherospermataceae), a few monocot families (Araceae, Iridaceae, Laxmanniaceae, Arecaceae and Rapateaceae) and two eudicot genera, Pedicularis L. (Orobanchaceae, Lamiales) and Limnanthes R.Br. nom. cons. (Limnanthaceae, Brassicaceae) (e.g., Walker 1974, Sampson 2000, Hesse and Zetter 2005).

Rigid stamens with basifixed anthers and abundant connective tissue as observed in the Catefica material occur in many early diverging angiosperms including the monocot family Araceae. In contrast, in other non-araceous monocot families that have zona-aperturate pollen, the anthers are versatile and dorsifixed. The anthers of Pedicularis and Limnanthes, are also versatile and dorsifixed and in both cases the ring-like colpus is formed from two fused colpi. Pollen of Limnanthes is also kidney- to hook-shaped in appearance with a strongly sculptured pollen wall, while pollen of Pedicularis is pilate-microechinate, disk-shaped with a groove-like aperture in dehydrated grains (Buchner et al. 1990, Hesse and Zetter 2005).

Among monocots, zona-aperturate pollen of Araceae (Grayum 1992, Hesse et al. 2001), Arecaceae (Harley and Baker 2001), Laxmanniaceae (Henderson 1982)
and Rapateaceae (Carlquist 1961, Venturelli 1988) are distinguished from the Catefica pollen in having a non-reticulate pollen wall. Reticulate pollen is reported for some zona-aperturate pollen of Iridaceae, but those zona-aperturate grains are typically much larger than those from Catefica and none has a reticulum as coarse as that in the Catefica pollen grains (e.g., Goldblatt and Le Thomas 1997).

May (1975) suggested a possible relationship of Dichastopollenites to members of the Nymphaeaceae, such as Nymphaea odorata Aiton and N. tuberosa Paine that have zona-aperturate pollen. However, the pollen wall in Nymphaeaceae typically has small spines or projections and is not reticulate like the Catefica grains. A further distinction is that in zona-aperturate pollen of Nymphaeaceae the aperture is typically displaced towards the distal pole dividing the grain into unequal, rather than equal halves (Taylor et al. 2015).

In Magnoliales, the zona-aperturate pollen of Eupomatia R.Br. (Eupomatiaceae) is similar to the Catefica material in having a band-like aperture dividing the grains into two equal halves, but Eupomatia pollen is psilate and atectate rather than reticulate (Woodland and Garlick 1982, Sampson 2000). In Annonaceae, zona-aperturate pollen is recorded in Guattaria Ruiz et Pav., which also has atectate pollen, and in Letestudoxa Pellegr., which has a verrucate tectum (Doyle and Le Thomas 2012). In Laurales, zona-aperturate pollen occurs in the Atherospermataceae together with dicolpate pollen in which the apertures are meridional and run through the poles (Sampson 1975, 2000). In zona-aperture grains, the encircling aperture is mostly of unequal width, but in some taxa it is of the same width throughout (Sampson 1996) as in the Catefica pollen. However, in Atherospermataceae, the pollen wall is tectate-columellate formed from partly fused hemispherical processes (Sampson 2000) rather than reticulate and anther dehiscence in the Atherospermataceae and all other core Laurales is by apically hinged valves rather than by longitudinal slits. Among extant Laurales only Calycanthaceae, the sister group to other extant genera, is comparable to the Catefica stamen in having laterally hinged valves that are extorse, as is inferred for the Catefica fossil. Pollen grains of extant Calycanthaceae are dicolpate with meridionally placed apertures and a tectate-perforate or microreticulate pollen wall (Sampson 2000, Paudel and Heo 2020). The pollen wall of the Early Cretaceous calycanthoid flower Virginianthus E.M.Friis, H.Eklund, K.R.Pedersen et P.R.Crane is coarsely reticulate but these grains are monocolpate (Friis et al. 1994).

Based on the combined stamen and pollen morphology we suggest that the most likely phylogenetic position of the Catefica fossil is close to extant magnoloids, perhaps close to the base of the Laurales, but the band-like aperture of Eupomatia may also be a significant similarity. A secure systematic assignment of the fossil is not possible with the information available currently.

Similar stamens and in situ pollen have not been observed in other mesofossil floras. Several species of dispersed Dichastopollenites pollen have been reported in late Aptian-Albian palynofloras from Portugal (Heimhofer et al. 2007, Horikx et al. 2016), but none of them are identical with the in situ Catefica pollen. Zona-aperturate pollen grains described in situ from elongated inflorescence axes from the mid-Cretaceous Dakota Formation of Kansas, USA (Dilcher 1979) are reticulate similar to the Catefica grains but the reticulum is much denser and the muri are rounded rather than sharp as in the Catefica pollen. The inflorescence axes are strongly compressed and there are currently no details on floral organisation.

**Genus Elasmostemon E.M.Friis, P.R.Crane, K.R.Pedersen, M.M.Mendes et J.Kvaček gen. nov.**

**Type.** Elasmostemon paisii E.M.Friis, P.R.Crane, K.R.Pedersen, M.M.Mendes et J.Kvaček gen. et sp. nov.

**Plant Fossil Names Registry Number.** PFN0002792 (for new genus).

**Etymology.** From Greek elasma for lamina and stemon for stamen.

**Generic diagnosis.** Stamen laminar. Anthers tetrasporangiate, dithecate. Thecae positioned close to the stamen margin and separated by a massive, broad connective. Stamen apex rounded without an apical extension. Dehiscence longitudinal. Staminial tissue with larger cells, probably ethereal oil cells. Pollen monocolpate, circular in equatorial view, semitectate-reticulate. Reticulum loosely attached, heterobrochate. Aperture long, reaching the equator, with distinct margins. Columellae short.

**Comments on the genus.** The broad and flattened stamen and monoaperturate pollen strongly suggest a position among basal grade angiosperms. Laminar or laminar-like stamens that have pollen sacs positioned at, or close to, their margin occur among some extant ANA-grade angiosperms (Austrobaileya C.T.White and Nymphaeaceae) and Magnoliales, and ethereal oil cells like those seen in the fossil stamens are also present in stamens of Austrobaileya and Magnoliales (e.g., Canright 1952, Endress and Hufford 1989). Stamens of Austrobaileya are flattened as in the Catefica fossils and Austrobaileya pollen is also reticulate-columellate. However, in Austrobaileya the two thecae are close together on either side of the mid-line of the stamen with little connective tissue between them (Canright 1952, Endress and Hufford 1989). Pollen of Austrobaileya is also much larger, between 51 and 100 µm, than the pollen of the Catefica material (Halbritter 2016). Stamens of Nymphaeaceae lack oil cells and the pollen is non-reticulate and often zona-aperturate (see discussion of “Stamen with zona-aperturate pollen” above).

In Magnoliales stamens of Degeneria I.W.Bailey et A.C.Sm. (Degeneriaceae) and Galbulimima F.M.Bailey (Himantandraceae) are broad as in the Catefica stamen, but pollen in Degeneria is psilate with granular infractetal layer and pollen in Galbulimima is atectate (Endress and Hufford 1989). Eupomatia (Eupomatiaceae) also has laminar-like stamens, but the pollen is zona-aperturate. In Magnoliaceae, the thecae are laminar or marginal and pollen is typically psilate. Semitectate-reticulate pollen is known among other Magnoliaceae, including species of Horsfieldia Willd., Myristicaceae (Sauquet and Le Thomas 2003) and several Annonaceae (Walker 1971), but stamens in these two families are not laminar.

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Elasmostemon paisii E.M. FRIS, P.R. CRANE, K.R. PEDERSEN, M.M. MENDES ET J. KVAČEK sp. nov.

Text-figs 25a–h, 26a–c

Holotype. S105281 (Catefica sample 151; figured Text-fig. 25d–h).

Plant Fossil Names Registry Number. PFN002793 (for new species).

Paratypes. S115859, S172560 (Catefica sample 49).

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

Etymology. In honor of Professor João Pais (1949–2016) for his contribution to the palaeobotany and geology of Portugal.

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 stratum and age. Almargem Formation, Early Cretaceous (Aptian-early Albian).

Specific diagnosis. As for the genus.

Dimensions. Stamen fragments 0.6–1.7 mm long (full length unknown); 0.5–0.7 mm broad.

Description and remarks. The material comprises two small stamen fragments (S105281 and S115859) that are about 0.6–0.8 mm long and 0.5 mm broad (Text-fig. 25a, d) and a larger fragment (S172560), about 1.6 mm and 0.7 mm broad (Text-fig. 26a–c). The three fragments preserve different parts of the stamen, and apparently also slightly different developmental stages. They are treated here as a single species based on the stamen shape, the orientation and positioning of the narrow pollen sacs, and the shared in situ monocolpate, semitectate-reticulate pollen (Text-figs 25a–h, 26a–c). The stamens are broad, tetrasporangiate and dithecate, and abaxially-adaxially flattened. The stamen apex, preserved in specimens S115859 and S172560, is rounded without an apical extension (Text-figs 25a, 26a). The stamen base is not preserved in any of the specimens and the full length of the stamen is unknown. In specimen S115859 the marginal tissue appears to be abraded. The pollen sacs are...
arranged in two pairs on one surface of the stamen close to the stamen margins. It is unknown whether the pollen sacs are on the abaxial or adaxial stamen surface. The two pairs of pollen sacs are separated from each other by a broad zone of connective tissue but are oriented such that they converge and meet near the stamen apex (Text-fig. 25a, d). Dehiscence of the pollen sacs is longitudinal. In the two smaller fragments the thecae are not open, while in the larger specimen the thecae are dehisced with their walls curved back (Text-fig. 26a). Larger cells, interpreted as ethereal oil cells, are closely spaced in the staminal tissue and particularly well-preserved in specimen S115859 as shallow depressions surrounded by several cells that produce rounded swellings (Text-fig. 25a, b). In the other two specimens these cells are obscured by poor preservation.

Mature pollen grains are exposed by fractures in the undehisced, smaller specimens. In the larger, dehisced specimen most of the pollen had been shed, but a group of grains, perhaps immature, remained attached to the inside of the anther wall. Pollen grains of specimen S115859 were described and figured earlier as Pollen type D.8 (Friis et al. 1999). Grains from specimen S105281 are very similar
but folded, which obscures the apertures. The pollen is circular in equatorial view, about 15–17 µm in diameter, and monocolpate. The exine is semitectate-reticulate with a heterobrochate, loosely attached reticulum (Text-fig. 25c, e–h). The aperture is long, reaches to the equator, and has distinct margins (Text-fig. 25e). Lumina are rounded to angular, with larger lumina up to about 1.6 µm in diameter and smaller lumina about 0.2–0.5 µm in diameter. Muri are narrow, about 0.2 µm wide, with a flattened profile and smooth surface (Text-fig. 25h). Columellae are short, about 0.2 µm long (Text-fig. 25h).

Pollen grains in S172560 vary markedly in size and may be immature but are also partly obscured by residual organic material. They show a gradation, from grains that are almost smooth, to grains with a very weakly developed reticulum (Text-fig. 26b, c). Pollen grains in specimen S172560 are also smaller than in the two other specimens, about 12 µm in diameter, and in some grains the reticulum is denser. The inner surface of the anther wall in the dehisced specimen is finely granular, probably reflecting the presence of tiny orbicules.

**Affinity and other occurrences.** For the possible systematic relationships of *Elasmostemon paisii* see comments on the genus above. The stamen fragments are closely similar to the specimen described below as “Laminar stamen with monocolpate reticulate pollen”. However, the pollen in the two stamen types differ in the details of their wall structure. Similar stamens have not been encountered in other mesofossil floras from Portugal. *Melloniflora* E.M.Friis, P.R.Crane et K.R.Pedersen, and several different isolated stamens from the Early Cretaceous Puddledock flora of Virginia, USA, have pollen sacs that are embedded in the staminal tissue in a non-marginal position, but they differ in their larger size and their more elongate, scale-like form (Friis et al. 2020b).

**Laminar stamen with monocolpate reticulate pollen**

*Text-fig. 26d–g*

**Description and remarks.** The material comprises a single stamen, about 1.8 mm long and up to about 0.6 mm broad (Text-fig. 26d) with monosporangiate, semitectate-reticulate-foveolate pollen in situ (Text-fig. 26f, g). The stamen is broad and elongate. The anther is basifixted and there is no trace of a filament indicating that the anther may have been sessile (Text-fig. 26d). The anther is tetrasperangiate, dithecate, narrowly elongate, and abaxially-adaxially flattened. The stamen apex is rounded, apparently with a short apical extension (Text-fig. 26d). The anther is curved, most likely towards the centre of the flower, suggesting
that the pollen sacs are in an adaxial position (Text-fig. 26d). The four pollen sacs are arranged in two pairs close to the margins of the stamen and converge toward the stamen apex. The pollen sacs are undehisced and are separated by a broad connective, except near the apex where they meet (Text-fig. 26d). Larger, rounded cells, probably the remains of ethereal oil cells, are scattered in the staminal tissue (Text-fig. 26d).

Pollen grains are seen in a fracture in one of the pollen sacs (Text-fig. 26f, g). The grains are folded, covered by orbicules and appear monoaperturate, but the aperture is not well-exposed in any of the grains (Text-fig. 26f, g). Pollen grains are circular in equatorial view, about 14 µm in diameter. The exine is semitectate-reticulate apparently with lumina grading from small to larger (Text-fig. 26f, g). Muri are smooth with a slightly rounded profile, and about 0.8 µm wide. Sometimes they are extended laterally (Text-fig. 26g). The muri are supported by short columellae (Text-fig. 26g). The inner surface of the anther wall (Text-fig. 26e) and the exposed pollen grains (Text-fig. 26f, g) are covered by spherical orbicules of different sizes that often have a tiny central depression (Text-fig. 26e–g).

**Affinity and other occurrences.** The specimen is closely similar to the stamen and stamen central depression (Text-fig. 26e–g). Spherical orbicules of different sizes that often have a tiny or Magnoliales (see discussion above). Close and are most likely related to extant Austrobaileyales produced the two stamen types are probably systematically E. paisii. The exposed pollen grains (Text-fig. 26f, g) are covered by orbicules and appear monoaperturate, but the aperture is not well-exposed in any of the grains (Text-fig. 26f, g). However, this single specimen differs from E. paisii in the details of the pollen wall and the dense covering of orbicules. The plants that produced the two stamen types are probably systematically close and are most likely related to extant Austrobaileyales or Magnoliales (see discussion above).

**Genus Valvidistemon E.M. Friis, P.R. Crane, K.R. Pedersen, M.M. Mendes et J.Kvacek gen. nov.**

**Type.** Valvidistemon globiferus E.M. Friis, P.R. Crane, K.R. Pedersen, M.M. Mendes et J.Kvacek gen. et sp. nov.

**Plant Fossil Names Registry Number.** PFN0002794 (for new genus).

**Etymology.** From Greek valvida for valve and stemon for stamen.

**Generic diagnosis.** Stamen small with a poorly differentiated base. Anther tetrasporangiate, dithecate. Dehiscence valve by two laterally hinged valves over each theca. Connective between thecae massive. Apical extension of the connective prominent, only slightly shorter than the anther, globose, overhanging the thecae. Pollen small, semitectate-reticulate.

**Comments on the genus.** Similar stamens with valvate dehiscence, laterally hinged valves, poor differentiation between stamen base and anther, and a prominent globose apical extension of the connective, are characteristic of several extant members of Annonaceae (e.g., Endress and Hufford 1989, Van Heusden 1992). Comparable stamens also occur in extinct and extant members of Platanaceae (Friis et al. 1988, Endress and Hufford 1989), but in Platanaceae the stamens have a distinct filament, and the pollen is tricolpate.

The stamen is assigned here to a new genus. We are not aware of similar stamens that have been described in the fossil record and because information on other floral parts are missing detailed comparison with extant angiosperms is currently not possible.

**Valvidistemon globiferus E.M. Friis, P.R. Crane, K.R. Pedersen, M.M. Mendes et J.Kvacek sp. nov.**

**Holotype.** S107779 (Catifica sample 49; figured Text-fig. 27a–d).

**Plant Fossil Names Registry Number.** PFN002795 (for new species).

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

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

**Type stratum and age.** Almargem Formation, Early Cretaceous (Aptian-early Albian).

**Specific diagnosis.** As for the genus.

**Dimensions.** Stamens up to about 0.9 mm long and 0.2 mm in broad.

**Description and remarks.** The material comprises a single stamen, about 0.6 mm long with semitectate-reticulate pollen in situ (Text-fig. 27a–d). The stamen consists of a short base that is poorly differentiated from the basifixted anther. The anther is tetrasporangiate and dithecate with an almost spherical apical extension of the connective that overhangs the thecae (Text-fig. 27a, b). Epidermal cells of the connective tissue between the thecae are slightly elongate and arranged in longitudinal rows (Text-fig. 27c). The four pollen sacs are arranged in two pairs in a lateral position and are separated by a broad connective that is equally thick on both adaxial and abaxial sides (Text-fig. 27a, b).

Dehiscence is valvate by laterally hinged valves that result from a distal and proximal bifurcation of the stomium (Text-fig. 27c). Valves are preserved on one side of the stamen (Text-fig. 27a, c), but are broken off on the other side exposing the distinct, quadrangular cells of the endothecium (Text-fig. 27b).

The thecae are dehisced. Most pollen has been shed and only a few grains remain adhering to the inside of the anther wall (Text-fig. 27d). Pollen grains are about 15 µm in diameter. The grains are folded and while the apertures of all the grains are poorly exposed the pollen appears monoaperturate, probably monocolpate. The pollen wall is semitectate-reticulate with a homobrochate reticulum (Text-fig. 27d). There is no trace of orbicules on the inside of the anther wall.

**Affinity and other occurrences.** Detailed consideration of possible systematic affinities is not possible given the limited material and information available. Similar stamens have not been observed in other Early Cretaceous mesofossil floras from Portugal and North America.
Text-fig. 24. Scanning electron microscope (SEM) images of “Stamen with zona-aperturate pollen”; Catefica locality, Portugal.

a) Dorsal view of elongated anther showing the broad connective and very narrow pollen sacs; b) Lateral view of elongated anther showing the broad dorsal and ventral surfaces of the connectives and very narrow pollen sacs; c) Apex of elongated anther showing dorsal and ventral surfaces and very narrow pollen sacs; d) Lateral view of narrow pollen sac showing in situ pollen; e) Detail of pollen grain showing the solid band of exine above the aperture (asterisk); f) Detail of pollen grain showing the solid
**Genus Endressistemon E.M.FRIS, P.R.CRANE, K.R.PEDERSEN, M.M.MENDES et J.KVAČEK gen. nov.**

*Type.* *Endressistemon cateficensis* E.M.FRIS, P.R.CRANE, K.R.PEDERSEN, M.M.MENDES et J.KVAČEK sp. nov.

**Plant Fossil Names Registry Number.** PFN002796 (for new genus).

**Etymology.** In honor of Peter K. Endress for his many contributions to understanding the flower and stamen morphology of angiosperms.

**Generic diagnosis.** Staminate structure consisting of a short, common stalk bearing two fully developed lateral stamens with a median axis-like structure between them. Stamens tetrasporangiate and dithecate with sessile, basifixed anthers attached directly to the common stalk. Thecae straight and parallel in each stamen, but the thecae of the two stamens diverging apically. Apex of the two stamens with prominent coriaceous projection that is also seen on the median axis-like structure. A bundle extends from the common base into the apical projection of the two stamens and the median axis-like structure. Pollen grains monocolpate, semitectate-reticulate.

**Comments on the genus.** Interpreting the morphology and likely relationships of this androecial structure is not straightforward but based on the distinctive apical projection of the stamens, and the monocolpate pollen, we infer a systematic position among the grade of angiosperms. This interpretation would be consistent with the suggestion that the tough apical projection of the *Hedyosmum* stamen could be remains of a subtending bract fused with the stamen (Endress and Doyle 2015, Doyle and Endress 2018).

Among extinct plants, the Early Cretaceous *Archaefructus* G.SUN, DILCHER, SHAO L.ZHENG et Z.K.ZHOU also has two or three stamens borne together, but in *Archaefructus*, the anthers are not sessile and not borne on a common stalk and the stamen apices are less prominent (Sun et al. 1998).

**Endressistemon cateficensis E.M.FRIS, P.R.CRANE, K.R.PEDERSEN, M.M.MENDES et J.KVAČEK sp. nov.**

*Text-fig. 28a–g.*

**Holotype.** S107778 (Catefica sample 49; figured Text-fig. 28a, b, c, f).

**Plant Fossil Names Registry Number.** PFN002797 (for new species).

**Paratypes.** S107751, S107768, S107769, S266022 (Catefica sample 49).

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

**Etymology.** From the Catefica locality where the fossils were collected.

**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 stratum and age.** Almargem Formation, Early Cretaceous (Aptian-early Albian).

**Specific diagnosis.** As for the genus.

**Dimensions.** Stamens up to about 0.9 mm long and 0.2 mm in broad.

**Description and remarks.** The material includes isolated staminal structures each consisting of two lateral stamens and in some specimens a median axis-like structure. The two stamens and axis-like structure are borne on a short, common stalk (Text-fig. 28a–e). The anthers are basifixed, tetrasporangiate and dithecate (Text-fig. 28a, b).

The stamens are up to about 0.9 mm long including the common stalk and the apical projection, and the anther is about 0.2 mm broad. The stamen base is short, about 0.1 mm long (Text-fig. 28a, b, d, e). Apically the two stamens have a prominent peltate to wing-like projection that is coriaceous and sometimes leaf-like (Text-fig. 28a–e). A similar band of exine above the aperture (asterisk); g) Detail of tectum showing heterobrochate reticulum with lumina of two different sizes supported by long columellae (arrows); h) Detail of pollen grain showing the aperture extending over the ends of the grain (asterisks); i) Detail of tectum showing heterobrochate reticulum with lumina of two different sizes supported by long columellae (arrows). Specimen, Catefica 49-S171527 (a–i). Scale bars = 600 μm (a, b), 100 μm (c), 20 μm (d), 6 μm (e, f, h), 3 μm (g), 1.5 μm (i).
projection is also present at the tip of the median axis-like structure in the holotype (Text-fig. 28a, b, e, f). In another specimen (S107769) the median axis-like structure is seen between the two stamens (Text-fig. 28c) in the same position as in the holotype, but in this specimen the axis-like structure is broken and has no apical projection. In the holotype three distinct ribs, which probably reflect the position of vascular bundles, extend from the common stalk into the apical projections (Text-fig. 28b, e). It is possible that these bundles are in an abaxial position, but the orientation of the staminal structure and which side is adaxial and which side is dorsal is unknown. Dehiscence of the anthers is longitudinal and in dehisced stamens, the anther wall is rolled back indicating valvate dehiscence (Text-fig. 28a, c).
Pollen grains were observed in situ in one specimen (Text-fig. 28g). They are monocolpate, semitectate-reticulate, circular in equatorial view, 10–11 µm in diameter, with a homobrochate reticulum. The aperture is long, reaching almost to the equator.

Affinity and other occurrences. The monocolpate pollen indicates that *Endressistemon* is a non-eudicot, most likely related to the basal grade of early angiosperm lineages (see discussion above). While it is not possible to place the fossils in any extant family or order a relationship to Chloranthaceae seems most likely. Currently *Endressistemon* has only been recovered from the Catefica mesofossil flora, where it is restricted to the basal part of the exposure.

cf. *Endressistemon* sp. 1
Text-fig. 29a, b

Description and remarks. The material includes a pair of compressed stamens resembling the staminate structures of *Endressistemon cateficensis* described above. The stamens are up to 0.8 mm long including the apical projection, and about 0.3 mm broad. The apical projection is longer than the thecae, about 0.45 mm long, and tapers to a long, pointed tip (Text-fig. 29a). The two stamens adhere together closely, but their bases are missing, and whether the stamens had separate distinct bases or a shared base, or whether the base was lost during fossilization, is not known. Anther dehiscence is longitudinal.

Pollen grains observed in situ (Text-fig. 29b) are monocolpate, semitectate-reticulate, circular in equatorial view, about 9 µm in diameter. The aperture is long, reaching almost to the equator, and the aperture margin is distinct. The reticulum is homobrochate (Text-fig. 29b).

Affinity and other occurrences. The stamens and in situ pollen are closely similar to those of *Endressistemon cateficensis* described above, but the pollen sacs are more rounded and the apical projection is much longer. Because of the missing stamen base it is uncertain whether the two taxa are closely related.

cf. *Endressistemon* sp. 2
Text-fig. 29c, d

Description and remarks. The material comprises a single stamen fragment, about 0.8 mm long including the apical projection, and about 0.3 mm broad. The apical projection is compressed covering the distal portions of the thecae (Text-fig. 29c).

Pollen grains in situ are poorly exposed and the aperture configuration is uncertain, although it is clear that the grains are not tricolpate and we assume that the pollen is monoaperturate. Pollen is semitectate-reticulate, circular in equatorial view, about 9 µm in diameter. The reticulum is homobrochate and only loosely attached to the main body of the pollen (Text-fig. 29d).

Affinity and other occurrences. The stamen fragment is closely similar in general morphology to the individual stamens of *Endressistemon cateficensis*, but slightly larger and the reticulum of the pollen grains is more open and only loosely attached to the main body of the grains.

cf. *Endressistemon* sp. 3
Text-fig. 29e–g

Description and remarks. The material comprises a single pollen from which the stamen base is missing. The anthers are basified, tetrasporangiate and dithecate (Text-fig. 29e). The stamens are up to about 0.7 mm long, including the apical projection, and about 0.3 mm broad over the anther. Apically the stamen has a prominent, coriaceous projection that is peltate to wing-like (Text-fig. 29e). Dehiscence is longitudinal and the anther wall is rolled back indicating valvate dehiscence (Text-fig. 29e).

Pollen grains in situ are monocolpate, semitectate-reticulate, circular in equatorial view, 13 µm in diameter, with a homobrochate reticulum (Text-fig. 29f, g). The grains are folded and the extent of the aperture is not fully exposed.

Affinity and other occurrences. The stamen is similar to stamens of some extant Annonaceae (see comments on *Endressistemon* above), but also to the individual stamens of *Endressistemon cateficensis* and it is possible that it was originally part of a similar staminate structure. The pollen grains in situ are also similar to those of *Endressistemon cateficensis*, but are larger and the two taxa are probably not conspecific.

Clade Monocotyledons

Genus *Pennipollis* E.M.Friis, K.R.Pedersen et P.R.Crane, 2000

*Pennipollis tenuis* E.M.Friis, K.R.Pedersen et P.R.Crane, 2000

Description and remarks. Two fruits, about 0.8–1.3 mm long and 0.5 mm broad, were recovered from Catefica sample 50. The fruits (not figured) are strongly flattened and elliptical in outline with a very thin fruit wall and thin, longitudinal ridges, probably from vascular bundles, that extend for the full length of the fruits.

Affinity and other occurrences. The fruits are closely similar in size, shape and texture to those of *Pennipollis tenuis* described from the Vale de Água and Buarcos mesofossil floras (Friis et al. 2000). The fruits from Catefica have not been studied using SEM and it is unknown whether they have adhering pollen of *Pennipollis* E.M.Friis, K.R.Pedersen et P.R.Crane as is known for *Pennipollis tenuis* from Vale de Água and Buarcos.

*Pennipollis* and the associated *Pennistemon* E.M.Friis, K.R.Pedersen et P.R.Crane and *Pennipollis*, collectively referred to as the *Pennipollis* plant (Friis et al. 2011), were placed in the monocots mainly based on the distinct acumellate pollen wall (Friis et al. 2000), although an affinity with Chloranthaceae has also been suggested (see Doyle and Endress 2014).

So far, only two fruits have been recovered from Catefica and *Pennipollis* grains have not been recognized in the palynological preparations. In the Vale de Água and Buarcos mesofossil floras remains of the *Pennistemon* plant are abundant. Dispersed *Pennipollis* pollen has also been
Text-fig. 26. Scanning electron microscope (SEM) images of stamens and pollen grains of *Elasmostemon paisii* gen. et sp. nov. (a–c) and laminar stamens with monocolpate reticulate pollen sp. (d–g); Catefica locality, Portugal. a) Stamen fragment with basal portion missing showing two pairs of pollen sacs on one surface of the stamen close to the margin and separated by a broad connective, except near the apex where the thecae meet; note that the thecae are dehisced with the walls of the pollen sacs curled back; b) Pollen grains inside a dehisced pollen sac; note variation in size and development of the reticulum; c) Detail of (b) showing monocolpate, reticulate pollen with lumen of reticulum varying markedly in size but partly obscured by residual organic
reported in early Aptian to middle Albian palynological assemblages from coastal sections in Portugal (Heimhofer et al. 2007) and from the dispersed palynoflora of Casal do Borracho (Torres Vedras) (Mendes et al. 2018a). *Pennipollis* pollen is also widespread in Early Cretaceous palynofloras from other regions (see Friis et al. 2000).

Non-eudicot angiosperms of uncertain affinity

Remarks. Under this heading we describe several angiosperm taxa that have monoaperturate pollen indicating a phylogenetic position among non-eudicot angiosperms, but for which assignment to monocots or early diverging dicots is not possible based on the features currently available.

**Genus Kempia** E.M.Friis, P.R.Crane et K.R.Pedersen, 2019

*Kempia longicolpites* E.M.Friis, P.R.Crane et K.R.Pedersen, 2019

Description and remarks. The material comprises two adhering stamens (only one cut stamen illustrated) with dithecate, tetrasporangiate anthers (Text-fig. 30a) and in situ pollen. The stamens are about 1 mm long and 0.25 mm broad with a distinct, triangular apical extension of the connective. One stamen was cut transversely into two pieces to expose the pollen for SEM. The other stamen was removed for TEM. Stamens and anthers are closely similar to *Kempia longicolpites* described from the Torres Vedras locality (Friis et al. 2019a) and the specimen is assigned here to the same species. Pollen grains are small, about 11–12 µm long, monoaperturate and with the colpus extending beyond the full length of the grains. The exine is semitectate-reticulate, columellate (Text-fig. 30b–f) with the reticulum and columellae only loosely attached to the foot layer (Text-fig. 30f). The muri have a rounded profile and a smooth surface (Text-fig. 30e). The foot layer is thick, and the endexine is restricted to the apertural region (Text-fig. 30e).

Affinity and other occurrences. *Kempia longicolpites* was first described from the Torres Vedras locality (Friis et al. 2019a) and is currently known from only the Torres Vedras and Catefica mesofossil floras.

**Genus Piercipollis** E.M.Friis, P.R.Crane et K.R.Pedersen, 2019

*Piercipollis* sp.

Description and remarks. The material comprises two isolated pollen grains, one observed as
a contaminant in a cluster of Araucariacites pollen (Text-fig. 31a, b), and another included in a coprolite (not illustrated). The pollen grain illustrated is monocolpate, small, almost circular in equatorial outline, about 14–18 µm in diameter. The colpus is long, extending to the equator and has clearly delimited margins (Text-fig. 31b). The exine is semitectate-reticulate and columellate. The reticulum is coarse and homobrochate with polygonal to rounded lumina up to about 0.15 µm in diameter. Muri are smooth with a slightly rounded profile and long, scattered columellae (Text-fig. 31b).

Affinity and other occurrences. The pollen grains resemble pollen of Piercipollis simplex E.M.Fris,
P.R. Crane et K.R. Pedersen described from the Torres Vedras locality (Friis et al. 2019a), but the reticulum is more dense and the lumen are smaller, more like the lumen in grains of Piercipollis sp. 2, also from the Torres Vedras locality (Friis et al. 2019a).}

Genus Teebacia E.M. Friis, P.R. Crane et K.R. Pedersen, 2019

Teebacia sp.

Description and remarks. The material consists of several isolated pollen grains observed adhering to the outer surface of a flower of Saportanthus parvus (Text-fig. 31c–e). The pollen grains are small, about 14 µm long, almost circular in equatorial outline, and monocolpate. The colpus is partly concealed and its full length is unknown, but it does not extend beyond the equator. The exine is semitectate-reticulate and columellate (Text-fig. 31e). The reticulum is coarse and heterobrochate with lumina of various sizes (Text-fig. 31e). The muri have a rounded profile and are prominently ornamented with narrow, transverse ridges that extend laterally (Text-fig. 31e). Columellae are scattered with fine granular ornamentation (Text-fig. 31e).

Affinity and other occurrences. The genus Teebacia was established for anthers with in situ pollen from the Torres Vedras locality (Friis et al. 2019a). The pollen grains from Catefica are closely similar in their overall appearance to pollen of the type species, Teebacia hughesii E.M. Friis, P.R. Crane et K.R. Pedersen, but the Catefica grains are smaller and the transverse ribbing of the muri is coarser and more pronounced. The Catefica pollen is more similar to grains recorded from the Vale de Água mesofossil flora as “Pollen Type I.1” that are 13–14 µm in diameter and that show similar coarse transverse ribbing on the muri (Friis et al. 1999).

Stamen with monocolpate, reticulate pollen

Description and remarks. The material comprises a single stamen with a triangular tetrasporangiate anther that broadens from the base (Text-fig. 32a). The stamen is associated with a small bract (Text-fig. 32a) and the anther is therefore sessile or the filament is very short. The stamen is about 0.75 mm long and about 0.45 mm wide at its broadest point near the apex, but there is no apical extension of the connective. Pollen in situ (Text-fig. 32b–e) is monoaperturate, almost circular in equatorial outline and about 14 µm in diameter. The aperture is rounded, about 10 µm long, with a distinctly delimited margin (Text-fig. 32b, d). The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 32c). Lumina are irregular, up to about 1 µm in diameter. Muri are narrow, 0.2 µm wide, and ornamented with minute
irregularly arranged verrucae. Columellae are about 1 µm long and widely spaced (Text-fig. 32c, e).

**Affinity and other occurrences.** The finely verrucate supratectal ornamentation of the muri is similar to that of pollen produced by many chloranthoids from the Early Cretaceous, but such a distinctly delimited aperture is not known in any extant or fossil chloranthoid. It is also possible that the grains are not fully developed or that they represent parts of zono-aperturate grains, but the material of these unusual grains is currently insufficient for definitive interpretation. Similar pollen has not been observed in other Early Cretaceous floras from Portugal.

**Clade Eudicot angiosperms**

**Remarks.** Plant fossils that can be assigned with certainty to eudicot angiosperms are not common in the Catcifica mesofossil flora and eudicot pollen grains are also rare in the palynological assemblages. Only six taxa have been recognized: *Paisia pantoporata*, which has pentamerous flowers and pantoporate pollen, and five different kinds of tricolpate pollen, which occur in situ in stamens, or that are found in pollen clumps. We also include here a single fruiting structure treated as *Paisia* sp., and several isolated *Paisia*-like follicles, although their eudicot affinity is not completely certain and in the counts they are treated as angiosperms of uncertain affinity.

**Genus Paisia E.M.Friis, M.M.Mendes et K.R.PederSEN, 2018**

**Paisia pantoporata E.M.Friis, M.M.Mendes et K.R.PederSEN, 2018**

**Text-fig. 33a–c**

**Description and remarks.** *Paisia pantoporata* is based on about 60 specimens of fossil flowers and isolated floral parts recovered from the Catcifica mesofossil flora (for a full description and discussion see Friis et al. 2018a). Flowers are small, about 1 mm long and 1.2 mm in diameter, actinomorphic and pentameras with a perianth consisting of a single whorl of five tepals, an androecium consisting of a single whorl of stamens, and a gynoecium of five free carpels (Text-fig. 33a, c). The organs of the three whors are arranged on the same radius with the incurved margins of each tepal embracing a stamen (Text-fig. 33c). Stamens have a short, stout filament that merges above into the anther. Anthers are tetrasporangiate with two pairs of pollen sacs borne laterally and separated by a massive connective.

Pollen grains are small, spheroidal, about 11–14 µm in diameter and pantoporate with six to eight pores. The pollen wall is tectate-punctate with spiny supratectal ornamentation (Text-fig. 33b). The carpels are follicular, narrowly elliptical to obovate with a ventral slit that extends for the full length of the carpel. Each carpel has one dorsal and two ventral bundles and contains about 20–30 seeds borne in two rows along the full length of the ventral suture.

**Affinity and other occurrences.** Panto- porate pollen occurs scattered among all major groups of angiosperms. However, the characters of the pollen combined with the pentameras organisation indicate that *Paisia pantoporata* is most likely an extinct lineage of basal eudicots, probably most closely related to extant Ranunculales.

Flowers of *Paisia pantoporata* have so far been recovered only from the Catcifica locality. Pollen of *Paisia pantoporata* is also encountered in the palynological strew preparations from Catcifica, where it occurs in clumps of several grains. Pantoporate pollen grains of the kind produced by *Paisia pantoporata* have not been reported from other palynofloras. Pantoporate pollen grains are not uncommon in Early Cretaceous palynofloras (for references see Ibrahim et al. 2015, Friis et al. 2018a), but grains similar to pollen of *Paisia pantoporata* have not been reported from other mesofossil floras or dispersed palynofloras.

**Remarks.** The single specimen is similar to *Paisia pantoporata* in its receptacle with apical facets, the cellular details of the pedicel and carpel wall, and the gynoecium of free, follicular carpels. However, the specimen differs in its trimerous gynoecium and should probably be assigned to a new species, either in *Paisia* or in a new extinct genus (Friis et al. 2018a).

**Description and remarks.** The material comprises a single specimen described previously from the Catcifica locality (Friis et al. 2018a). The specimen consists of a long axis terminating in a floral structure of which only the gynoecium is preserved. The receptacle has poorly-defined scars from shed floral parts and the structure is apparently preserved at a post-anthetic stage (Text-fig. 33d). The gynoecium is apocarpous consisting of three ovoid to elliptic follicular carpels. Each carpel has about ten ovules/seeds borne in two longitudinal rows along the entire ventral suture.

**Affinity and other occurrences.** The material includes several isolated follicles probably derived from apocarpous gynoecia. The follicles vary considerably in size and shape, and range from narrow elongated-ellipsoidal to obovate. Follicles are 0.7–1.7 mm long, 0.35–0.7 mm broad in the dorsi-ventral direction, and 0.3–6.2 mm wide (Text-figs 34a–h, 35a–e, 36a–e).

The follicles have a distinct ventral suture with a deciduous stigma that extends along the full length of the follicle. In some specimens there is a distinct papillate zone that extends along both sides of the ventral suture from the follicle base to the apex (Text-fig. 34a–d). This papillate zone is possibly stigmatic. In many specimens the follicles have a distinct apical cleft (Text-figs 34d, 35a, d, 36b, d).

The follicles contain many anatropous ovules/seeds that are borne on placenta that extend on either side of the ventral suture for the full length of the follicle. In most specimens the ovules/seeds are arranged in two distinct rows (Text-figs 34e–h, 35e), but in one specimen (Text-fig. 36a–e) this is less distinct and the ovules/seeds are more crowded. This specimen is larger than the other follicles and clearly more mature. There are smaller undeveloped ovules in its
lower part (Text-fig. 36c) but there are larger, probably mature, seeds in the upper part (Text-fig. 36c). Whether the crowding of the seeds is due to the stage of maturity of the follicles, or because this larger specimen represents another species, is uncertain. The epidermal cells of the ovules/seeds have slightly raised anticlinal walls that give the surface a striate-reticulate appearance (Text-figs 34e, f, 36c).

The follicle wall is thick. It consists of an inner layer of transversely aligned fibres (Text-fig. 34e), a middle layer that is one to two cell layers deep and an outer epidermis of smaller, thin-walled cells (Text-figs 34g, 35e). The mesocarp is composed of large, isodiametric, thick-walled cells that have a rounded cell lumen (Text-figs 34e, f, h, 35e). The follicle is supplied by one dorsal and two ventral bundles (Text-figs 34g, h, 35e, 36e).

Affinity and other occurrences. The follicles are closely similar to the follicles seen in flowers of *Paisia pantoporata* in their elongate shape and in the anatomical details of the follicle wall. However, the carpels in the *Paisia* flowers are immature and the stigmatic zone is indistinct. Other features seen in the isolated follicles, such as the apical cleft, and a papillate zone extending along the margins of the ventral suture, are also not seen in *Paisia pantoporata*. It is possible that the isolated follicles represent different developmental stages of a single species, perhaps *Paisia pantoporata*. However, it is also possible that they represent additional species of *Paisia* or a closely related genus.

Isolated follicular fruits occur in other mesofossil floras from Portugal, but *Paisia*-like follicles like those described here are known only from Catefica.

**Isolated eudicot stamens and pollen clumps with tricolpate pollen in situ**

Five different kinds of eudicot have been identified from the Catefica mesofossil flora based on isolated stamens and pollen clumps with different kinds of tricolpate pollen. Dispersed tricolpate pollen grains are typically assigned to species of dispersed pollen genera such as *Foveotricolpites* R.L. PIERCE, *Psilatecolpites* HAMMEN ex HAMMEN et WYMSTRA, *Reticolpites* HAMMEN ex HAMMEN et WYMSTRA, *Rhoipites* WODEHOUSE, *Rousset* SAT.K.SRIVAST., or *Striatopolis* KRUTZSCH and *Tricolpites* COOKSON ex COUPER. However, the application of these pollen genera is typically very broad and their type specimens have been studied and illustrated mainly using light microscopy. Light microscope resolution is insufficient for detailed comparison with specimens studied using scanning electron microscopy, including the specimens described here from Catefica. New genera are probably warranted for the Catefica material, but for present purposes we simply refer to the five different taxa as “Stamen/pollen clump with tricolpate pollen sp. 1 – sp. 5.”
Stamen with tricolpate pollen sp. 1
Text-fig. 37a–f

Description and remarks. The material comprises a single fragmentary stamen, about 2.3 mm long and 0.5 mm wide. The anther is tetrasporangiate and dithecate with long narrow pollen sacs (Text-fig. 37a). Pollen grains in situ are small, almost spherical, about 21 µm in diameter and tricolpate (Text-fig. 37b–d). The colpi are long, reaching almost to the poles, and have a distinct margin (Text-fig. 37b–d). The grains are semitectate-retticulate with a heterobrochate reticulum that is coarse in the mesocolpium zones but finer over the poles and along the margins of the colpi (Text-fig. 37b–d). The muri are smooth, about 0.4 µm wide, with a rounded to flattened profile. Columellae supporting the muri are short and densely spaced (Text-fig. 37f).

Orbicules are densely-scattered on the inner surface of the anther wall and over the surface of the pollen grains (Text-fig. 37e). Orbicules are up to about 1 µm long, irregular in shape and have a solid base of laterally fused spheres with rod-like projections (Text-fig. 37e).

Affinity and other occurrences. The triaperturate pollen grains clearly indicate a relationship to eudicots, but relationships to extant taxa within the group are uncertain.

In the mesofossil floras from Portugal this taxon is currently known only from Catefica. The in situ pollen grains are identical in size, shape and most features of the reticulum to the dispersed pollen Retitri-Liliret described by Penny (1991) from the Aptian of Egypt, but in that material the polar regions are foveolate to psilate rather than finely reticulate.

Stamen with tricolpate pollen sp. 2
Text-fig. 38a–e

Description and remarks. The material comprises a single fragment of a tetrasporangiate, dithecate stamen, about 0.9 mm long and 0.3 mm wide (Text-fig. 38a). Pollen grains in situ are tricolpate, prolate-spheroidal, about 25 µm in diameter, and with an almost circular equatorial amb (Text-fig. 38b, d, e). The apertures are long with irregular margins and a coarsely verrucose aperture membrane (Text-fig. 38c).
fig. 38b, d, e). The grains are semitectate-microreticulate, and uniformly heterobrochate over the entire surface of the grain (Text-fig. 38b, d, e). The muri are about 0.4 µm wide, almost smooth with faint transverse striations and a rounded to flattened profile (Text-fig. 38c). The infratectal layer is granular to irregularly columellate (Text-fig. 38c). Small irregular spherical orbicules are scattered over the surface of the pollen grains (Text-fig. 38b, e).

**Affinity and other occurrences.** The triaperturate pollen grains clearly indicate a relationship to eudicots, but relationships to extant taxa within the group are uncertain.

In the mesofossil floras from Portugal this taxon is currently known only from Catefica. The pollen is distinguished from all other tricolpate pollen recorded from Catefica by its microreticulate tectum and irregular aperture margins.

**Pollen clump with tricolpate pollen sp. 3**

*Text-fig. 39a–e*

**Description and remarks.** The material comprises a single pollen clump, probably a fragment of an anther, about 0.5 mm long and 0.3 mm wide (Text-fig. 39a). The pollen clump consists of densely packed pollen grains that are all of the same kind. The grains are tricolpate, small, about 21 µm in equatorial diameter (Text-fig. 39b, d, e). The equatorial outline is slightly triangular, with apertures placed in the middle of the sides (Text-fig. 39b, d). The apertures are long with a distinct margin and a coarsely verrucate aperture membrane (Text-fig. 39b, d). The grains are semitectate-reticulate between the colpi and foveolate to punctate over the poles and along the margins of the colpi (Text-fig. 39b, d, e). The muri are smooth, about 1.1 µm wide, with a rounded to flattened profile and are supported by short, densely spaced columellae (Text-fig. 39c). No orbicules were observed on the surface of the pollen grains.

**Affinity and other occurrences.** The triaperturate pollen grains clearly indicate a relationship to eudicots, but relationships to extant taxa within the group are uncertain.

In the mesofossil floras from Portugal this taxon is known only from Catefica. The pollen is distinct from that of “Stamen with tricolpate pollen sp. 1”, which has a microreticulate tectum in the polar regions and along the apertures, and has smaller and larger lumen intermixed in the mesocolpium regions.

**Pollen clump with tricolpate pollen sp. 4**

*Text-fig. 40a–e*

**Description and remarks.** The material comprises a single isolated pollen grain observed in the
palynological preparations and a pollen clump about 0.8 mm long and 0.5 mm wide. The pollen clump has an irregular shape and remains of an outer epidermis suggesting that is probably a fragment of an anther (Text-fig. 40a). The pollen clump consists of densely-packed pollen grains, all of the same kind. The grains are tricolpate, prolate and small, with a polar axis about 22 µm long and an equatorial diameter of about 19 µm (Text-fig. 40b, c). The equatorial outline is triangular, with apertures placed in the middle of the sides (Text-fig. 40c). The apertures are long with a distinct margin and a coarsely verrucate aperture membrane. The grains are semitectate-reticulate in the mesocolpium zones, striato-reticulate over the poles, and microreticulate to foveolate along the colpi margins (Text-fig. 40b, c). The muri are smooth, about 0.6 µm wide, with a high profile and are supported by long, densely-spaced columellae (Text-fig. 40d, e). The foot layer seen
in broken grains is thick (Text-fig. 40e). No orbicules were observed on the surface of the pollen grains.

Affinity and other occurrences. The triaperturate pollen grains clearly indicate a relationship to eudicots, and while relationships to extant taxa within the group are uncertain there are strong similarities between the striato-reticulate exine sculpture in the polar regions of the pollen grains, with the similar exine sculpture of pollen known in situ from fossil flowers of Lusistemmon K.R.Pedersen, Balthazar, P.R.Crane et E.M.Friis (Pedersen et al. 2007) and Spanomera Drinnan, P.R.Crane, E.M.Friis et K.R.Pedersen (Drinnan et al. 1991), both of which are related to extant Buxales.

In the mesofossil floras from Portugal this taxon is currently known only from Catifica. The pollen is distinguished from all other tricolpate pollen from Catifica by the striato-reticulate tectum in the polar regions.

Pollen clump with tricolpate pollen sp. 5
Text-fig. 41a–d

Description and remarks. The material includes a single pollen clump with a regular broadly elliptical shape and an irregular surface. The specimen is about 0.7 mm long and 0.6 mm wide and is probably a coprolite (Text-fig. 41a). The pollen clump consists of densely packed pollen grains, all of the same kind. The grains are tricolpate, prolate and small, about 21 µm in equatorial diameter (Text-fig. 41b, c). The equatorial outline is triangular to circular, with apertures placed in the middle of the sides (Text-fig. 41c). The apertures have a distinct margin and an apparently smooth aperture membrane. The grains are semitectate-reticulate, with a uniform, coarse reticulum over the whole grain (Text-fig. 41b, c). The muri are smooth, about 0.1 µm wide, with a rounded to flattened profile. The muri are supported by long, densely-spaced columellae that are loosely attached to the thin foot layer (Text-fig. 41d). No orbicules were observed on the surface of the pollen grains.

Affinity and other occurrences. The triaperturate pollen grains clearly indicate a relationship to eudicots, but relationships to extant taxa within the group are uncertain. In the mesofossil floras from Portugal this taxon is currently known only from Catifica. The pollen is distinguished from all other tricolpate pollen from Catifica by the uniformly coarse reticulate tectum over the whole of the grain.

Angiosperms of uncertain affinity

Remarks. Under this heading, we describe those angiosperm fossils from the Catifica locality, including flowers, fruits and seeds, that cannot be placed with certainty in any of the major extant lineages of angiosperms. The most characteristic types are described under separate headings, several other poorly known taxa are mentioned only briefly to illustrate the diversity of the flora.

Tricarpellate flower sp. 1
Text-fig. 42a–g

Description and remarks. The material comprises several flower buds with an inferior gynoeonium (Text-fig. 42a–g). Five specimens were studied using SRXTM, which reveals a trimerous perianth, androecium and gynoeonium. The flowers are pedicellate (Text-fig. 42d, e). The perianth apparently consists of two tepal whorls, but in all specimens studied using SRXTM the floral organs are closely compressed, tepals appear folded in the bud and with tepal appendages (Text-fig. 42f) complicating a full reconstruction of the flower. The flowers are triangular in cross-section (Text-fig. 42f, g) with a distinct depression in the corners immediately above the insertion of the perianth apparently separating the outer perianth lobes (Text-fig. 42a, b, d, e), while the inner tepals apparently have a narrow base. In one specimen the narrow base can be seen in the split between two outer tepals (Text-fig. 42d). The androecium apparently consists of two alternating trimerous whorls of stamens (Text-fig. 42f). The gynoeonium is inferior consisting of three carpels (Text-fig. 42f, g). Above the insertion of the perianth and androecium, the carpels are free, strongly flattened laterally and radially elongate (Text-fig. 42f). Below the insertion, the gynoeicum is syncarpous, trilocular with axile placenta and numerous ovules (Text-fig. 42g). None of the flowers is mature and the pollen is unknown.

Affinity and other occurrences. Fossil flowers or flower buds comparable to those described above have not been described from other mesofossil floras and the material represents a new genus and species. A preliminary assessment of the flower suggests a possible relationship to monocotyledons. There are several similarities to extant members of the Bromeliaceae that also have trimerous flowers, tepal appendages and inferior, trilocular gynoeconium (e.g., Sajo et al. 2004). There are also other groups of monocots with comparable flower morphology, although the possibility of a relationship to magnoliid angiosperms cannot be ruled out. A more comprehensive study including formal description of the new taxon and an analysis of its relationship is in preparation (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress).

Tricarpellate flower sp. 2
Text-fig. 43a–e

Description and remarks. The material consists of a single flower with a tricarpellate gynoeconium that has been studied using SRXTM (Text-fig. 43a–e). The specimen is lignitised and cellular details are not well preserved. The flower is perigynous with a very broad and prominent triangular hypanthal rim (Text-fig. 43a, b) with a slit at each of the three corners (Text-fig. 43b). The nature of these slits is currently unknown, but they are perhaps related to the perianth or stamens, which are not preserved. The floral structure was probably preserved in a very early post-anthetic stage as ovules are not fully developed. The flower is triangular in transverse section and probably trimerous in all parts (Text-fig. 43b). The gynoeicum is tricarpellate, syncarpous with a single apical style. Only one of the three locules is fully developed (Text-fig. 43c). The two other locules are undeveloped and were perhaps compressed during fossilization.
Text-fig. 34. Synchrotron radiation X-ray tomographic microscopy (SRXTM, a–h) images of “Paisia-like follicle”; Catefica locality, Portugal. a–d) Volume rendering of follicles in lateral (a, c) and ventral (b, d) views showing the decurrent stigmatic region that extends from base of the follicle to the apex; note papillate zone forming a probable stigma along the full length of the ventral suture; e) Longitudinal section (volume rendering cut at orthoslice yz0326) near the base of the follicle showing two ovules with a striate-reticulate surface (asterisks); note transverse fibers lining the inner follicle wall and large cells of the mesocarp; f) Transverse section (volume rendering cut at orthoslice xy2475) of follicle showing two rows of ovules borne on placentae on
Ovules are borne along the full length of the ventral margin in the well-developed locule, both above and below the level at which the perianth is inserted (Text-fig. 43c–e). Ovules are thin-walled, apparently anatropous and surrounded by an amorphous substance that partly fills the locule space (Text-fig. 43c–e). This amorphous substance may be the fossilised remains of a mucilaginous secretion from either the ovules or the carpels.

Affinity and other occurrences. The trimerous organisation of the flowers, along with the semi-inferior ovary and the secretion surrounding ovules are the most distinctive features of this fossil. Such secretions are not common among angiosperms, but have been described for several taxa of monocots (Igersheim et al. 2001) and together with the trimerous floral organisation this may suggest a possible monocot relationship. Similar flowers have not been encountered in other Early Cretaceous mesofossil floras and the fossil represents a new genus and species. A detailed description and complete analysis is in preparation (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress).

Hexacarpellate flower

Description and remarks. The material comprises a single floral structure, probably preserved around anthesis since the perianth parts are spreading and the ovules are small and do not fill out the locules. The flower is radially symmetrical, epigynous, with six tepals alternating with six carpels (Text-fig. 44a, d). The perianth is undifferentiated and the tepals are fused for part of their length above the hypanthial rim. The gynoecium is either side of the ventral suture (asterisks); note also the pronounced and densely-spaced papillae around the ventral suture; g) Transverse section (orthoslice xy1988) of follicle showing two ventral vascular bundles and one dorsal bundle (arrows) and ovules/seeds borne on two placentae, one on either side of the ventral suture; note the remains of the small thin-walled cells of the outer epidermis that cover the thicker-walled cells of the mesocarp; h) Transverse section (orthoslice xy2860) of follicle showing two ventral bundles and one dorsal bundle (arrows) and ovules/seeds in two rows on the placentae, one on either side of the ventral suture; note the remains of small epidermal cells and the large rounded cells of the mesocarp with thicker walls. Specimens, Catefica 49-S174916 (a, b), Catefica 49-S174917 (c–f, h), Catefica 50-S171525 (g). Scale bars = 300 μm (a–c), 100 μm (d, e).
Text-fig. 36. Synchrotron radiation X-ray tomographic microscopy (SRXTM, a–e) images of "Paisia-like follicle"; Catefica locality, Portugal. 

a, b) Volume rendering of follicle in lateral (a) and ventral (b) views showing the decurrent stigmatic region that extends from the follicle base to the apex but lacks a distinct papillate zone; 
c) Longitudinal section (volume rendering cut at orthoslice yz0341) of follicle showing under-developed ovules towards the base and numerous well-developed ovules/seeds in the upper part suggesting that the follicle is probably mature; 
d) Dorsal view of follicle apex showing the cleft in the presumed stigmatic apical region; e) Transverse section (orthoslice xy1294) of follicle with one dorsal and two ventral bundles and two placentae bulging into the locule, one on either side of the ventral suture; note the strongly compressed outer epidermis and the homogenized cells of the mesocarp. Specimen, Catefica 49-S174915 (a–e). Scale bars = 300 μm (a–d), 100 μm (e).
syncarpous with six locules (Text-fig. 44d). The placentae are close to the center of the gynoecium and each locule has many ovules arranged in two lines from the base of the locule to the apex (Text-fig. 44c). The ovules are small and do not fill the locule space. A distinct vascular bundle extends along the length of the central axis that runs through the gynoecium and there are six dorsal bundles that extend from the base of the gynoecium to the hypanthial rim, where they separate to supply both the carpels and the tepals. No stamens have been observed, but linear structures adhering to the tepal lobes (Text-fig. 44b) may be the remnants of filaments. The outer epidermis of the hypanthium and tepals consists of small, almost isodiametric cells with thick cell walls that are covered by a thick cuticle (Text-fig. 44a, c, d).

Affinity and other occurrences. The flower is partly abraded and lacks the apical parts of the perianth and the stigmatic region. It is uncertain whether the stamens were shed or whether the flower was unisexual (pistillate). Perianth and carpels each appear to be arranged in a single whorl of six. It is uncertain whether septa are fused at the center or merely closely appressed. These uncertainties

Text-fig. 37. Scanning electron microscope (SEM) images of “Stamen with tricolpate pollen sp. 1”; Catefica locality, Portugal. a) Stamen fragment showing the elongate, tetrasporangiate anther but with the base and apex poorly preserved; b–d) Pollen grains from stamen fragment in equatorial view showing the long colpi and well-developed, heterobrochate reticulum with very distinct large and small lumina; e) Detail of pollen wall showing orbicules with irregular projections; f) Detail of pollen wall showing smooth muri supported by short, densely spaced columellae. Specimen, Catefica 50-S170419 (a–f). Scale bars = 600 μm (a), 6 μm (b–d), 1.5 μm (e, f).
impede more precise comparison with flowers of extant angiosperms. However, there is some resemblance to the flowers of early diverging monocots in the Alismatales, such as Hydrocharitaceae and Juncaginaceae, both of which include taxa with flowers that have inferior ovaries and a hexacarpellate gynoecium. Flowers with an inferior ovary and a gynoecium of six carpels are also known for Aristolochiaceae (magnoliids).

**Staminate structure**

**Text-fig. 45a–c**

**Description and remarks.** The material includes two staminate structures that were illustrated previously with line drawings (Friis et al. 2006, 2011). Each has about 20 stamens densely-crowded in a spherical head that was slightly compressed during fossilization (Text-
fig. 45a–c). The spherical head has small bracts below and is borne on a distinct stalk (Text-fig. 45a–c). The stamens appear to be borne in four whorls with increasing number of stamens towards the apex of the structure, but a helical arrangement cannot be ruled out completely. Anthers are basifixed, sessile and tetrasporangiate, with a flattened apical extension of the connective that has distinct openings that may be secretory (Text-fig. 45a–c). No pollen was observed on the surface of the structure or in situ in the anthers and the structures were probably preserved at a pre-anthetic stage. We originally interpreted these structures as composed of naked, unistaminate flowers, but this is not certain and their organization is not fully understood.

Affinity and other occurrences. We previously compared these fossils with the staminate inflorescences of extant *Hedyosmum*. This was done based on similarities between the Catefica fossils and staminate structures from other Early Cretaceous mesofossil floras from Portugal that have *Asteropollis*-type pollen in situ and that are clearly chloranthoid (Friis et al. 2006, 2011). However, the Catefica specimens, differ from these other fossils in several respects, particularly in the smaller number of stamens, the distinct bracts, and the possible secretory openings in the sterile tissue. Further, the arrangement of stamens is not unequivocally whorled as it is in the chloranthoid fossils (Friis et al. 2019a; E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress). The lack of pollen in the Catefica structures also impedes a more precise placement of the fossils and with the information currently available, we include these fossil here among “Angiosperms of uncertain affinity”. So far this taxon is only reported from the Catefica mesofossil flora.
Rugulate fruit
Text-fig. 46a–d

Description and remarks. The material consists of a single fruit with a distinct rugulate surface. The fruit is isolated and there is no information on how it was borne on the plant. The fruit is more or less elliptical in outline, about 1.3 mm long and 0.7 mm broad, slightly flattened laterally with an almost straight ventral margin and a rounded dorsal margin (Text-fig. 46a, b). The stigma is sessile and slightly raised at the apex of the fruit. Many pollen grains, all of the same kind, are embedded in a secretion on the stigmatic surface. The grains are semi-tectate-reticulate, about 11 µm in diameter and appear to be pantoporate (Text-fig. 46d), but the stigmatic secretion obscures most of the grains and the apertures are not well exposed.

Cells of the outer epidermis have isodiametric facets and are covered by a thick cuticle (Text-fig. 46c). The irregular fruit surface most likely reflects the irregular surface of an endocarp, which is characteristic of many drupaceous fruits and often indicates animal dispersal.

Affinity and other occurrences. The phylogenetic position of this fossil is uncertain. This taxon is currently known only from the Catefica mesofossil flora.

One-seeded fruit sp. 1
Text-fig. 47a–f

Description and remarks. The material includes tiny fruits, each with a single seed that fills out the whole locule (Text-fig. 47a–f). The fruits are about 0.65–
0.7 mm long and 0.55–0.65 mm broad in the dorsi-ventral direction, with a ventral margin that is sinuous and a dorsal margin that is rounded (Text-fig. 47a, b). The base of the fruit is rounded with the short stalk curved towards the ventral side (Text-fig. 47a, b). The stigmatic region is indistinct. The fruit wall is several cell layers thick, and thicker on the ventral side (Text-fig. 47c). A single bundle enters the fruit through the stalk and divides into bundles that extend along the ventral and dorsal sides (Text-fig. 47c). The seed cavity is slightly sinuous and contains a single anatropous seed with two integuments. The outer integument consists of an outer epidermis of thin-walled cells, and an inner layer of smaller, thick-walled cells (Text-fig. 47c–e). The inner integument is thin, membranous and composed of cells with wavy anticlinal walls (Text-fig. 47c–f). The micropyle is formed from the inner integument (Text-fig. 47f).
Text-fig. 42. Scanning electron microscope (SEM, a, b, e) and synchrotron radiation X-ray tomographic microscopy (SRXTM, c, d, f–g) images of “Tricarpellate flower sp. 1”; Catefica locality, Portugal. a, b) Flower bud in two different lateral views showing semi-inferior ovary and perianth; c) Longitudinal section (orthoslice yz0340) through flower bud in (a and b) showing the semi-inferior gynoecium and perigynous insertion of other floral parts; d) Volume rendering of flower bud with pedicel preserved; note the depression/split in one of the corner apparently separating two perianth lobes of the outer perianth whorl (t-o) and exposing one tepal of the inner whorl (t-i); e) Flower bud with pedicel preserved; note broad tepals of the outer whorl (t-o) and tepal of the inner whorl abraded exposing a broad stamen (st); f, g) Transverse sections through flower bud in (a and b) at two different levels above the insertion of the perianth (f, rec-file 1310; g, xy0280) showing the trimerous organization of the flower and the free, laterally flattened carpels; yellow indicates the two whorls of the androecium, each with three stamens. Specimens, Catefica 50-S171520 (a–c, f), Catefica 50-S174902 (d), Catefica MM154-P0271 (e), Catefica 49-S175354 (g). Scale bars = 300 μm (a–e).
**Affinity and other occurrences.** The fruits and seeds are highly similar to those of certain members of the monocot order Alismatales, but further details are required for a more precise systematic assignment (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress). Similar fossils are known from the Torres Vedras locality (Friis et al. 2019a: text-fig. 54g, h).

**One-seeded fruit sp. 2**
Text-fig. 48a–c

**Description and remarks.** The material includes several small fruits each with a single seed. The fruits are broadly elliptical in lateral view, rounded to angular in transverse section, and about 1 mm long and 0.8 mm in diameter (Text-fig. 48a, c). Remains of perianth parts and a stamen at the base of the fruit (Text-fig. 48a) show that the fruit was derived from a hypogynous and structurally bisexual flower. The fruit surface is almost smooth with small, scattered scale-like trichomes (Text-fig. 48b). Seeds inside the fruits appear to be mature with remains of nutritive tissue (Text-fig. 48c).

**Affinity and other occurrences.** Similar fossils are known from other Early Cretaceous mesofossil floras from Portugal and North America where different developmental stages are present, including ovules that are not fully mature and have a distinct endothelium (Friis et al. 2019d).

**Unassigned, unnamed fruits**
Text-fig. 48d–f

**Description and remarks.** In addition to the angiosperm fruits described under separate headings, the Catefica mesofossil flora comprises about ten other species of fruits that are typically preserved only as fragments or lack critical features that would enable more detailed analysis. Two of these fruits are figured here. The first fruit is about 0.7 mm long and 0.5 mm broad in the dorsi-ventral direction (Text-fig. 48d) with the ventral side slightly sinuous and the stigmatic region slightly pointed (Text-fig. 48d). The fruit surface is almost smooth with scattered openings in the epidermis that are interpreted as burst secretory cells (Text-fig. 48e). The second fruit is about 0.5 mm long and 0.35 mm in diameter (Text-fig. 48f). The rounded, slightly bulging apical region is interpreted as stigmatic. The fruit surface is finely rugulate.

**Affinity and other occurrences.** Internal features are unknown for all of the “Unassigned, unnamed fruits” included here and their systematic affinity is unknown. So far they appear to be unique to the Catefica mesofossil flora, and contribute to its diversity, but they are not included in the species counts.

**Genus Pazliopsis E.M.Friis, P.R.Crane et K.R.Pedersen, 2018**

**Pazliopsis sp.**
Text-fig. 48g, h

**Description and remarks.** The material comprises several small, isolated, bilaterally symmetrical seeds that are about 0.85 mm long, and 0.75 mm broad in the dorsi-ventral direction (Text-fig. 48g). The seeds are anatropous and bitegmic. They are elliptical to almost circular in outline, rounded at the chalazal end and truncate at the micropylar end. The hilar scar is almost circular in outline and lacks a hilar rim. The outer epidermis of the outer integument consists of palisade-shaped cells with thickened wavy anticlinal walls that result in a jigsaw-puzzle like surface pattern (Text-fig. 48h). The inner integument is membranous.

**Affinity and other occurrences.** The seeds described here closely resemble seeds of Pazliopsis reyi E.M.Friis, P.R.Crane et K.R.Pedersen from the Torres Vedras mesofossil flora in shape, surface ornamentation and seed coat anatomy (Friis et al. 2018c, 2019a). However, the seeds from Catefica are larger and the hilar scar is not as pronounced as in the seeds from Torres Vedras. The Catefica seeds are also circular rather than elongate-ovate. *Pazliopsis reyi* is thought to be related to members of extant Austrobaileyales and Nymphaeales (Friis et al. 2018c).

**Follicular fruit with exotestal seeds**
Text-fig. 48i

**Description and remarks.** The material includes isolated seeds and a fragment of a follicular fruit containing two seeds (Text-fig. 48i). The seeds are small, almost spherical, about 0.7 mm long, about 0.6 mm in diameter, and anatropous. The micropylar-hilar region is slightly raised. The seed surface is rugulate-ribbed with irregular longitudinal ribs extending from the micropylar-hilar region to the chalazal region. Ribs over the raphe are narrower than over the main body of the seed. The cell outlines formed by the anticlinal walls of the outer cells of the seed coat are weakly sinuous.

**Affinity and other occurrences.** These fossils are common in many of the mesofossil floras from Portugal including Buarcos, Famaicoã and Vale de Água. The seeds have many features in common with seeds of extant Austrobaileyales and Nymphaeales and formal description and systematic analysis of the species is in preparation based on a broader range of fossils from other mesofossil floras (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress).

**Foveolate seeds sp. 1**
Text-fig. 49a–e

**Description and remarks.** The material includes several small exotestal, foveolate seeds that are broadly ovate in outline, about 0.9 mm long and 0.85 mm broad in dorsi-ventral direction. The seeds are isolated and there is no information on the fruit in which they were borne. The seeds are anatropous, bilaterally symmetrical, and bitegmic with a pointed micropylar region and a rounded chalazal region (Text-fig. 49a–e). In the specimen illustrated there is the remains of a presumed secretion from the micropyle. The seed surface is foveolate with deep pits that obscure the underlying jigsaw puzzle-like pattern formed from the undulate anticlinal walls of the exotesta cells (Text-fig. 49b).

Micropyle and hilum are close to each other, and the hilum lacks a hilar rim. Internally the micropyle and hilum...
are separated by a zone of sclerenchyma tissue (Text-fig. 49c, e). The course of the raphe is indistinct on the seed surface but is marked by rows of slightly narrower cells. The micropyle is formed from the inner integument (Text-fig. 49c–e).

The seed coat is composed mainly of exotesta, while the mesotesta/endotesta and tegmen are typically collapsed. The exotesta is one cell layer deep and consists of palisade-shaped sclerenchyma cells that are about 80 µm tall over most of the
seed, but much shorter around hilum and micropyle (Text-
fig. 49c, e). The anticlinal walls of the exotestal cells are
thickened and strongly undulate towards the outside. The
tiny embryo is surrounded by remains of cellular nutritive
tissue (Text-fig. 49c–e).

Affinity and other occurrences. Features
of the seed coat, including the undulate anticlinal walls
of the exotesta, indicate close relationship to other Early
Cretaceous seeds that have been compared to seeds of extant
Nymphaeales and Austrobaileyales (e.g., Friis et al. 2018c).
The Catefica seeds described here are conspecific with seeds
from other Early Cretaceous mesofossil floras of Portugal
(e.g., Famalicão and Buarcos) and formal description and
naming of the taxon will be based on this more informative
material from other localities (E. M. Friis, P. R. Crane and
K. R. Pedersen, work in progress). The seeds also closely
resemble seeds described below as “Foveolate seeds sp. 2”,
which differ in having coarser surface ornamentation.

**Foveolate seed sp. 2**
Text-fig. 50a–f

Description and remarks. The material
includes small exotestal, foveolate seeds. The seeds are
broadly elliptical in outline, about 0.75 mm long and 0.5 mm broad in dorsi-ventral direction, with a rounded chalazal region and a truncate apex resulting from a slightly sunken hilar-micropylar region. The seeds are isolated and there is no information on the fruit in which they were borne. The seeds are anatropous, and bitegmic with bilateral symmetry (Text-fig. 50a–f). The seed surface is coarsely pitted with the pits arranged in irregular transverse rows (Text-fig. 50a).

Micropyle and hilum are close to each other, and the hilum lacks a hilar rim (Text-fig. 50b). Internally, small, thin-walled cells of the meso- and endotesta, together with sclerenchyma cells of the outer integument, form a plug around the micropyle (Text-fig. 50c, e, f). The course of the raphe is indistinct on the seed surface. The micropyle is formed from the inner integument (Text-fig. 50e, f).

The seed coat is composed mainly of exotesta that is one cell layer deep and consists of palisade-shaped sclerenchyma cells that are about 120 µm tall over most of the seed (Text-fig. 50c–f). The anticlinal walls of the exotestal cells are undulate towards the outside resulting in a faint jigsaw puzzle-like pattern on the seed surface (Text-fig. 50a). Mesotesta and endotesta are few cell layers thick and consist of small, thin-walled cells. The inner integument is membranous (Text-fig. 50d).

Affinity and other occurrences. The seeds closely resemble those described here as “Foveolate seed sp. 1”, but differ in the coarser pitting of the exotesta and in details of the hilar-micropylar region, including the well-developed meso- and endotesta tissue around the micropyle. The Catefica seeds described here are conspecific with seeds from other Early Cretaceous mesosossil floras from Portugal (Famalicão and Buarcos) and formal description and naming of the taxon will be based on the more informative material from these other localities (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress).

Unassigned, unnamed exotestal seeds

Description and remarks. In addition to the various exotestal seeds described separately above the Catefica mesosossil flora includes a few other kinds of exotestal seeds (not illustrated), each of which is represented by only a single specimen. The seeds are about 1 mm long, circular in lateral view, about 1 mm broad and all have a smooth surface with a jigsaw-puzzle pattern formed from the sinuous anticlinal walls of the outer cells of the exotestal seed coat. For one specimen where internal details are known, the seed coat is bitegmic with palisade shaped exotestal cells with anticlinal cell walls that are straight for most of their length, but strongly wavy towards the inner and outer surface of the exotesta.

Affinity and other occurrences. These seeds are a new and distinct species, but in their general appearance and in the jigsaw-puzzle like pattern on the surface of the exotesta, these seeds are similar to several kinds of exotestal seeds described from other Early Cretaceous mesosossil floras that are related to the Nymphaeales-Austrobaileyales (e.g., Friis et al. 2018c, 2019a). This relationship is also supported by the internal features known for one of the seeds, but critical features such as arrangement of micropyle and hilum are unknown for the Catefica material.

Discussion

The Catefica mesosossil flora

In addition to the angiosperm remains described here, the Catefica mesosossil flora includes numerous unidentified wood fragments and cuticles, as well as small vegetative remains of mosses, lycopsids, ferns, conifers and possibly also the BEG group (Bennettitales-Erdtmanithecales-Gnetales). Many small, complete or fragmentary non-angiosperm reproductive
structures are also present. In addition to angiosperm flowers, fruits, inflorescences, infructescences, seeds and stamens, there are lycopsid and salvinianean megaspores, sporangia and sori of ferns, and cones, cone scales, seeds and pollen sacs of several kinds of conifers, as well as seeds assigned to the BEG group. Some of these fossils have already been formally described, such as most of the BEG seeds including *Battenispernum hirsutum* M.M.Mendes, K.R.Pedersen et E.M.Friis, *Buarcospermum tetragonium* E.M.Friis, K.R.Pedersen et P.R.Crane, *Lignierispernum maroneae* E.M.Friis, K.R.Pedersen et P.R.Crane, *Lobospermum glabrum* E.M.Friis, K.R.Pedersen et P.R.Crane, *Lobospermum rugosum* E.M.Friis, K.R.Pedersen et P.R.Crane, *Quadrispermum parvum* E.M.Friis, K.R.Pedersen et P.R.Crane and *Tomcatia taylorii* E.M.Friis, K.R.Pedersen et P.R.Crane (Friis et al. 2009b, 2013, 2019e, Mendes et al. 2020). Other non-angiosperm fossils from the Catefica locality that have been described and formally named include remains of *Costatoperforosporites friisiae* M.M.Mendes, E.Barrón, Batten et Pais, a schizaealean fern (Mendes et al. 2017), the araucarian conifer *Callialastrobus soussai* J.Kvaček et M.M.Mendes (Kvaček and Mendes 2020), the podocarpaceous conifer *Frisisia lusitanica* M.M.Mendes et J.Kvaček (Mendes and Kvaček 2020), and the cheirrolepidiaceous conifer *Watsoniocladus cunhae* J.Kvaček et M.M.Mendes (Kvaček and Mendes 2021). Separate, more detailed accounts of all non-angiosperm plant fossils are in preparation (J. Kvaček, M. M. Mendes, E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress).

The Catefica angiosperms

A total of 1,407 angiosperm specimens were separated from Catefica samples 49, 50, 150–154, 242, 342, 343, 358–362, 381 and 382. Of these, 880 are from Catefica sample 49 (Text-fig. 51, Tab. 2). Sixty-seven angiosperm species were identified in the total assemblage from all samples, and of these Catefica sample 49 contained 45 species (Text-fig. 51, Tab. 2). Some of the species are based on isolated pollen, or on isolated stamens with in situ pollen, and were perhaps produced by the same plants as some of the floral structures for which pollen is unknown. Such overlaps would reduce the total number of species recognized.

Non-eudicot angiosperms (ANA-grade, chloranthoids, magnoliids, monocots) dominate the Catefica mesofossil flora with 43 species that can be assigned with confidence to these groups. These species account for 65 % of all the angiosperm species recognized. Only six species can be confidently assigned to eudicot angiosperms. The remaining species are of uncertain relationships, but most are probably non-eudicots. In sample 49 there are 32 non-eudicot species, corresponding to 72 % of all the angiosperm species recognized in that sample. Non-eudicot angiosperms are also quantitatively dominant accounting for 83 % of all angiosperm specimens in the total counts and 79 % of all angiosperm specimens in sample 49 (Text-fig. 51).

The most prominent component of the Catefica mesofossil flora are chloranthoid angiosperms, which make up 40 % of all specimens and 28 % of all species in the total
angiosperm count. Similarly, they account for 41 % of the specimens and 27 % of all angiosperm species in sample 49 (Text-fig. 51). Most abundant among the chloranthoid fossils are fruits and seeds of Canrightia (45 % of the chloranthoid specimens in the total count, 44 % of the chloranthoid specimens in sample 49), fruits and seeds of Canrightiopsis (30 % of the chloranthoid specimens in the total count, 24 % of the chloranthoid specimens in sample 49) and flowers and fruits of Hedyflora (21 % of the chloranthoid specimens in the total count, 30 % of the chloranthoid specimens in sample 49). All other chloranthoid taxa are represented by only one to six specimens, most of them isolated stamens or groups of stamens, and together constitute 1 % or less of all chloranthoid specimens.

Magnoliid angiosperms are also significant in the Catefica mesofossil flora, particularly with regard to diversity. Of all angiosperm specimens in the total count 30 % are flowers, fruits, seeds and stamens related to Magnoliidae (species of Serialis), Caneales (Catanthus), Laurales (Saportanthus parvus) and Piperales (Aristospermum, Appomattoxia, Goczania). In sample 49 magnolioid angiosperms account for 22 % of all angiosperm specimens.

Several of the other non-eudicot taxa are probably related to ANA-grade angiosperms, chloranthoids or magnoliids (“Uncertain position at the level of ANA-grade angiosperms-Chloranthaceae-magnoliids”), but cannot be placed with certainty in any of these groups. These include fruits and seeds of Anacostia, Choffaticarpus, Ibericarpus and several isolated stamens or stamens in groups that contain in situ monocolpate (Elasmostemon, Endressiastemon, cf. Endressiastemon, “Laminar stamen with monocolpate reticulate pollen”, Valvidiastemon), or zona-aperturate pollen (“Stamen with zona-aperturate pollen”). For other non-eudicots, such as Kempia, Piercipollis, Teebacia and “Stamen with monocolpate, reticulate pollen”) a monocot affinity cannot be excluded.

One species, Paisia pantoporata, is assigned unequivocally to eudicot angiosperms based on its pentameric flowers and pantoporate pollen and a further five species are assigned to the eudicots based on their tricolpate
pollen. Eighteen angiosperm species lack critical features to place them with certainty in any of the major angiosperm groups. However, preliminary phylogenetic assessments suggest that they would add to the total of non-eudicot rather than eudicot angiosperms. The two kinds of tricarpellate flowers (“Tricarpellate flower sp. 1” and “Tricarpellate flower
sp. 2”) and the small one-seeded fruits (“One-seeded fruit sp. 1”) may be monocotyledons. Others that we include as “Angiosperms of uncertain affinity”, such as Pazliopsis sp., the “Follicular fruit with exotestal seeds”, “Foveolate seed sp. 1”, “Foveolate seed sp. 2”, and other exotestal seeds, are probably related to ANA-grade or magnoliid angiosperms. Notably, in addition to the possible monocot representatives mentioned above, the only other taxon from Catifica assigned to the monocots is Pennicarpus sp.

**Angiosperm pollen in the Catifica mesofossil flora**

Thirty-four different kinds of angiosperm pollen grains have been observed in situ in stamens, in pollen clumps or attached to various plant fragments (Text-fig. 52). This number represents about half of all angiosperm taxa reported from the Catifica mesofossil flora. The pollen grains are minute to small with the smallest ranging between 8–11 μm in diameter (Saportanthus parvus, Endressistemon portugallicus, cf. Endressistemon sp. 1 and sp. 2) and the largest ranging between 24–26 μm in diameter (Clavatipollenites sp. 2, Tricolpate sp. 2). Chloranthoid pollen ranges in diameter from 12–26 μm, while the tricolpate pollen grains range between 19–25 μm.

Of the different aperture configurations among the pollen types identified in the mesofossil flora, most (25, 75 %) are monoaperturate-reticulate (monocolpate, trichotom-, tetrachotomo-, pentachotomocolpate). Five tricolpate-reticulate pollen types correspond to about 15 % of the pollen species. The remainder belong to a monoaperturate-tectate (monocolpate) type, a zona-aperturate-reticulate
type, and a pantoporate-echinate type. The aperture configuration in *Saportanthus parvus* is uncertain, but these grains are classified here as monoaperturate-striate, based on comparison with other species of *Saportanthus*. Among the monoaperturate pollen, six species have a branched aperture (trichotomo-, tetrachotomo-, pentachotomocolpate). Pollen was not observed for *Anacostia* from Catefica, but is known from other mesofossil floras to be monocolpate-trichotomocolpate, which raises the number of species with a branched pollen aperture to seven, corresponding to about a quarter of all the monoaperturate pollen types.

**Comparison with other Early Cretaceous mesofossil floras**

Numerous mesofossil floras, ranging in age from late Barremian-Aptian through to early Cenomanian, have been discovered in Portugal and eastern North America. These mesofossil floras provide a more detailed insight into the changing patterns of systematic relationships through the earliest angiosperm diversification than is possible based on leaves or pollen alone (e.g., Friis et al. 2011). So far, only the Torres Vedras mesofossil flora has been studied in the same detail as the Catefica flora (Friis et al. 2019a), but similar accounts are in preparation for other Early Cretaceous floras (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress), and the information already available highlights some general patterns.

Several of the Catefica flowers, fruits and seeds are known only from the Catefica mesofossil flora including *Canrightia foveolata*, *Catanthus dolichostemon*, *Mugi-deiriflora portugallica*, *Paisia pantoporata* and the two tricarpellate flowers. Flowers of *Saportanthus parvus* are also characteristic for the Catefica mesofossil flora, although this species may also be present in the Chicalhão mesofossil flora (“Flower sp. 2”; Mendes et al. 2014). Many of the isolated stamens are also unique for the Catefica mesofossil flora, and thin inner integument (ii). Specimen, Catefica 153-S172332 (a–f). Scale bars = 300 μm (a–f).
Table 2. Mesofossils recognized in Catefica samples 49, 50, 150–154, 242, 342, 343, 358–362, 381, 382.

| Taxon/Sample | 49 | 50 | 150 | 151 | 152 | 153 | 154 | 242 | 342 | 343 | 358 | 359 | 360 | 361 | 362 | 381 | 382 | all |
|--------------|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Mugideiriflora portugallica | 3 | 1 | | | | | | | | | | | | | | | 4 |
| Canrightia resinifera | 148 | 4 | 3 | 5 | 8 | 17 | 23 | 14 | 2 | 6 | 11 | 3 | 244 |
| Canrightia foveolata | 11 | 1 | 1 | | | | | | | | | | | | | | 13 |
| Canrightia sp. | | | | | | | | | | | | | | | | | |
| Canrightiopsis crassiuscula | 6 | 1 | 2 | 1 | | | | | | | | | | | | | | 12 |
| Canrightiopsis intermedia | | | | | | | | | | | | | | | | | | 1 |
| Canrightiopsis sp. | 80 | 1 | 3 | 8 | 7 | 4 | 12 | 1 | 1 | | | | | | | | | 158 |
| Hedyflora crystallifera | 111 | 2 | 1 | | 1 | | 2 | | | 1 | | | | | | | | 121 |
| Proencistemon portugallicus | 2 | 2 | 1 | | | | | | | | | | | | | | 6 |
| Proencistemon sp. | | | | | | | | | | | | | | | | | | 1 |
| Clavatipollenites type sp. 1 | | | | | | | | | | | | | | | | | | 1 |
| Clavatipollenites type sp. 2 | | | | | | | | | | | | | | | | | | 1 |
| Clavatipollenites type sp. 3 | | | | | | | | | | | | | | | | | | 1 |
| Clavatipollenites type sp. 4 | 1 | | | | | | | | | | | | | | | | | |
| Asteropollis type sp. 1 | 3 | | | | | | | | | | | | | | | | | 3 |
| Asteropollis type sp. 2 | 1 | | | | | | | | | | | | | | | | | 1 |
| Asteropollis/Clavatipollenites type sp. 1 | | | | | | | | | | | | | | | | | | 1 |
| Asteropollis/Clavatipollenites type sp. 2 | 1 | | | | | | | | | | | | | | | | | 1 |
| Asteropollis/Clavatipollenites type sp. 3 | 1 | | | | | | | | | | | | | | | | | 1 |
| Serialis communis | 25 | | | | | | | | | | | | | | | | | 25 |
| Serialis crassiuscula | 36 | | | | | | | | | | | | | | | | | 36 |
| Serialis spp. | 74 | 50 | 11 | 3 | 8 | 10 | 100 | | | | | | | | | | | 256 |
| Catantus dolichostemon | 8 | 3 | 2 | | 1 | | | 2 | | | | | | | | | | 16 |
| Saportanthus parvus | 25 | 3 | 3 | 2 | 2 | 1 | | 1 | | | | | | | | | | 41 |
| Aristospermum haberi | 19 | 6 | 1 | 1 | 1 | 3 | 2 | 1 | 2 | 4 | 2 | 42 |
| Appomattoxia sp. | 3 | 1 | | | | | | | | | | | | | | | 4 |
| Goczania rugosa | 3 | 2 | | | | | | | | | | | | | | | 5 |
| Anacostia portugallica | | | | | | 1 | | 1 | | 1 | | 3 | | | | | | | |
| Chofaticarpus compactus | 62 | 7 | 2 | | 1 | | | | | | | | | | | | | | 72 |
| Ibericarpus cuneiformis | 59 | 12 | | | | | | | | | | | | | | | | 71 |
| Stamen with zona-aperturate pollen | 1 | | | | | | | | | | | | | | | | | 1 |
| Elasmostemon paisii | 2 | 1 | 1 | | | | | | | | | | | | | | 4 |
| Laminar stamen/monocolpate reticulate pollen | 1 | | | | | | | | | | | | | | | | | 1 |
| Valvistemon globiferus | 1 | | | | | | | | | | | | | | | | | 1 |
| Endressistemon cateficensis | 5 | | | | | | | | | | | | | | | | | 5 |
| cf. Endressistemon sp. 1 | 1 | | | | | | | | | | | | | | | | | 1 |
| cf. Endressistemon sp. 2 | 1 | | | | | | | | | | | | | | | | | 1 |
| cf. Endressistemon sp. 3 | 1 | | | | | | | | | | | | | | | | | 1 |
| Pennicarpus tenuis | 2 | | | | | | | | | | | | | | | | | 2 |
| Kempia longicolpites | 1 | | | | | | | | | | | | | | | | | 1 |
| Piercipollis sp. | 1 | 1 | | | | | | | | | | | | | | | | 2 |
| Teebacia sp. | | | | | | | | | | | | | | | | | | 1 |
| Stamen with monocolpate reticulate pollen | 1 | | | | | | | | | | | | | | | | | 1 |
| Paisia pantoporata | 27 | 17 | 1 | 2 | 2 | 3 | | | | | 2 | | 1 | | 55 |
| *Paisia sp. | | | | | | | | | | | | | | | | | | |
| Paisia-like | 45 | | | | | | | | | | | | | | | | | 46 |
| Tricolpate pollen sp. 1 | 1 | | | | | | | | | | | | | | | | | 1 |
*paeisi, Endressistemon cateficensis*, the three species of *Endressistemon, Valvidistemon globiferus*, “Stamen with zona-aperturate pollen” and “Laminar stamen/monocolpate reticulate pollen”. For comparison, in the Torres Vedras mesofossil flora about 20 different kinds of stamens are known, but none shows a conspicuous connective between the pollen sacs or an extension of the connective above the pollen sacs (Friis et al. 2019a). The Puddledock mesofossil flora from Virginia, USA, of early-middle Albian age is the only other mesofossil flora with a comparably high proportion of stamens with massive connective between and above the pollen sacs (Crane et al. 1994, Friis et al. 2020b), but none of the stamens from Catefica match any of those from Puddledock.

| Taxon/Sample                      | 49 | 50 | 150 | 151 | 152 | 153 | 154 | 242 | 342 | 343 | 358 | 359 | 360 | 361 | 362 | 381 | 382 | all |
|----------------------------------|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Tricolpate pollen sp. 2          |    |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1   |
| Tricolpate pollen sp. 3          |    |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1   |
| Tricolpate pollen sp. 4          |    | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| Tricolpate pollen sp. 5          |    |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1   |
| Tricarpellate flower sp. 1       |    | 2  |     |     |     |     | 2   |     |     |     |     |     |     |     |     |     |     | 7   |
| Tricarpellate flower sp. 2       |    | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1   |
| Hexacarpellate flower             |    | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1   |
| Staminate structure               |    | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1   |
| Rugulate fruit                    |    | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 2   |
| One-seeded fruit sp. 1            | 37 | 1  | 2   |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 42  |
| One-seeded fruit sp. 2            | 1  | 1  |     |     |     |     | 1   | 1   |     |     |     |     |     |     |     |     |     | 3   |
| Fruit spp.                       | 5  | 1  | 1   |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 8   |
| Pazlopsi sp.                      | 16 | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 36  |
| Follicular fruit with exotestal   | 36 |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 20  |
| Fruit sp.                        | 2  | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 36  |
| Foveolate seeds sp. 1             | 2  |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 2   |
| Foveolate seeds sp. 2             | 2  | 1  |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 3   |
| Exotestal seed spp.               | 2  |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 2   |
| Reticulate seed sp. 1             | 9  |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 9   |
| **TOTAL**                        | 880| 128| 23  | 13  | 20  | 31  | 36  | 46  | 21  | 4   | 7   | 12  | 137 | 25  | 8   | 5   | 1407|     |

Text-fig. 51. Number of specimens and number of species for the five categories of angiosperms distinguished from the Catefica mesofossil flora.
The Torres Vedras and the Catefica mesofossil floras were collected in the same region only about 5 km apart and both are from the Almargem Formation. However, while the Torres Vedras mesofossil floras is in the Lower Almargem Formation, the Catefica mesofossil flora is probably slightly younger and is most likely from the basal part of Upper Almargem Formation. Both mesofossil floras are similar in the number of angiosperm species recognized: 64 species recorded from Torres Vedras, compared to 67 angiosperm species from Catefica. However, in the Torres Vedras mesofossil flora angiosperms are much less common, angiosperms are quantitatively subordinate to other kinds of plants and most angiosperm species are represented by only one or two specimens. In the Catefica mesofossil flora, angiosperms are dominant, both in the number of specimens and in the number of species. In the Catefica mesofossil flora some species are very abundant and represented by more than hundred specimens, for example, Canrightia resinifera (244 specimens), Canrightiopsis spp. (158 specimens), Hedyflora crystallifera (121 specimens) and Serialis spp. (256 specimens). In the Torres Vedras mesofossil flora none of the angiosperm species approaches that level of abundance.

In both the Catefica and Torres Vedras mesofossil floras the angiosperm component is dominated by specimens of non-eudicot angiosperms and this is mirrored in the distribution of species among the major angiosperm groups. About ten of the Catefica species and 14 of the Catefica genera (Anacostia, Appomattoxia, Asteropollis, Canrightia, Choffaticarpus, Clavatipollenites, Goczania, Hedyflora, Kempia, Pazliopsis, Pennicarpus, Piercipollis, Serialis, Teebacia) are also reported from Torres Vedras. Also significant is that the Catefica and Torres Vedras mesofossil floras are both characterized by a high proportion of chloranthoid angiosperms: 18 taxa from Catefica and 12 from Torres Vedras. However, while the Catefica and Torres Vedras mesofossil floras share several chloranthoid genera, the species are different.

The eudicot element in the Catefica and Torres Vedras mesofossil floras also differs. Eudicots are not common in either mesofossil flora, but are more diverse at Catefica, with six species currently reported, of which five are known to have tricolpate pollen. Furthermore, in all five species the three apertures are regularly positioned, and the pollen wall is tectate-reticulate. In contrast, all three of the tricolpate pollen types reported from the Torres Vedras mesofossil flora show some irregularity in the position of the apertures and the pollen wall is tectate-perforate or microreticulate-perforate.

The mesofossil flora from the Buarcos locality (e.g., Friis et al. 2011) has not yet been assessed in comparable detail to the Catefica and Torres Vedras mesofossil floras, but nevertheless there are many obvious similarities between the fossil assemblages at Catefica and at Buarcos. The number of taxa shared between Catefica and Buarcos appears to be about the same as between Catefica and Torres Vedras. For example, taxa shared between Catefica and Buarcos include Aristaspermum huberi, Choffaticarpus compactus, Canrightia resinifera, Canrightiopsis intermedia, “Foveolate seed sp. 2”, Hedyflora crystallifera, “One-seeded fruit sp. 1”, “Follicular fruit with exotestal seeds”, Pennicarpus tenuis and Serialis communis. However, the Catefica and Buarcos mesofossil floras differ in the kinds of the fossils preserved. For example, the Buarcos flora includes very few stamens. Also, only one tricolpate pollen type has been recorded so far and it is similar to pollen from Torres Vedras in being tectate-perforate.

The relationship of the Catefica mesofossil flora to that from the Vale de Água locality (e.g., Friis et al. 2011) shows an analogous pattern to the relationship between the Catefica and Buarcos plant fossil assemblages. While the Catefica and Vale de Água mesofossil floras share some species, such as Canthus dolichostemon, Canrightia resinifera, Canrightiopsis intermedia, “Foveolate seed sp. 2”, Hedyflora crystallifera, Serialis communis and Serialis crassistesta, the overall aspect of the two mesofossil floras is different. The Vale de Água mesofossil flora has a much greater diversity of exotestal seeds that are probably related to ANA-grade angiosperms. The Arazed and Famalicão mesofossil floras also contain diverse and abundant exotestal seeds and differ from the Catefica mesofossil flora in that respect (Friis et al. 2018c, 2019c).

Early Cretaceous mesofossil floras containing rich assemblages of angiosperm flowers, fruits, seeds and stamens are also reported from Potomac Group sediments of eastern North America (e.g., Crane et al. 1994, Friis et al. 2011), and although several in depth studies of individual taxa have been published, none of the Potomac Group mesofossil floras have been studied in full detail. The most diverse mesofossil floras from Potomac sediments are those from the Puddledock and Kenilworth localities, in Virginia and Maryland respectively, which are both of early-middle Albian age and thus slightly younger that the Catefica mesofossil flora (e.g., Friis et al. 1994, 1995, 1997, 2016,
2018b, d, e, 2020a, b, von Balthazar et al. 2007, 2008, 2011). Nevertheless, both the Puddledock and Kenilworth mesofossil floras are broadly comparable in their composition to the mesofossil flora at Catefica and other Early Cretaceous mesofossil localities in Portugal. They are dominated by taxa related to ANA-grade angiosperms, chloranthoids and magnoliids, although the angiosperm component is more diverse and includes a greater proportion of eudicot taxa. These slight differences perhaps reflect the slightly younger age of the Puddledock and Kenilworth mesofossil floras.

Conclusion

The Catefica flowers, fruits, seeds and stamens are among the oldest and most informative angiosperm reproductive structures known and they provide direct evidence of angiosperm floral structure, reproductive biology and phylogenetic diversity from a very early phase of angiosperm diversification. ANA-grade angiosperms, chloranthoids and magnoliids are the most prominent components of the mesofossil flora. Remains of chloranthoid angiosperms are especially common and diverse comprising around 40% of the specimens, and more than 25% of the species. Eudicots are subordinate comprising only 3–4% of all angiosperm specimens and about 9% of all species. One of the eudicot angiosperms, Paisia pantoporata, is thought to represent an extinct lineage near the base of the core eudicots. In this respect, the results from our detailed survey of the Catefica mesofossil flora are the same as the results from the slightly older Torres Vedras mesofossil flora (Friis et al. 2019a), and the same pattern is seen clearly in other species-rich Early Cretaceous mesofossil floras from Portugal, such as those from Arazede, Buarcos, Famalicão and Vale de Água (e.g., Friis et al. 2010a, b, 2011).

Also significant, and of general importance, is that although many of the Early Cretaceous fossils can be placed with confidence in major clades of angiosperms, very few can be placed unequivocally at the level of families or orders, not always because of lack of information, but also because the fossils possess combinations of characters not seen among living taxa. These Early Cretaceous fossils probably represent extinct lineages near the base of the angiosperm tree and reflect a hitherto unanticipated diversity within and among those few relatively depauperate lineages that can be recognized today and often have few surviving members. While angiosperms are a significant component of the Catefica mesofossil flora, both in terms of diversity and in number of specimens, their systematic diversity compared to the diversity of extant angiosperms is very restricted.

All the angiosperm remains recovered in the Catefica mesofossil flora are reproductive structures such as flower, fruits, seeds and stamens. There are no fragments of angiosperm wood or leaves. The lack of angiosperm wood in the flora, together with the predominance of angiosperm taxa of probable herbaceous or shrubby nature, such as the diverse assemblage of chloranthoid angiosperms, suggests open vegetation with small mainly herbaceous and shrubby angiosperms intermixed with mosses, lycopsids and ferns, as well as plants of the BEG-group that were probably also small herbaceous and shrubby. The woody component of the flora was dominated by conifers. This interpretation of the Catefica source vegetation as relatively open and dominated by angiosperms of small stature, is also consistent with the small size and tiny embryos of many of the Catefica seeds (Friis et al. 2015a) and the long-established idea that the earliest angiosperms were early successional colonizers of disturbed habitats.

Acknowledgements

We thank the Paul Scherrer Institute, Villigen, Switzerland for provision of synchrotron radiation beam time at the TOMCAT beamline X02DA of the Swiss Light Source. We are also grateful to Federica Marone for her help at the beamline (project 20070197, 20080872, 20100167, 20110963, 20130185, 20141047, 20160140, 20171476, 2019071, 20211671 to P. C. J. Donoghue, S. Bengtson, E. M. Friis and M. Rücklin), Anna Lindström for help with the SRXTM analyses, and Pia Bomholt Jensen for her help with SEM at the University of Aarhus. We also thank Patrick S. Herendeen and Steven R. Manchester for valuable comments to the manuscript. Support for this research was also obtained from the Swedish Research Council (2014-5228 to E. M. Friis), United States National Science Foundation (BSR-8708460, DEB-9616443, DEB-1348456, DEB-1748286, to PRC and colleagues) the Oak Spring Garden Foundation, the Czech Grant Agency (project 20-06134S) and the Portuguese Science Foundation (FCT), under the projects UIDB/04292/2020 and UIDP/04292/2020, granted to MARE, and LA/P/0069/2020, granted to the Associate Laboratory ARNET.

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Appendix I

Overview of Catefica specimens analyzed for internal features using synchrotron radiation X-ray tomographic microscopy (SRXTM).

| Filename     | Specimen info     | Taxon              | keV | Objective | Comments                       |
|--------------|-------------------|--------------------|-----|-----------|--------------------------------|
| P0292_10x    | Catefica MMM      | Paisia sp.         | 10  | ×10       |                                |
| P0292_10xb   | Catefica MMM      | Paisia sp.         | 10  | ×10       |                                |
| P0338_20x    | Catefica MMM      | Paisia pantoporata | 10  | ×20       |                                |
| P0355_10x    | Catefica MMM      | Battenispermum hirsutum | 10  | ×10       | Lateral stacking 2 blocks      |
| P0357_10x    | Catefica MMM324   | Axis – uncertain   | 10  | ×10       | Stacked 2 blocks               |
| S100754new   | Catefica 49       | Tomcatia taylorii  | 10  | ×20       | S100254new incorrect number; 3 blocks |
| S100757new   | Catefica 49       | Tomcatia taylorii  | 10  | ×10       |                                |
| S101214a     | Catefica MMM      | Battenispermum hirsutum | 10  | ×10       |                                |
| S118680a     | Catefica 49       | Tomcatia taylorii  | 10  | ×10       |                                |
| S118688phase | Catefica 49       | Catanthus dolichostemon | 20  | ×10       |                                |
| S156531a     | Catefica 49       | Piasia pantoporata | 10  | ×4        |                                |
| S156532a     | Catefica 49       | Axis – uncertain   | 10  | ×4        |                                |
| S156533a     | Catefica 49       | Axis – uncertain   | 10  | ×4        |                                |
| S156535a     | Catefica 49       | Bryophyta          | 10  | ×10       |                                |
| S156536a     | Catefica 49       | Axis – uncertain   | 10  | ×10       | Stacked 2 blocks               |
| S156537a     | Catefica 49       | Axis – uncertain   | 10  | ×10       |                                |
| S156538a     | Catefica 49       | Axis – uncertain   | 10  | ×10       | Stacked 2 blocks               |
| S156539a     | Catefica 49       | Battenispermum hirsutum | 10  | ×4        |                                |
| S156540a     | Catefica 342      | Lignierisperma maroneae | 10  | ×4        |                                |
| S156541a     | Catefica 342      | Coniferales        | 10  | ×10       | Stacked 2 blocks               |
| S171508b     | Catefica 50       | Canrightia resinifera | 10  | ×10       |                                |
| S171509a     | Catefica 50       | Canrightia resinifera | 10  | ×20       | Stacked 2 blocks               |
| S171510a     | Catefica 50       | Canrightia resinifera | 10  | ×10       |                                |
| S171511a     | Catefica 50       | Canrightia resinifera | 10  | ×20       |                                |
| S171513a     | Catefica 343      | Piasia pantoporata | 10  | ×10       |                                |
| S171514b     | Catefica 343      | Piasia pantoporata | 10  | ×20       |                                |
| S171514c     | Catefica 343      | Piasia pantoporata | 10  | ×20       | Stacked 2 blocks               |
| S171515a     | Catefica 343      | Piasia-like follicle | 10  | ×20       |                                |
| S171516a     | Catefica 343      | Leaves? – uncertain | 10  | ×10       |                                |
| S171517a     | Catefica 342      | Tricarpellate flower sp. 1 | 10  | ×20       |                                |
| S171518a     | Catefica 342      | Tricarpellate flower sp. 1 | 10  | ×20       |                                |
| S171519a     | Catefica 342      | Piasia pantoporata | 10  | ×10       |                                |
| S171520a     | Catefica 342      | Tricarpellate flower sp. 1 | 10  | ×10       |                                |
| S171521a     | Catefica 342      | Tricarpellate flower sp. 1 | 10  | ×10       |                                |
| S171522a     | Catefica 342      | Tricarpellate flower sp. 1 | 10  | ×10       |                                |
| S171523a     | Catefica 342      | Piasia-like follicle | 10  | ×20       | Stacked 3 blocks               |
| S171524a     | Catefica 342      | Piasia-like follicle | 10  | ×20       | Stacked 3 blocks               |
| S171525a     | Catefica 342      | Piasia-like follicle | 10  | ×20       | Stacked 2 blocks               |
| S171526-01a  | Catefica 342      | Piasia pantoporata | 10  | ×20       | Stacked 2 blocks               |
| S171526-02a  | Catefica 342      | Piasia pantoporata | 10  | ×20       |                                |
| S171526a     | Catefica 342      | Piasia pantoporata | 10  | ×20       |                                |
| S171527a     | Catefica 342      | Stamen with zonaperturate pollen | 10  | ×10       |                                |
| S171528a     | Catefica 342      | Axis – uncertain   | 10  | ×10       | Stacked 4 blocks               |
| S171529a     | Catefica 342      | Piasia pantoporata | 10  | ×20       | Stacked 2 blocks               |
| S171530a     | Catefica 342      | Piasia pantoporata | 10  | ×20       |                                |
| S172313a     | Catefica 342      | Hedyflora crystallifera | 10  | ×10       |                                |
| Specimen Code | Taxon Name | Description | Magnification | Comment |
|---------------|------------|-------------|---------------|---------|
| S172314a      | Catifaca 49 | Tricarpellate flower sp. 1 | 10 × 10 |         |
| S172315a      | Catifaca 49 | Uncertain | 10 × 10 |         |
| S172316a      | Catifaca 49 | Foveolate seed sp. 1 | 10 × 10 |         |
| S172317a      | Catifaca 49 | Exotesta seed | 10 × 10 |         |
| S172318a      | Catifaca 49 | Coprolite | 10 × 10 |         |
| S172319a      | Catifaca 49 | Psilophyc sp. | 10 × 10 |         |
| S172320a      | Catifaca 49 | Chafficarpus compactus | 10 × 10 |         |
| S172321a      | Catifaca 49 | Chafficarpus compactus | 10 × 10 |         |
| S172322a      | Catifaca 49 | Chafficarpus compactus | 10 × 10 |         |
| S172323a      | Catifaca 49 | Chafficarpus compactus | 10 × 10 |         |
| S172324a      | Catifaca 49 | Hexameric flower/fruit | 10 × 20 | Stacked 2 blocks |
| S172325a      | Catifaca 49 | Hexameric flower/fruit | 10 × 20 | Stacked 2 blocks; rec only B1 |
| S172326a      | Catifaca 49 | Axis – uncertain | 10 × 20 |         |
| S172327a      | Catifaca 49 | Paisia-like follicle | 10 × 20 | Stacked 3 blocks |
| S172329a      | Catifaca 153 | Quadrispermum parvum | 10 × 20 | Scan interrupted! |
| S172329b      | Catifaca 153 | Quadrispermum parvum | 10 × 20 | Stacked 2 blocks |
| S172330a      | Catifaca 153 | One-seeded fruit sp. 2 | 10 × 10 |         |
| S172331a      | Catifaca 153 | Canrightiosis crassistesta | 10 × 20 |         |
| S172332a      | Catifaca 153 | Foveolate seed sp. 2 | 10 × 20 | Stacked 2 blocks; rec only B1 |
| S172333a      | Catifaca 153 | Canrightiosis crassistesta | 10 × 10 |         |
| S172354a      | Catifaca 49 | Canthus dolichostemon | 10 × 10 | Stacked 2 blocks |
| S172355a      | Catifaca 49 | Canthus dolichostemon | 10 × 10 | Stacked 2 blocks |
| S172356a      | Catifaca 49 | Canthus dolichostemon | 10 × 10 | Stacked 2 blocks |
| S172359a      | Catifaca 49 | Quadrispermum parvum | 10 × 20 | Stacked 2 blocks |
| S174008a      | Catifaca 50 | Canrightia sp. | 10 × 20 |         |
| S174038a_B1_B2_B3 | Catifaca 49 | Lycopsid axis | 10 × 10 | Stacked 3 blocks |
| S174039a      | Catifaca 49 | Canrightiosis crassistesta | 10 × 10 |         |
| S174040a      | Catifaca 49 | Canrightiosis crassistesta | 10 × 10 |         |
| S174093a      | Catifaca 49 | Axis – uncertain | 10 × 10 | Moved during scan |
| S174114b      | Catifaca 49 | Saporantus parvus | 10 × 10 |         |
| S174159a      | Catifaca 49 | Canrightiosis crassistesta | 10 × 10 |         |
| S174160a      | Catifaca 49 | Lycopsid axis | 10 × 10 |         |
| S174161a      | Catifaca 49 | One-seeded fruit sp. 1 | 10 × 10 | Stacked 2 blocks |
| S174162a      | Catifaca 342 | Chafficarpus compactus | 10 × 10 |         |
| S174248_10x_ | Catifaca 49 | Canrightiosis crassistesta | 10 × 10 |         |
| S174249a      | Catifaca 49 | Canrightia foveolata | 10 × 10 | Stacked 2 blocks |
| S174249a_B1a_ | Catifaca 49 | Canrightia foveolata | 10 × 10 | Rescanned top |
| S174249Re_B1_B2 | Catifaca 49 | Canrightia foveolata | 17 × 10 | Stacked 2 blocks |
| S174250a      | Catifaca 359 | Axis – uncertain | 10 × 10 |         |
| S174251a      | Catifaca 49 | Bryophyta | 10 × 20 |         |
| S174254L      | Catifaca 150 | Mugideiriflora portugalinca | 10 × 10 | Lateral stacking |
| S174254La     | Catifaca 150 | Mugideiriflora portugalinca | 10 × 10 | Lateral stacking |
| S174255L_B1_B2_B3 | Catifaca 150 | Canthus dolichostemon | 10 × 10 | Stacked 3 blocks |
| S174299a_B1_B2 | Catifaca 152 | Axis – uncertain | 10 × 10 | Stacked 2 blocks |
| S174301_10x_ | Catifaca 242 | Saporantus parvus | 10 × 10 |         |
| S174301_20x_ | Catifaca 242 | Saporantus parvus | 10 × 20 | Stacked 2 blocks |
| S174309a      | Catifaca 154 | Canrightiosis crassistesta | 10 × 10 |         |
| S174310a      | Catifaca 154 | Canrightiosis crassistesta | 10 × 10 |         |
| S174311_10x_ | Catifaca 343 | Canrightiosis crassistesta | 10 × 10 |         |
| S174312_10x_ | Catifaca 153 | Canrightia resinifera | 10 × 10 |         |
| S174313_B1_B2 | Catifaca 153 | Hexameroes flower/fruit | 10 × 10 | Stacked 2 blocks |
| S174314_10x_ | Catifaca 153 | One-seeded fruit sp. 2 | 10 × 10 |         |
| S174356a      | Catifaca 360 | Saporantus parvus | 10 × 10 |         |
| S174373_10x_ | Catifaca 50 | Paisia pantoporotata | 10 × 10 |         |
| S174373_10x_ | Catifaca 361 | Paisia pantoporotata | 10 × 10 |         |
| S174676_10x_ | Catifaca 49 | Axis – uncertain | 10 × 10 |         |
| S174767_10x_ | Catifaca 49 | Serialis communis | 10 × 10 |         |
| S174768_20x_ | Catifaca 49 | Serialis communis | 10 × 20 | Stacked 2 blocks |
| S174769_20x_ | Catifaca 49 | One-seeded fruit sp. 1 | 10 × 20 |         |
| Image Code     | Catefica   | Taxon Name                          | Magnification | Description                      |
|---------------|------------|-------------------------------------|---------------|----------------------------------|
| S174899_10x   | Catefica 50| Catanthus dolichostemon             | 10 ×10        | Stacked 2 blocks                 |
| S174900_10x   | Catefica 50| Mugideiriflora portugallica         | 10 ×10        |                                  |
| S174901_10x   | Catefica 50| Tricarpellate flower sp. 2          | 10 ×10        |                                  |
| S174902_10x   | Catefica 50| Tricarpellate flower sp. 1          | 10 ×10        |                                  |
| S174903_10x   | Catefica 50| BEG new taxon                       | 10 ×10        |                                  |
| S174903_20x   | Catefica 50| BEG new taxon                       | 10 ×20, apex  |                                  |
| S174904_10x   | Catefica 50| Canrightiopsis crassitesta          | 10 ×10        |                                  |
| S174905_10x   | Catefica 50| Canrightiopsis crassitesta          | 10 ×10        |                                  |
| S174906_10x   | Catefica 50| Canrightia resinifera               | 10 ×10        |                                  |
| S174907_10x   | Catefica 50| Ibericarpus cuneiformis             | 10 ×10        |                                  |
| S174908_10x   | Catefica 50| Choffaticarpus compactus            | 10 ×10        |                                  |
| S174909_10x   | Catefica 50| Tricarpellate flower sp. 2          | 10 ×10        |                                  |
| S174910_20x   | Catefica 50| Paisia-like follicle                | 10 ×20        | Stacked 2 blocks                 |
| S174911_20x   | Catefica 49| Uncertain structure                 | 10 ×20        | Stacked 2 blocks                 |
| S174912_20x   | Catefica 49| Axis – uncertain                    | 10 ×20        |                                  |
| S174913_20x   | Catefica 49| Appomatoxosia sp.                   | 10 ×20        |                                  |
| S174914_20x   | Catefica 49| Paisia-like follicle                 | 10 ×20        | Stacked 2 blocks                 |
| S174915_10x   | Catefica 49| Paisia-like follicle                 | 15 ×10        | Stacked 2 blocks                 |
| S174916_20x   | Catefica 49| Paisia-like follicle                 | 10 ×20        | Stacked 2 blocks                 |
| S174917_20x   | Catefica 49| Paisia-like follicle                 | 10 ×20        | Stacked 2 blocks                 |
| S174919_20x   | Catefica 49| Leaf-uncertain                      | 10 ×20        | Stacked 2 blocks                 |
| S174920_20x   | Catefica 49| Paisia-like follicle                 | 10 ×20        | Stacked 2 blocks                 |
| S174921_20x   | Catefica 49| Serialis sp.                        | 10 ×20        | Stacked 2 blocks                 |
| S174922_20x   | Catefica 49| One-seeded fruit sp. 1              | 10 ×20        | Stacked 2 blocks                 |
| S174923_20x   | Catefica 49| One-seeded fruit sp. 1              | 10 ×20        | Stacked 2 blocks                 |
| S174924_20x   | Catefica 49| One-seeded fruit sp. 1              | 10 ×20        | Stacked 2 blocks                 |
| S174925_20x   | Catefica 49| One-seeded fruit sp. 1              | 10 ×20        |                                  |
| S174926_20x   | Catefica 49| Fruit with exotestal seed           | 10 ×20        |                                  |
| S174927_20x   | Catefica 49| One-seeded fruit sp. 1              | 10 ×20        |                                  |
| S174928_20x   | Catefica 49| Canrightia resinifera               | 10 ×20        |                                  |
| S174929_20x   | Catefica 49| Paisia-like follicle                 | 10 ×20        |                                  |
| S174930_20x   | Catefica 49| Coprolite                           | 10 ×20        |                                  |
| S175178_10x   | Catefica 49| Canrightia foveolata                | 10 ×10        | Stacked 2 blocks                 |
| S175179_10x   | Catefica 49| Canrightia foveolata                | 10 ×10        |                                  |
| S175353_10x   | Catefica 49| Tricarpellate flower sp. 2          | 10 ×10        | Stacked 2 blocks                 |
| S175354_10x   | Catefica 49| Tricarpellate flower                | 10 ×10        |                                  |
| S260004_10x   | Catefica 49| Canrightiopsis crassitesta          | 10 ×10        |                                  |
| S260038_10x   | Catefica 50| Mugideiriflora portugallica         | 10 ×10        |                                  |
| S260039_10x   | Catefica 50| Axis – uncertain                    | 10 ×10        |                                  |
| S260045_10x   | Catefica 49| Aristostpermum huberi               | 10 ×10        | Stacked 2 blocks                 |
| S260046_10x   | Catefica 49| Seed reticulate                     | 10 ×10        | Stacked 2 blocks                 |
| S260047_10x   | Catefica 49| Catanthus dolichostemon             | 10 ×10        | Stacked 2 blocks                 |
| S260048_10x   | Catefica 49| Seed reticulate                     | 10 ×10        | Stacked 2 blocks                 |
| S260049_10x   | Catefica 49| Aristostpermum huberi               | 10 ×10        | Stacked 2 blocks                 |
| S266050_10x   | Catefica 49| Serialis sp.                        | 10 ×10        |                                  |
| S266052_10x   | Catefica 49| Coniferales                         | 10 ×10        | Stacked 2 blocks                 |
| S266053_10x   | Catefica 49| Coniferales                         | 10 ×10        | Stacked 2 blocks                 |
| S266054_10x   | Catefica 49| Coniferales                         | 10 ×10        |                                  |
| S266055_10x   | Catefica 49| Coniferales                         | 10 ×10        | Stacked 2 blocks                 |
| S266056_10x   | Catefica 49| Coniferales                         | 10 ×10        |                                  |
| S266214_10x   | Catefica 362| One-seeded fruit sp. 2            | 10 ×10        |                                  |